University of Nevada, Reno

**Long-Term Effects of Thinning and Prescribed Fire on Tree Growth and Bark Beetle Demography in a Jeffrey Pine Stand**

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Natural Resources and Environmental Science

by

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# OVERALL ABSTRACT

Forest thinnings implemented with cut-to-length and whole-tree harvesting systems followed by underburning were evaluated for their effects on long-term individual tree and stand level growth responses as well as bark beetle demography in pure, uneven-aged Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) accompanied by isolated California white fir (*Abies concolor* var. lowiana [Gord.] Lemm.). Based on both dimension and volume growth measures, trees of the unburned whole-tree treatment combination exhibited the greatest individual growth responses. At the stand level, a diminished volume growth response in the whole-tree treatment was especially pronounced in the burned portion, mostly attributable to exaggerated stocking losses, while a superior response in the unburned cut-to-length combination likely reflected not only the absence of detrimental fire impacts but also the benefits of on-site slash retention. For stand level biomass, diminished growth in the whole-tree treatment was again evident, with that in the burned portion again most pronounced, while biomass accrual in the unburned cut-to-length treatment combination was generally comparable to that in the unthinned control. Regarding bark beetle prevalence as quantified through pitch tube counts, the Jeffrey pine beetle (*Dendroctonus jeffreyi* Hopkins) generally preferred larger trees before treatment implementation, but after exhibiting mixed pretreatment tendencies concerning stand density demonstrated a posttreatment proclivity toward higher density. Cut-to-length thinning followed by underburning increased the pine beetle population while whole-tree thinning unaccompanied by burning reduced it. Tree mortality was induced by the bark beetle infestation but was not its sole cause. Pitch tube abundance on white fir far exceeded that on Jeffrey pine, and the greatest influence on the fir engraver (*Scolytus ventralis* LeConte) population was the prevalence of its host tree. Increasingly utilized in forest restoration efforts in the western USA, the responses presented herein to these

thinning and burning practices provide natural resource managers insight into potentially compromised outcomes when implemented in Jeffrey pine and similar dry site forest types.

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# OVERALL INTRODUCTION

Past land use activities such as logging and grazing along with fire exclusion practices have altered forest successional patterns, leading to heightened stand densities and fuels accumulations (Parsons & DeBenedetti, 1979; Agee & Skinner, 2005). These, in combination with warmer temperatures, earlier snow melt, longer fire seasons, and prolonged droughts have contributed to a decline in forest health in the western USA. Two of the most prominent threats to these forests are catastrophic wildfire (Calkin et al., 2005; Stephens, 2005; Westerling et al., 2006; Miller et al., 2009) and epidemic bark beetle outbreaks (Goyer, Wagner, & Schowalter, 1998; Raffa et al., 2008; Bentz et al., 2009). To help mitigate these threats, silvicultural practices such as thinnings and prescription fire, often implemented in concert, have been increasingly utilized to restore forested ecosystems that are considered outside of their historical range of variability, concerning structural attributes and fuels accumulations (Agee, 1993), including Jeffrey pine dry site forest types of the eastern Sierra Nevada.

Thinnings, also known as density management, are often employed to improve vigor of residual stems through a reduction in competition for limiting resources such as water and nutrients, which in turn promotes their resistance to insects, disease, and other stressors (Fiddler et al., 1989; Stone, Kolb, & Covington, 1999; Nyland, 2002; Rippy et al., 2005; Walker et al., 2006; Fecko et al., 2008). Density management can also reduce canopy crowding as well as remove suppressed stems that constitute ladder fuels, restoring stand characteristics that minimize crown fire hazard and thus reduce the risk of catastrophic wildfire, stand replacing (Graham et al., 1999; Agee & Skinner, 2005). Another prominent restoration practice is prescription fire, which is often implemented to reintroduce fire into forested ecosystems that have been altered by its exclusion in order to restore the historical fire regime and therefore potentially alter wildfire behavior by reducing ground, surface, and ladder fuels accumulations and increasing canopy base height (Agee & Skinner, 2005; Stephens & Moghaddas, 2005).

The purpose of this study was to ascertain the long-term effects of density management and prescription fire on stand development and bark beetle activity in a Jeffrey pine dry site forest type. Specifically, cut-to-length and whole-tree harvesting approaches along with prescription fire were evaluated individually and in combination for their long-term influences on individual tree and stand level growth as well as their individual and interactive effects on Jeffrey pine beetle and fir engraver beetle demography during a posttreatment period of approximately one decade. Chapter One of this thesis is dedicated to examining the long-term effects of these practices on stand development while Chapter Two focuses on pre- and posttreatment beetle demography. The implications of these findings may provide natural resource managers insight into potential compromised outcomes concerning long-term growth and bark beetle activity when these practices are implemented in dry site forest types.

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# CHAPTER ONE

## Long-Term Growth Responses of a Jeffrey Pine Stand to Mechanized Thinning and Prescribed Fire

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### ABSTRACT

Forest thinnings implemented with cut-to-length and whole-tree harvesting systems followed by underburning were evaluated for their effects on individual tree and stand level growth responses in pure, uneven-aged Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) accompanied by isolated California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.). Based on both dimension and volume measures, trees of the unburned whole-tree treatment combination exhibited the greatest individual growth responses. At the stand level, a diminished volume growth response in the whole-tree treatment was especially pronounced in the burned portion, mostly attributable to exaggerated stocking losses, while a superior response in the unburned cut-to-length combination likely reflected not only the absence of detrimental fire impacts but also benefits of on-site slash retention. For stand level biomass, diminished growth in the whole-tree treatment was again evident, with that in the burned portion again most pronounced, while biomass accrual in the unburned cut-to-length treatment combination was generally comparable to that in the unthinned control. Increasingly utilized in forest restoration efforts in the western USA, the responses presented herein to these thinning and burning practices provide natural resource managers insight into potential compromised outcomes when implemented in Jeffrey pine and similar dry site forest types.

### KEYWORDS

stand density management, cut-to-length harvesting, whole-tree harvesting, prescription fire, tree dimensions, stand volume, stand biomass, *Pinus jeffreyi*, *Abies concolor*

# INTRODUCTION

Wildfire risk to forests of the western United States is on the rise and the acreages burned, although variable from year to year, as well as fire severity have also been on a protracted rise (Calkin et al., 2005; Stephens, 2005; Westerling et al., 2006; Miller et al., 2009). This has compromised watershed integrity, yields of commercial wood fiber, wildlife habitat, and scenic amenities. There are several factors that have contributed to this increase, including warmer temperatures, earlier snow melt, longer fire seasons, and past logging, grazing and fire exclusion practices that have altered successional patterns and elevated fuel accumulations (Parsons & DeBenedetti, 1979; Agee & Skinner, 2005; Westerling et al., 2006). Consequently, many forest restoration efforts currently underway are directed toward creating forest structures and compositions that permit stands to be more resistant and resilient to wildfire (Fule et al., 2001; Taylor, 2007; Fecko et al., 2008a; North et al., 2009). In some cases, these restoration practices are applied directly to the stand itself while in others they involve a reduction in forest floor fuels, and frequently both are implemented concurrently within individual stands.

Historically, silviculturists have used thinning to accelerate the growth of residual stems and to capture fiber volume before it is sacrificed through natural self-thinning (Li, 1923; Zeide, 2001; Nyland, 2002). Other benefits of thinning forest stands have been realized, particularly regarding improved vigor of residual stems through a reduction in competition for limiting resources such as water and nutrients, which in turn promotes the resistance to insects, disease, and other stressors (Fiddler et al., 1989; Stone, Kolb, & Covington, 1999; Nyland, 2002; Rippy et al., 2005; Walker et al., 2006a; Fecko et al., 2008b). However, this practice is also being employed as a wildfire mitigation technique. Thinnings, specifically low thinnings and possibly free thinnings (Helms, 1998), remove biomass in the form of suppressed trees that would otherwise succumb to competition, and such removals reduce the prevalence of ladder fuels and therefore crowning risk along with later accumulations of surface fuels, all of which serve to diminish wildfire size and severity (Graham et al., 1999; Pollet & Omi, 2002; Agee & Skinner, 2005; Stephens & Moghaddas, 2005).

Another prominent forest practice with implications for wildfire mitigation is prescription fire. This practice is currently being implemented to mimic the historic fire cycles of natural ecosystems, particularly those that have previously experienced frequent, low-to-moderate severity surface fires, which may aid in the restoration of historic stand characteristics that foster greater resistance and resilience to stand-replacing wildfires (Arno, 2000; Husari et al., 2006; Vaillant, Fites-Kaufman, & Stephens, 2009; Fettig et al., 2010; Fule et al. 2012). More specifically, prescribed fire is being used to reduce surface and ground fuels, prepare seed beds for natural regeneration, and to modify understory vegetation which can function as a competitor of stand constituents and regulator of regeneration establishment as well as a ladder fuel (Gaines, Kallander, & Wagner, 1958; Sackett, 1980, 1984; Reinhardt et al., 1991; Pyne, Andrews, & Laven, 1996; Arno, 2000; Bailey & Covington, 2002; Nyland, 2002; Walker et al., 2006b, 2011; Knapp et al., 2007; Wayman & North, 2007; Salverson et al., 2011a, 2011b). Prescribed fire has also been used to enhance wildlife habitat (Wright & Bailey, 1982; Pyne, Andrews, & Laven, 1996; Nyland, 2002) and to elevate availability of such critical nutrients as N, but evidently this is very nutrient and site specific (Wright & Bailey, 1982; Agee, 1993; Fisher & Binkley, 2000; Murphy et al., 2006; Johnson et al., 2008). Nevertheless, it has been documented that when underburning is not preceded by density management it can exacerbate stand mortality (Wright & Bailey, 1982; Arno, 2000; Pyne, Andrews, & Laven, 1996). Even when accompanied by density management, there is some recognition of a mortality risk in residual stems following an underburn and that the magnitude of the risk depends on several factors, including burn severity, stand vigor prior to underburning, and the diameter class and species composition of the residual stand (Thomas & Agee, 1986; Breece et al., 2008; Fecko et al., 2008a; Schwilk et al., 2009; Vaillant, Fites-Kaufman, & Stephens, 2009; Ryan et al., 2010). Mortality can ensue from a direct burning effect such as severe crown or cambial injury or may occur indirectly as a result of opportunistic insects or pathogens (Bradley & Tueller, 2001; Maloney et al., 2008; Schwilk et al., 2009; Fettig et al., 2010). Despite the immediate effectiveness of underburning in reducing fuel loading and enhancing the ability of a stand to endure catastrophic wildfire, the long-term effects of prescribed fire on the mortality of residual stems has not been comprehensively assessed.

The purpose of the study presented here was to ascertain the influences of density management and prescription fire, individually and interactively, on long-term stand development in a prominent forest cover type of the eastern slopes of the Sierra Nevada. Specifically, the responses of a residual Jeffrey pine stand on a dry eastern Sierran site were quantified eleven growing seasons following thinnings, implemented through two distinctly different harvesting approaches, and ten seasons after subsequent underburning. The implications of these findings may provide natural resource managers insight into potential compromised outcomes of these practices when implemented in dry site forest types.

## MATERIALS AND METHODS

### Study Site

The stand chosen for this study is uneven-aged, second growth, and pure Jeffrey pine with a minor representation of white fir. The site consists of 12.1 ha located on the east side of the Sierra Nevada in Nevada County, CA and is a component of the Tahoe National Forest (39°25’45”N, 120°8’30”W). The elevation is 1800 m and the aspect is generally northeast. The soils are of the Kyburz-Trojan complex (USDA Forest Service, 1994) and are well drained with a gravelly sandy loam surface layer and an andesitic substratum. The slope varies from 3 to 12% with the majority of the site falling within 3 to 6%. Based on the 55-year average, annual precipitation is 69 cm and is predominantly snowfall. At the time of treatment installation, the stand was 105 years old based on dominant and codominant crown class trees and the site quality is $SI_{100}$21 (index height in meters) for Jeffrey pine (Fecko et al., 2008c).

Treatment Installation

In September 2000, the study site was divided into three subunits of equal proportion with one of three thinning treatments randomly assigned to each subunit, specifically a cut-to-length harvesting system, a whole-tree harvesting system, or an unthinned control. As reviewed by Walker et al. (2006b), cut-to-length and whole-tree systems vary greatly in their harvesting approach and site impacts. The former system utilizes two machines, one which processes the trees at the stump, thereby creating residual organic materials that it concentrates into slash mats, while the second machine self-loads the logs and forwards them to a landing. Both machines travel over the slash mats, minimizing the disturbance of mineral soil as well as its compaction, but the mats also constitute elongated surface fuel concentrations. Whole-tree harvesting systems involve two machines as well, one of which fells selected trees and bunches them for transport while the second machine skids them to a landing where further processing ensues. All organic residues created by the harvest are extracted from the stand, minimizing wildfire risk but also exposing mineral soil and increasing associated impacts. The thinning treatments were implemented concurrently over four days in October 2000 using a Timberjack 1270 processor combined with a Timberjack 1210 forwarder (Timberjack Forestry Group, Moline, IL, USA) for the cut-to-length system while the whole-tree system used a Timbco 445 feller-buncher (Timbco Hydraulics, Inc., Shawano, WI, USA) and a Caterpillar 518 grapple skidder (Caterpillar, Inc., Peoria, IL, USA). For both treatments, a free thinning approach (Nyland, 2002) was followed to release select dominant and codominant crown class trees that displayed good growth form and crown development. Trees that were removed varied in crown class but few were < 25.4 cm DBH (bole diameter 1.37 m aboveground) and those < 20.3 cm DBH were intentionally felled only when they posed an obstacle to the harvesting operation (Fecko et al., 2008a).

In May 2002, a prescribed underburn was implemented on one-half of each of the three subunits dedicated to the individual thinning treatments. The subunits were divided by 1.0-m-wide hand lines and one of the two portions of each subunit was randomly designated to be burned while the other was to remain unburned. For the stand portions to be burned, a strip head fire ignition pattern was applied beginning at 6:00 p.m. with the treatment of all three portions completed at 11:00 p.m. of the same day. At the time of ignition the air temperature was 16°C, relative humidity was 48%, and the wind speed was 5.5 km $hr^{-1}$, with variation over the course of the 5-hr burn period ranging from 14 to 18°C, 39 to 50%, and 4.8 to 6.6 km $hr^{-1}$, respectively. The fuel moisture content was 8% for 1-hr, 10% for 10-hr, 14% for 100-hr, and 25% for 1000-hr timelag categories. The average rate of spread of the prescribed fire was approximately 58 m $hr^{-1}$ and the average flame length was approximately 0.7 m.

## Data Collection

During the designation of the subunits in September 2000, 30 permanent 0.08-ha circular plots were established for measurement of mensurational variables with 10 plots located in each of the three subunits, and within each subunit, 5 in the portion to be burned with the remaining 5 in the portion to remain unburned. At the implementation of the thinning treatments, all residual trees ≥ 20.3 cm DBH in every plot were measured for total height, DBH, and live crown length and then tallied by species. Subsequently, tree heights and live crown lengths were used to calculate live crown percentages, and average DBH values by plot were calculated using the quadratic mean formula (Curtis & Marshall, 2000). Basal area by plot was derived from quadratic mean DBH in combination with plot stem counts (Davis et al., 2001). Ultimately, the stem count and basal area for each plot were expanded to reflect equivalent 1.0-ha values.

For volume determination, three measures were used, specifically board feet volume, cubic feet volume, and cubic meter volume, with board feet and cubic feet units constituting the most common expression of volume in the USA while cubic meter units are most common where the metric system prevails (Husch, Beers, & Kershaw, 2003). Preliminary volume determinations were species specific regardless of the units used. For board feet volume of Jeffrey pine, the USDA Humboldt-Toiyabe National Forest Jeffrey Pine and Ponderosa Pine-Board Foot Volume Table was used, which is based on the Scribner Decimal C log rule with utilization to a 6-in merchantable top diameter and which incorporates both tree height and DBH in volume determinations. For Jeffrey pine cubic feet volume, the USDA Humboldt-Toiyabe National Forest Jeffrey Pine and Ponderosa Pine Cubic Foot Volume Table, which is also based on utilization to a 6-in merchantable top diameter and incorporates height and DBH dimensions, was used. White fir board feet and cubic feet volumes were derived from the McDonald & Skinner (1989) tables, with the former again based on the Scribner Decimal C log rule while both employ a 6-in merchantable top diameter and rely upon DBH measurements exclusively. Cubic meter volume for both Jeffrey pine and white fir was directly derived from the respective cubic feet volumes. Once individual tree volumes by species were obtained based on each specified unit, they were summed by plot and then combined across species within each plot. For stand level volumes, plot volumes based on board feet and cubic feet were expanded to reflect equivalent 1.0-ac values while those for cubic meters were further expanded to reflect a 1.0-ha equivalent value. Derived from the DBH measurements of all tallied trees within each plot, biomass for individual above-ground tree components, specifically foliage, branch, bole bark, and bole wood plus the total, was calculated by species using the formulas of Gholz et al. (1979) and then combined across species by plot, with all plot sums ultimately expanded to reflect equivalent 1.0-ha values. A final inventory identical to that detailed above in every respect was conducted in September 2011 and all extrapolated values regarding tree dimensions, density, volume, and biomass were again calculated. The availability of initial and final data permitted the calculation of the changes in all variables over the course of the study.

For the purpose of assessing influences of competing understory vegetation on overstory responses to the thinning and fire treatments, a 54-$m^2$ circular plot was established with the same center as each of the 0.08-ha plots for the mapping of shrub and herbaceous understory species, which permitted expression of their prevalence on a percent ground cover basis. Cover by each species encountered was determined individually, and then all were grouped together for the calculation of total percent ground cover. The understory inventory was conducted in August 2005, and the methods employed are described in greater detail in Salverson et al. (2011b).

Statistical Analysis

Because field logistics involving the implementation of the thinning and prescribed fire treatments necessitated that the thinning treatments be assigned to individual subunits of the stand with the underburn then assigned to one-half of each subunit, it was necessary to test for the independence of the plots within each thinning and burning treatment combination using initial data for variables germane to this study. The chosen variables were tree height, DBH, live crown length, basal area, and stem count. For each variable, residual values were calculated, which were defined as the difference between the mean for a given variable of the five plots of each treatment combination and the values obtained from the individual plots for the selected variable. Subsequently, the residual value of one plot was designated as the independent variable and that of the immediately adjacent plot the dependent variable which was repeated sequentially within each treatment combination, yielding one value of each for each plot pair, four values of each for each of the six treatment combinations, and thus a total of 24 values of each for the entire stand. These values were then incorporated into simple linear regression models by variable. For each regression, models were considered to be significant, signifying a lack of independence among the plots within treatments, only when $p \leq .05$ according to the $F$ test. None of the models proved to be significant, indicating that responses from individual plots were not significantly influenced by those from immediately adjacent plots for any of these variables.

Excluding the changes occurring between the initial and final inventories, data pertaining to the tree dimensions, density, volume, and biomass components of the study were analyzed using repeated measures, mixed model analysis of variance (ANOVA) to test for effects of thinning and prescribed fire treatments, the year of inventory, and all possible interactions. This analysis incorporated both the compound symmetry covariance structure and the first-order autoregressive structure. For each variable, the covariance structure relied upon was that providing the lowest value for Akaike's Information Criterion (bias-corrected version, AICC). For changes between the initial and final inventories pertaining to the various study components, two-way ANOVA was used to test for thinning and fire treatment effects plus their interaction. In every ANOVA indicated above, main effects and their interactions were considered significant only when $p \leq .05$ according to the $F$ test. Subsequently, differences among means were evaluated using the least significant difference (LSD) test with $\alpha = .05$. For the statistical analysis of the understory data used in this study, refer to Salverson et al. (2011b).

Additional statistical analysis consisted of two series of simple linear regression models used to investigate relationships between variables selected as particularly pertinent to each of the components of the study. The first series was divided into six subsets, with the first consisting of models incorporating all possible combinations of initial live crown length and percentage as independent variables with initial, final, and changes in height, DBH, basal area, tree count, individual tree board feet, cubic feet, and cubic meter volumes by species, stand board feet, cubic feet, and cubic meter volumes by species and across species, and foliage, branch, bole bark, bole wood, and total biomass by species plus the combined total across species serving as the dependent variables. Additionally, initial live crown length and percentage constituted the independent variables in models with final live crown length and percentage plus their changes as dependent variables. The second subset of this series was configured identically to the first except that final values for the independent variables were coupled with final values plus the changes regarding the dependent variables, and combinations involving live crown variables for both were excluded. The third subset was also configured identically to the first except that initial basal area and tree count replaced that of live crown length and percentage as the independent variables, and the initial values for the dependent variables were excluded as were the density variables in their entirety regarding the latter. The fourth subset employed final tree count alone as the independent variable but was otherwise identical to the third subset. For the fifth subset, initial foliar biomass of the individual tree species served as the independent variables while the suite of dependent variables employed in the first subset was replicated with the exception of initial foliar biomass. Additional stipulations regarding the fifth subset were that models involving volume or biomass as the dependent variables were matched within species to that specified in the independent variable and all models incorporating volume or biomass values across species were excluded. The last subset in this series was configured identically to the fifth subset except that final values replaced initial values regarding the independent variables and initial values were excluded from the suite of dependent variables. The second regression series incorporated percent cover by prominent understory species and the total cover of the understory community as independent variables while the suite of dependent variables identified above regarding the first subset of the first series was again employed except that all initial values for the latter were excluded. For both series, regression models were considered significant only when $p \leq .05$ according to the F test, but significant models explaining < 40% of the variation in the dependent variable are not reported here. All statistical analyses were performed using SAS (SAS Institute, Inc., Cary, NC).

## RESULTS

Tree Dimensions and Stand Density

When averaged across species, with the subject stand consisting of 96% Jeffrey pine and 4% white fir at both the initial and final inventories, ANOVA revealed that total tree height was significantly influenced by the year of inventory ($p < .0001$) and the fire treatment × year of inventory interaction ($p = .0071$) while the fire treatment was the sole significant influence on the change in height ($p = .0071$) over the course of the study (Table 1). Initially, the LSD test indicated that tree height in the unburned portion of the whole-tree subunit significantly exceeded that in the burned portion of the cut-to-length treatment and the unburned portion of the unthinned treatment with all other treatment combinations assuming intermediate values. At the final inventory, height in the unburned portion of the whole-tree subunit exceeded that in all other treatments except the unburned cut-to-length combination, and that in the latter also exceeded the height in the burned portion of this thinning treatment. Regarding the change in height, positive values prevailed regardless of treatment, and the pattern of disparities indicated by the LSD test noted above for height at the final inventory was replicated verbatim. For DBH, ANOVA identified fire treatment ($p = .0178$), year of inventory ($p < .0001$), and the thinning × fire treatment ($p = .0113$), thinning treatment × inventory year ($p = .0087$), and fire treatment × inventory year ($p = .0136$) interactions as significant, while the change in this dimension was influenced by the thinning ($p = .0087$) and fire ($p = .0136$) treatments. Regarding the differences among treatment combinations in initial, final, and change in DBH, the LSD test disclosed that trees in the unburned portion of the whole-tree subunit were larger throughout the study and also exhibited a greater response over the course of the study than in any other treatment combination, although the growth responses were positive without exception for this dimension.

For live crown variables, ANOVA identified significant influences of fire treatment ($p = .0058$) and of the thinning × fire treatment ($p = .0089$) and thinning treatment × year of inventory ($p = .0002$) interactions on crown length along with a fire treatment effect ($p = .0002$) on the change in length (Table 1). Initially, crown length in the burned portion of the unthinned treatment was significantly greater than that in the burned portions of the cut-to-length and whole-tree subunits according to the LSD test while it was greater in the unburned portions of all three thinning treatments than in the latter as well. At the final inventory, numerous disparities among treatment combinations were revealed by the LSD test. Specifically, crowns were larger in the unburned whole-tree combination than in all except the burned but unthinned combination, were larger in the latter than in the burned portions of the cut-to-length and whole-tree treatments, and were also larger in the unthinned and unburned combination than in the burned whole-tree combination. Regarding change in crown length, positive values were confined to the whole-tree subunit irrespective of fire treatment while losses prevailed in all remaining treatments, and the LSD test indicated that the losses incurred in the burned and unburned portions of the cut-to-length and unthinned subunits differed significantly from the gain in the unburned portion of the whole-tree treatment and that the loss in the unburned portion of the cut-to-length treatment along with those within both portions of the unthinned subunit differed from the gain in the burned portion of the whole-tree treatment. For live crown percentage, ANOVA revealed the influences of thinning ($p < .0001$) and fire ($p = .0199$) treatments, inventory year ($p < .0001$), and the thinning × fire treatment ($p = .0367$) and thinning treatment × year ($p < .0001$) interactions to be significant, while for the change in live percentage, thinning treatment proved to be the sole influence ($p < .0001$). According to the LSD test, the initial live percentage in the burned and unburned portions of the unthinned subunit significantly exceeded the percentages in all remaining treatments except that in the unburned portion of the cut-to-length treatment, that in the latter exceeded the initial percentages in the whole-tree subunit regardless of fire treatment, and the percentage was significantly greater in the unburned than in the burned portion of the whole-tree treatment. At the final inventory, the LSD test revealed a significantly greater live percentage in the unthinned and unburned combination than in the unburned cut-to-length and burned whole-tree combinations along with a percentage in the latter that was exceeded by those in the burned cut-to-length, unburned whole-tree, and burned but unthinned combinations. Significant disparities identified by the LSD test regarding the change in live percentage identified a higher percentage in the burned whole-tree combination, the only one producing a positive value, than those in all remaining treatments except for the unburned whole-tree combination, a value in the latter that exceeded those in all except the former and in the burned cut-to-length combination, and a value in the burned cut-to-length combination that exceeded those in the unburned cut-to-length and in the unthinned subunit regardless of fire treatment.

According to ANOVA, significant effects exerted on basal area consisted of those of thinning treatment ($p$ = .0235), year of inventory ($p$ < .0001), and their interaction ($p$ = .0176) while the change in basal area was affected by the thinning treatment ($p$ = .0176) alone (Table 1). When averaged across fire treatments, the basal area in the unthinned subunit was 29% greater than that in the cut-to-length subunit at the initial inventory and 31% greater than that in the whole-tree subunit, and the LSD test indicated that the basal area in the unburned portion of the unthinned subunit significantly exceeded those in the burned portion of the cut-to-length and the unburned portion of the whole-tree subunits. At the final inventory, significant disparities consisted of a higher basal area in the unburned portion of the unthinned subunit than in the burned portions of the cut-to-length and whole-tree subunits and the unburned portion of the latter. Regarding the change in basal area, increases were evident in all treatments, but the LSD test revealed that those in the unburned portions of the cut-to-length and unthinned treatments plus that in the burned portion of the latter exceeded the increase in the burned whole-tree treatment combination. Thinning treatment ($p$ = .0059) and the thinning × fire treatment ($p$ = .0050) and thinning treatment × inventory year ($p$ = .0393) interactions influenced tree count according to ANOVA with the former also influencing the change in count ($p$ = .0393). At the initial inventory, the count in the unthinned treatment was 19% and 42% greater when averaged across fire treatments than those in the cut-to-length and whole-tree treatments, respectively, and the LSD test disclosed that the count in the unburned and unthinned combination significantly exceeded those in the unburned portions of the cut-to-length and whole tree treatments while the counts in the burned portions of all three subunits also exceeded that in the latter. At the final inventory, it was revealed that the count in the unburned and unthinned combination was greater than those in all other treatments while that in the unburned portion of the whole-tree subunit was less than the counts in all other treatments. For the change in counts, increases were confined to the two portions of the unthinned subunit, and the LSD test indicated that these differed significantly from a loss in the burned portion of the whole-tree subunit.

Individual Tree Volume

ANOVA revealed significant influences of thinning ($p$ = .0241) and fire ($p$ = .0094) treatments plus their interaction ($p$ = .0127), the year of inventory and the thinning treatment × year and fire treatment × year interactions (all $p$ < .0001), as well as the thinning × fire treatment × inventory year interaction ($p$ = .0003) on individual tree board feet volume of Jeffrey pine (Table 2). The LSD test, however, indicated that significant differences among treatments were limited to a higher volume in the unburned whole-tree combination than that in all remaining treatments, disparities that were common to both inventories. As for the change in volume for this species, ANOVA disclosed that the thinning and fire treatments (both $p$ < .0001) and their interaction ($p$ = .0003) imposed significant influences. Over the course of the study, volume increases prevailed regardless of treatment, but the LSD test indicated that the increase in the unburned portion of the whole-tree subunit exceeded those in all other treatment combinations and that the increase in the unburned portion of the cut-to-length subunit exceeded those in all others except the two portions of the whole-tree subunit. For white fir, effects of all treatments and interactions on individual tree volume as well as on the change in volume were nonsignificant according to ANOVA. Nevertheless, the LSD test indicated that the volume in the unburned portion of the unthinned treatment exceeded that in the burned portion of the whole-tree treatment at the initial inventory, but thereafter all differences were nonsignificant as were those involving the change in volume. Regarding the latter, increases prevailed in all treatments except for the unburned cut-to-length combination where no change occurred, but a comparison of the changes over the course of the study between Jeffrey pine and white fir across treatments reveals that the average increase for the former surpassed that for the latter by 407%.

Significant influences on individual tree cubic feet volume of Jeffrey pine consisted of those of thinning ($p$ = .0343) and fire ($p$ = .0108) treatments plus their interaction ($p$ = .0128), the year of inventory and the thinning treatment × year and fire treatment × year interactions (all $p$ < .0001), as well as the thinning × fire treatment × inventory year interaction ($p$ = .0003), and because individual tree cubic meter volume was a direct transformation of cubic feet volume, influences on these two volume measures as revealed by ANOVA were identical in every respect (Table 2). Such an identicality also prevailed regarding the changes in individual tree cubic feet and cubic meter volumes for this species, with both affected by the thinning and fire treatments (each $p$ < .0001) and their interaction (each $p$ = .0003). As for the disparities among means revealed by the LSD test, those previously noted for the Jeffrey pine individual tree board feet volume and its change were replicated verbatim for both cubic feet and cubic meter volumes and their changes, respectively. For white fir, effects of all treatments and interactions on individual tree cubic feet and cubic meter volumes as well as on the changes in volumes were again nonsignificant according to ANOVA. However, as noted previously concerning board feet volume for this species, the LSD test revealed that at the initial inventory, the volumes in the unburned portion of the unthinned treatment significantly exceeded those in the burned portion of the whole-tree treatment. In a slight departure from the change in board feet volume for white fir, changes in cubic feet and cubic meter volumes included small losses regarding the unburned cut-to-length treatment combination.

Stand Volume

For stand volume variables, ANOVA identified the influences of the year of inventory ($p < .0001$) and the fire treatment × inventory year interaction ($p = .0248$) as significant on Jeffrey pine board feet volume per acre, but there was no designation of significant differences among any of the means for this species and variable by the LSD test (Table 3). Fire treatment alone ($p = .0248$) affected the change in volume for this species, however, and while increases over the course of the study prevailed regardless of treatment, the LSD test revealed that those in the burned portions of the cut-to-length and whole-tree treatments were exceeded by that in the unburned portion of the former. For white fir, all main and interaction effects on board feet volume per acre as well as on the change in this variable were nonsignificant according to ANOVA. Nevertheless, the LSD test indicated that at the final inventory, the volume in the unburned portion of the unthinned subunit exceeded that in the unburned portion of the whole-tree subunit, a disparity accentuated by the total lack of white fir in the latter throughout the study. Regarding the change in volume for this species, and notwithstanding the lack of significant differences among treatments here according to the LSD test, it is perhaps noteworthy that substantial losses were sustained in the burned portion of the cut-to-length treatment and in the unburned portion of the unthinned treatment over the course of the study. Significant influences identified by ANOVA on combined board feet volume per acre were limited to that of the year of inventory ($p < .0001$), while none were revealed regarding the change in this variable. Largely reflecting the dominance of Jeffrey pine in stand composition, however, and with volume increases again prevailing in all treatments, the LSD test disclosed differences among means concerning the latter that replicated verbatim those noted above for Jeffrey pine.

The same array of influences identified by ANOVA for board feet volume per acre of Jeffrey pine also affected cubic feet volume per acre for this species, specifically the year of inventory ($p < .0001$) and the fire treatment × inventory year interaction ($p = .0236$), while the fire treatment alone ($p = .0236$) again influenced the change in Jeffrey pine volume (Table 3).

Here also, however, the LSD test again did not designate any of the differences among means within either inventory as significant. For the change in cubic feet volume per acre, and in somewhat of a departure from the significant disparities regarding board feet volume, those pertaining to the cubic feet measure consisted of a lower value in the burned portion of the whole-tree subunit than in the unburned portions of the cut-to-length and unthinned subunits along with a lower value in the burned than in the unburned portion of the cut-to-length treatment, although positive values again prevailed without exception. Nevertheless, pronounced parallels between the cubic feet and board feet measures were also evident in white fir and in the combined volume. As for white fir, ANOVA again revealed all main and interaction effects on cubic feet volume per acre, and on its change, to be nonsignificant, differences among means identified by the LSD test were confined to the final inventory as before and consisted solely of a greater volume in the unburned portion of the unthinned treatment than in that of the whole-tree treatment where this species was absent entirely, and substantial losses were sustained over the course of the study in the burned portion of the cut-to-length treatment and the unburned portion of the unthinned treatment. Regarding the combined cubic feet volume per acre, the year of inventory ($p < .0001$) was identified by ANOVA as solely influential, while all effects on the change in this variable were identified as nonsignificant. The LSD test did, however, indicate differences among the means in regards to the latter that deviated slightly from those of the combined board feet volume and more so from those of the Jeffrey pine cubic feet volume, as the combined volume in the unburned portion of the cut-to-length treatment here exceeded only that in the burned portion of this thinning treatment. Nevertheless, volume increases over the course of the study again prevailed across all treatment combinations.

For the reason noted above in the individual tree volume subsection, ANOVA disclosed that the influences on cubic feet volume per acre and cubic meter volume per hectare were identical in every respect as was that concerning their respective changes (Table 3). Disparities among treatments identified by the LSD test, or the lack thereof, were identical in the two measures as well. Consequently, neither are reiterated here for the cubic meter measure.

Stand Biomass

For Jeffrey pine biomass, ANOVA revealed parallels among the different biomass components, specifically those of foliage, branch, bole bark, bole wood, and total biomass, concerning the significant influences of the inventory year (all $p < .0001$) and the thinning treatment × inventory year interaction ($p = .0012$, $p = .0242$, $p = .0022$, $p = .0284$, and $p = .0180$, respectively). However, the differences among treatment means identified by the LSD test were confined to the foliar biomass component at the final inventory, where the unburned portion of the unthinned treatment exceeded that of the burned cut-to-length treatment (Table 4). As for the change in Jeffrey pine biomass, ANOVA indicated that the thinning treatment alone affected each of the aforementioned biomass components plus the total ($p = .0012$, $p = .0242$, $p = .0022$, $p = .0284$, and $p = .0180$, respectively). Regarding the change in foliar biomass, the LSD test identified several significant disparities among treatments, specifically a greater value in the unburned portion of the unthinned subunit than in the whole-tree subunit irrespective of fire treatment along with greater values in both portions of the cut-to-length subunit and in the burned portion of the unthinned treatment than in the burned portion of the whole-tree subunit. Overall, and despite the gains in foliar biomass exhibited by all treatments, those in the whole-tree subunit were 52% and 60% less when averaged across fire treatments than those in the cut-to-length and unthinned subunits, respectively. Differences among treatment means for the change in the branch component consisted of greater values in the unburned portion of the cut-to-length subunit and in the unthinned subunit in its entirety than in the burned portion of the whole-tree subunit, although biomass increases again prevailed across all treatment combinations. The LSD test also revealed that the disparities among means for the change in bole bark biomass replicated verbatim those of foliar biomass, while those identified for the changes in bole wood and total Jeffrey pine biomass were identical to those of the branch component. Here again, positive values prevailed without exception. Specific to the changes in bole wood and total biomass, the gains in the burned portion of the whole-tree subunit were 46% less than the next smallest increase for each, namely that found in the unburned portion of this subunit.

ANOVA disclosed that all influences on the individual white fir biomass components and their total were nonsignificant (Table 4). The LSD test, however, detected significant differences among treatment means at the final inventory that were identical for each component as well as the total, with values in the unburned portion of the unthinned subunit exceeding those in the unburned whole-tree combination which again largely reflected the lack of white fir representation in the latter. For changes in the biomass of this species, no significant influences were identified by ANOVA nor were any significant disparities among means revealed by the LSD test. Nevertheless, unlike Jeffrey pine, numerically substantial losses occurred in certain treatment combinations for white fir regarding each of the four biomass components and the total, specifically in the burned portion of the cut-to-length treatment and in the unburned portion of the unthinned treatment.

Regarding combined total biomass and its change, the sole influence revealed by ANOVA for either was that of the year of inventory ($p < .0001$) on the former (Table 4). That the combined total was greater at the final than at the initial inventory in every treatment combination was apparent in the positive values prevailing in all treatments regarding the change in this variable. As for disparities among means according to the LSD test, only those in combined biomass at the final inventory were significant, with a higher total in the unburned portion of the unthinned treatment than in the burned portions of either the cut-to-length or whole-tree treatments.

## Tree and Stand Relationships to Overstory and Understory Variables

The first subset of the first simple regression series, which related a wide array of individual tree and stand variables to initial live crown development, produced 26 significant models (Table 5). Of those involving live crown length, a total of 17 models, initial DBH, final live crown length, the final values plus the changes for all three stand level Jeffrey pine volume measures as well as each of the three final combined volume values, specifically board and cubic feet volume per acre and cubic meter volume per hectare, along with the final values plus the changes for Jeffrey pine branch, bole wood, and total biomass, were all positively related to this independent variable. For models encompassing initial live crown percentage as the independent variable, eight positive relationships were disclosed which consisted of those between final live crown percentage, the change in basal area, and the change in total Jeffrey pine biomass as well as in each of its four biomass components, specifically that of foliage, branch, bole bark, and bole wood, plus that in combined total biomass, and this independent variable. Additionally, a negative correlation was revealed between the change in live crown percentage and the initial percentage that explained nearly two-thirds of the variation in the dependent variable, an amount greater than that explained in any other model of this subset. The second subset of this series, which replaced initial live crown development with its final values regarding the independent variables, generated eight significant models, all incorporating crown length as the independent variable to which final values for height and DBH as well as the final values plus the changes for all three individual Jeffrey pine volume measures, namely board feet, cubic feet, and cubic meter volume per tree, were each positively related. With the exception of the two involving changes in cubic volume, these models accounted for more than one-half of the variation in the dependent variables, and one of them, specifically the model involving DBH, accounted for more than 70% of such variation.

The third subset of the first regression series, which related an array of tree and stand variables to initial stand density, yielded 11 significant models involving basal area and an additional four involving tree count (Table 5). For the former, positive relationships prevailed exclusively, and these involved the final values for combined board feet and cubic feet volume per acre along with that for combined cubic meter volume per hectare, final Jeffrey pine stand level cubic feet and cubic meter volumes, final values for total Jeffrey pine biomass and for each of its individual biomass components, and the final combined total biomass. Three of these models, specifically those involving the combined stand level cubic volumes and the combined total biomass, accounted for more than three-fourths of the variation in the dependent variables, with the latter explaining over 80% of this variation. For models with initial tree count as the independent variable, final DBH and the changes in all three of the individual Jeffrey pine volume measures constituted the dependent variables, and for each of these four models, negative relationships prevailed. The fourth subset of this series, which incorporated final tree count as the sole independent variable, replicated the third subset concerning pertinent dependent variables. Except for the model involving DBH, however, the relationships were somewhat stronger.

The fifth subset of the first regression series, which related tree and stand variables to initial foliar biomass by species, produced 27 significant models with eight specific to Jeffrey pine and 19 to white fir regarding the independent variables (Table 5). Concerning the former, positive relationships prevailed without exception between the final values of all three Jeffrey pine stand level volume measures and each of its four biomass components plus the total and this independent variable. Collectively, these models were among the strongest thus far noted with at least two-thirds of the variation in the dependent variables explained. The models encompassing initial white fir foliar biomass as the independent variable revealed 11 positive correlations between the final values of each of the individual volume and stand level volume measures as well as the final values of each of the biomass components plus total biomass and this independent variable. All of these models produced strong correlations explaining more than 90% of the variation in the dependent variables except for those involving individual volume measures. Eight additional models specific to white fir in this subset involved changes in the three stand level volume measures and the four biomass components plus the total as the dependent variables, all negatively related to the initial foliar biomass of this species. Nevertheless, approximately two-thirds at least of the variation in the dependent variables was explained here.

For the sixth and final subset of the first regression series, which related tree and stand variables to final foliar biomass by species, 27 significant models were generated with 10 specific to Jeffrey pine and 17 to white fir regarding the independent variables (Table 5). For the former, the final values plus the changes in all three stand level volume measures and the final values of Jeffrey pine branch, bole bark, bole wood, and total biomass served as dependent variables. Positive correlations prevailed without exception, with approximately 50% or more of the variation in the dependent variables accounted for in the models involving volume measures and considerably more than 80% in those involving biomass. As for the models in which final white fir foliar biomass served as the independent variable, positive relationships were revealed between the final individual volume measures, the final stand level volume measures, and the final branch, bole bark, and bole wood biomass plus the total, and this independent variable. Of these, nearly all of the variation in the dependent variables was explained except for that in the models involving individual white fir volume. Additional significant models specific to this species related the changes in the stand level volume measures and those in branch, bole bark, bole wood, and total biomass to final foliar biomass, all of which revealed negative correlations of relatively modest strength.

The second simple regression series, which related a wide array of individual tree and stand variables to understory development by prominent species and in total, produced nine significant models, all of which featured Mahala mat (*Ceanothus prostratus* Benth.) cover as the independent variable (Table 6). These models portrayed positive correlations exclusively between the final values of all three white fir stand level volume measures, the final white fir total biomass and each of the four components, the combined total biomass, and this independent variable. Except for the latter, these models explained more than two-thirds of the variation in the dependent variables.

## DISCUSSION

Imposed on a Jeffrey pine stand of moderate pretreatment density on a site of low quality (Meyer, 1938), the thinnings implemented here using cut-to-length and whole-tree harvesting approaches each removed approximately 30% of the extant stocking, which constitutes a moderate thinning according to conventional guidelines (Smith et al., 1997). On average, the thinning intensity based on tree counts also revealed a density reduction of 30% although with a substantial difference between a lower cut-to-length and higher whole-tree treatment level. This disparity was largely a reflection of the variation in the spatial distribution of tree sizes across the stand. Unlike thinning practices, which by intent are employed to diminish density, prescribed fire may inadvertently do so as well when its implementation induces excessive mortality (Weaver, 1947). To a limited degree such was the case here, specifically when combined with the whole-tree harvesting approach, which was the only treatment combination to produce a loss in stem count that differed significantly from the gain in the unthinned control. Much of this mortality occurred in smaller trees within the first two post-fire growing seasons (Fecko et al., 2008a), which was consistent with the findings of earlier studies (Mutch & Parsons, 1998; Stephens & Finney, 2002; Agee, 2003; McHugh & Kolb, 2003; Fettig et al., 2010) and was attributable to the direct effects of fire injury, specifically a reduction in photosynthetic capacity caused by severe crown scorch and cambial injury due to excessive bole char (Harrington, 1987; Ryan & Reinhardt, 1988; Swezy & Agee, 1991; van Mantgem & Schwartz, 2004). In the study here, this may have been magnified by the severe drought sustained during this period (Fecko et al., 2008c). However, continued mortality was observed throughout the duration of the study, suggesting a cumulative effect of stress possibly resulting from soil compaction and diminishment of nutrient pools exacerbated by the whole-tree harvesting approach. Rubber tired skidders exert high ground pressure (Adams & Froehlich, 1981; Davis, 1992) and when coupled with the absence of slash accumulations can greatly diminish soil macro-porosity, thereby impairing hydraulic conductivity and thus water availability (Gomez et al., 2002; Page-Dumroese et al., 2006; Han et al., 2009). Resulting from both the mechanized and fire treatments, the removal of organic residues from the site, combined with the loss of antelope bitterbrush, the most prevalent understory species and a nitrogen-fixer (Busse et al., 2007; Salverson et al., 2011b), may have reduced availability of critical nutrients, especially N, P, and Ca, further diminishing tree vigor (Kimmins, 1977, 2004; Grigal, 2000; Johnson et al., 2008). Another possible contributor to the continued mortality may have been a bark beetle infestation, specifically by the red turpentine beetle (*Dendroctonus valens* LeConte), which often attacks western yellow pine stands following prescription fire and especially when tree vigor has been previously compromised (Bradley & Tueller, 2001; McHugh, Kolb, & Wilson, 2003; Parker, Clancy, & Mathiasen, 2006). This possibility will be examined further in a subsequent manuscript.

Based upon all of the variables employed here to assess individual tree responses to treatment, those in the whole-tree subunit provided the greatest evidence of a stimulatory effect, although it was largely confined to the unburned portion. Nevertheless, trees of the latter treatment combination exhibited the greatest overall growth in height, DBH, and live crown length as well as individual board feet, cubic feet, and cubic meter volumes over the course of the study, although in some individual comparisons within certain variables their superiority was manifested numerically rather than statistically. To some extent, the faster growth in this treatment combination was a reflection of the larger trees there initially due to the natural variation in tree sizes. However, the aforementioned higher harvesting intensity likely reduced between-tree competition, allowing for enhanced growth that may have been further amplified by the continued reduction in stem count as the study progressed (Fiddler et al., 1989; Kimmins, 2004). These assertions were corroborated somewhat by the negative relationships prevailing between final DBH as well as the changes in each of the individual Jeffrey pine volume measures and both the initial and final tree counts, which in total suggested that lower densities yielded greater growth increases in individual Jeffrey pine stems. Another possible contributor to the faster growth may have been the absence of white fir in this treatment combination. White fir is poorly adapted to sites receiving less than 89 cm of precipitation annually (Laacke, 1990) which probably limited its growth here, contributing to lower averages for individual tree growth measures where it was present even though it was a minor stand component. Due to its shade tolerance among other factors, this species is renowned for its persistence in high density stands (Laacke, 1990), however, and only in the unthinned treatment was there any indication of the fir exhibiting growth even remotely comparable to that of Jeffrey pine, specifically regarding the changes in the three volume measures. Nevertheless, for white fir, the values in the unthinned stand portion numerically exceeded those in the other treatments but did not differ statistically from them. A final contributor to the enhanced dimension and volume growth exhibited by trees in the unburned whole-tree combination may have been the expansion of their crowns during the study, another possible expression of their continued release from competition but also perhaps a reflection of the absence of any fire-induced crown loss, which has been documented to impair post-fire tree growth (Peterson et al., 1991; Moghaddas & Stephens, 2007). Several significant regression models developed here attested to the importance of crown development to individual tree growth in this stand, including positive relationships between initial DBH and initial live crown length, between final height as well as DBH and final crown length, and between the final values plus the changes for all three Jeffrey pine volume measures and the latter. In light of the above considerations, the detrimental effects of the burned whole-tree treatment combination with regard to mortality noted previously may have been more a reflection of fire impacts than those of harvesting approach despite the fact that stem losses in the unburned whole-tree treatment combination were substantial as well. A thinning treatment influence on live crown percentage in this study was manifested primarily in a greater average decrease in the unthinned subunit compared to those in the thinned subunits, which likely reflects the propensity of Jeffrey pine, a shade intolerant species (Jenkinson, 1990), to self-prune prodigiously (Lanner, 1999) when subjected to elevated crown competition. The only treatment combination with an increase in live crown percentage during the study was the burned whole-tree combination, which when coupled with the fact that this combination was the second of only two that exhibited an increase in live crown length, suggests that any loss to crown scorch at the implementation of the underburn was offset by subsequent crown expansion permitted by the continued reduction in stem count noted previously. In somewhat of an exception to the pattern here concerning the importance of live crown to the growth of individual trees, the burned cut-to-length combination generally exhibited growth responses that were comparable to the unthinned control despite a crown loss over the course of the study that was intermediate relative to those of the other treatment combinations, which may be indicative of bole damage resulting from the prolonged combustion of the slash mats produced by this harvesting approach.

Representing the integration of stocking level and individual tree growth as influenced by treatment, examination of stand level volume growth measures, specifically the changes in board and cubic feet volume per acre along with those in cubic meters per hectare, revealed that the fire treatment alone influenced Jeffrey pine stand volume growth, imposing a pronounced reduction in growth over the course of the study. This effect was apparent in all three volume measures and most evident within the cut-to-length subunit among the three thinning treatments, while the lowest overall increase in growth occurred in the burned whole-tree combination. In the absence of thinning, Collins, Moghaddas, & Stephens (2007) observed a small, albeit significant, reduction in stand level cubic volume growth in Sierra Nevada mixed conifer one year following the implementation of prescription fire. Comparatively, results presented here, specifically the small numerical reduction for Jeffrey pine in the burned unthinned combination compared to that in the unburned portion of this subunit, suggests that such a reduction may persist for an extended period. Nevertheless, the burned whole-tree combination exhibited the smallest stand volume gain, which conforms to the findings of Landsberg et. al (1984), Landsberg (1992), and Busse, Simon, & Riegel (2000), all of whom reported diminished annual stand cubic volume growth in ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.) when prescribed fire was implemented in previously thinned stands. The diminished stand level growth response by Jeffrey pine here was mostly attributable to the exaggerated loss in stocking level incurred by the whole-tree subunit, possibly resulting from the array of potential contributing maladies previously discussed in reference to this treatment combination. This assertion is supported in part by positive relationships displayed in the regression analysis between final values for stand level Jeffrey pine cubic volume measures and initial basal area as well as others between final combined board and cubic volume values and this independent variable. It is also probable that exaggerated stocking loss accounts for the fact that volume growth in the unburned whole-tree treatment combination was surpassed numerically by that in the unburned cut-to-length combination despite the superior individual tree growth in the former. The overall supremacy of the unburned cut-to-length combination among the six included in the study regarding stand level Jeffrey pine volume growth measures likely reflected not only the lack of fire impacts but also benefits of the on-site slash retention characteristic of this harvesting approach, possibly including a mulching effect that enhanced soil moisture retention (Fisher & Binkley, 2000; Fecko et al., 2008b) and the augmentation of critical nutrient pools (Tiedemann, Klemmedson, & Bull, 2000). Regarding the latter, forest floor levels of N, P, K, Ca, Mg and S are documented to have been elevated by the cut-to-length treatment on this site (Johnson et al., 2008). When combined with prescription fire, however, there was some additional evidence beyond that specific to Jeffrey pine noted above of a detrimental effect in this subunit likely associated with the slash mats, particularly within the combined cubic volume measures where there was significantly lower stand level growth in the burned than in the unburned portion. To a minor extent, this may reflect somewhat pronounced volume losses sustained by white fir in the burned portion of this subunit. In contrast to Jeffrey pine, white fir is poorly adapted to fire due in part to delayed self-pruning, lateness of thick bark development, a shallow root system, and copious pitch production (Ferrell, 1983; Lanner, 1983; Ferrell, Otrosina, & DeMars, 1994; Zouhar, 2001) combined with continuous exudation, all of which exacerbate its tendency to torch and succumb to cambial and root mortality (Lanner, 1999; Zouhar, 2001; Walker et al., 2012). This tendency may be particularly pronounced in the presence of slash mats where fire intensity tends to be elevated (Walker et al., 2006b; Fecko et al., 2008a). A profusion of regression models revealing positive relationships between the final stand level Jeffrey pine volume values and initial live crown length, between these values and both the initial and final foliar biomass for this species, and perhaps most pertinently, between the changes in these values and both initial crown length and final species-specific foliar biomass, seemingly supports an assertion that absence of any crown loss related to scorching in unburned stand portions was an important factor in the comparatively superior volume growth realized there. However, such a claim is compromised by the fact that the burned whole-tree treatment combination was one of only two for which live crown length increased over the course of the study, as previously noted, yet it produced the poorest overall stand volume growth attributable specifically to that in Jeffrey pine. There were also several significant regression models specific to white fir potentially pertaining to a fire impact on crown development and more specifically to its subsequent influence on stand level volume growth as manifested in final volumes that were positively related to initial and final foliar biomass and volume changes that were negatively related to these independent variables. Yet, again when assessed within the context of the analyses in total, an interpretation of the latter models as indicating that crown loss due to scorching culminated in volume losses in this species over the course of the study as was evident in the burned cut-to-length treatment combination was contradicted by the fact that the only other combination exhibiting a loss was that of the unburned and unthinned combination. Nevertheless, some significant regression models revealed associations between stand volume measures and understory vegetation, which may indirectly provide further evidence supporting the assertion that fire depressed volume increment in this study. Specifically, positive correlations were disclosed between final white fir board feet and cubic feet volume per acre plus the cubic meter volume per hectare values and mahala mat abundance, which is noteworthy for the fact that this shrub is renowned for its near complete fire resistance (USDA Natural Resources Conservation Service, 2012), although an affinity of white fir for mahala mat may also be reflected in these models as has been previously noted in regards to its regeneration (Tappeiner & Helms, 1971; Salverson et al., 2011a) with results here suggesting that this regeneration may persist until it contributes to stand volume.

Unlike stand volume growth, thinning was the overriding influence on total Jeffrey pine biomass and each of the four Jeffrey pine biomass components, specifically foliage, branch, bole bark and bole wood. This effect was most clearly reflected in the diminished biomass growth in the whole-tree subunit compared to the unthinned control and was particularly pronounced in the burned portion of the former. Nevertheless, other studies have also found depressed biomass accrual following imposed density reductions that persisted for prolonged periods (Velazquez-Martinez, Perry, & Bell, 1992; Mitchell et al., 1996). Here, the diminished growth was likely another manifestation of the previously noted higher harvesting intensity coupled with the continued reduction in stocking level incurred by this subunit. Bolstering this assertion were regression models revealing positive relationships between the final values for total Jeffrey pine biomass plus each of its components and initial basal area and between final combined total biomass and this independent variable. Among individual components, the abatement was most pronounced in foliage and bole bark, especially within the whole-tree subunit and again most prominently in the burned portion. The former suggests that the aforementioned individual crown expansion in this subunit was insufficient on a stand level basis to mitigate the exaggerated loss in stocking. In contrast, Barclay, Pang, & Pollard (1986) reported, on a stand level basis, a small numeric increase in new foliage production and a significant increase in that of old foliage in comparison to a control for post-thinned Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), although their finding concerning reduced bark growth was consistent with that here. Regardless, the unburned cut-to-length treatment combination produced Jeffrey pine biomass growth comparable to that in the unthinned subunit, suggesting that the attenuated accrual in the whole-tree treatment was not a reflection of a thinning impact per se but rather of the thinning approach employed. Also noteworthy is the fact that the burned portions of each subunit had lower numeric values compared to those in the unburned portions and that the effect of fire, especially on foliage, may have been somewhat masked by the biomass equations of Gholz et al. (1979) used in this study. These equations incorporate DBH exclusively among measured dimensions, and in order to discern a fire effect a substantial mortality concentrated in larger trees, which tend to have thicker bark and thus greater fire resistance, would have had to occur. Consequently, any potential effect of crown scorch on foliar biomass was undetectable and may explain the lack of a significant fire treatment effect. Nevertheless, biomass measures were largely analogous to those of stand level volume in that an extensive array of regression models demonstrated relationships between their values for Jeffrey pine and crown development, expanded in this case to include live crown percentage among the independent variables, a parallel extending essentially verbatim to white fir, although for both species the aforementioned precautions are warranted when these are interpreted in the context of the overall analysis. Regarding white fir, there were no significant treatment effects on any biomass measure, but the burned cut-to-length combination exhibited the greatest numerical losses which likely reflect the lack of fire resistance previously noted for this species, a trait possibly exacerbated here by the combustion of the slash mats.

In summary, thinning and burning treatments increasingly utilized in forest restoration efforts in the western USA were evaluated for their long-term influences on individual tree and stand level growth measures in pure, uneven-aged Jeffrey pine with a minor stand component of white fir. Individually, trees in a stand subunit subjected to whole-tree thinning exhibited the greatest evidence of a subsequent stimulatory effect evident in both dimension and volume measures, although it was largely confined to the unburned portion. However, at the stand level, a diminished volume growth response occurred in the whole-tree subunit, especially in the burned portion, mostly attributable to exaggerated stocking losses, while a superior response in the unburned portion of a subunit in which cut-to-length thinning was implemented likely reflected not only the absence of detrimental fire impacts but also benefits of on-site slash retention. Regarding stand level biomass, diminished growth in the whole-tree subunit was again evident, with that in the burned portion again most pronounced, while biomass accrual in the unburned cut-to-length treatment combination was generally comparable to that in the unthinned control. These findings advance the understanding of the likely responses to density management and prescription fire of Jeffrey pine and similar dry site forest cover types.

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**TABLE 1** Mensurational Characteristics of a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1]

| Inventory | Thinning and burning treatment | Height (m) | DBH (cm) | Live crown (m) | Live crown (%) | Basal area ($m^2$ $ha^{-1}$) | Total trees (stems $ha^{-1}$) |
|---|---|---|---|---|---|---|---|
| Initial[2] | Cut-to-length | | | | | | |
| | Burned | 16.1b | 33.6b | 8.5bc | 53.2bc | 17.4b | 203ab |
| | Unburned | 18.2ab | 37.6b | 10.5ab | 57.6ab | 18.5ab | 178bc |
| | Whole-tree | | | | | | |
| | Burned | 17.1ab | 33.5b | 6.8c | 39.7d | 18.7ab | 210ab |
| | Unburned | 19.8a | 45.0a | 10.1ab | 50.5c | 16.5b | 111c |
| | Unthinned | | | | | | |
| | Burned | 17.5ab | 37.3b | 11.1a | 63.9a | 21.2ab | 193ab |
| | Unburned | 16.2b | 34.6b | 10.3ab | 64.1a | 25.1a | 262a |
| Final | Cut-to-length | | | | | | |
| | Burned | 17.5c | 36.1b | 8.2cd | 47.1ab | 19.8b | 198b |
| | Unburned | 20.7ab | 41.9b | 9.3bcd | 44.6bc | 22.6ab | 168b |
| | Whole-tree | | | | | | |
| | Burned | 19.0bc | 37.3b | 7.6d | 40.0c | 20.0b | 183b |
| | Unburned | 23.3a | 51.3a | 11.4a | 48.7ab | 18.8b | 94c |
| | Unthinned | | | | | | |
| | Burned | 19.9bc | 40.6b | 9.9ab | 50.3ab | 25.5ab | 198b |
| | Unburned | 18.6bc | 37.5b | 9.6bc | 51.5a | 29.6a | 267a |
| Change in values[3] | Cut-to-length | | | | | | |
| | Burned | +1.4c | +2.5b | –0.3bc | –6.1b | +2.4ab | –5ab |
| | Unburned | +2.5ab | +4.3b | –1.2c | –13.0c | +4.1a | –10ab |
| | Whole-tree | | | | | | |
| | Burned | +1.9bc | +3.8b | +0.8ab | +0.3a | +1.3b | –27b |
| | Unburned | +3.5a | +6.3a | +1.3a | –1.8ab | +2.3ab | –17ab |
| | Unthinned | | | | | | |
| | Burned | +2.4bc | +3.3b | –1.2c | –13.6c | +4.3a | +5a |
| | Unburned | +2.4bc | +2.9b | –0.7c | –12.6c | +4.5a | +5a |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test.
[2]Prescribed underburn not yet implemented.
[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in mean values.

**TABLE 2** Individual Tree Volumes in Pure, Uneven-Aged Jeffrey Pine as Influenced by Mechanized Thinning and Prescription Fire[1]

| Inventory | Thinning and burning treatment | Board feet volume | | Cubic feet volume | | Cubic meter volume | |
|---|---|---|---|---|---|---|---|
| | | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir |
| Initial[2] | Cut-to-length | | | | | | |
| | Burned | 75b | 65ab | 15.0b | 16.2ab | 0.43b | 0.46ab |
| | Unburned | 137b | 27ab | 25.9b | 6.9ab | 0.73b | 0.19ab |
| | Whole-tree | | | | | | |
| | Burned | 92b | 5b | 18.0b | 1.4b | 0.51b | 0.04b |
| | Unburned[4] | 246a | – | 44.1a | – | 1.25a | – |
| | Unthinned | | | | | | |
| | Burned | 112b | 61ab | 22.6b | 15.2ab | 0.64b | 0.43ab |
| | Unburned | 83b | 93a | 17.1b | 22.3a | 0.48b | 0.63a |
| Final | Cut-to-length | | | | | | |
| | Burned | 109b | 76a | 21.3b | 18.2a | 0.60b | 0.51a |
| | Unburned | 211b | 27a | 38.4b | 6.5a | 1.09b | 0.18a |
| | Whole-tree | | | | | | |
| | Burned | 143b | 9a | 26.9b | 2.5a | 0.76b | 0.07a |
| | Unburned[4] | 377a | – | 64.8a | – | 1.84a | – |
| | Unthinned | | | | | | |
| | Burned | 157b | 91a | 30.4b | 21.5a | 0.86b | 0.61a |
| | Unburned | 119b | 109a | 23.6b | 26.3a | 0.67b | 0.74a |
| Change in volume[3] | Cut-to-length | | | | | | |
| | Burned | +34c | +11a | +6.3c | +2.0a | +0.17c | +0.05a |
| | Unburned | +74b | 0a | +12.5b | –0.4a | +0.36b | –0.01a |
| | Whole-tree | | | | | | |
| | Burned | +51bc | +4a | +8.9bc | +1.1a | +0.25bc | +0.03a |
| | Unburned[4] | +131a | – | +20.7a | – | +0.59a | – |
| | Unthinned | | | | | | |
| | Burned | +45c | +30a | +7.8c | +6.3a | +0.22c | +0.18a |
| | Unburned | +36c | +16a | +6.5c | +4.0a | +0.19c | +0.11a |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test.
[2]Prescribed underburn not yet implemented.
[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in mean values.
[4]White fir not present.

**TABLE 3** Stand Volumes in Pure, Uneven-Aged Jeffrey Pine as Influenced by Mechanized Thinning and Prescription Fire[1]

| Inventory | Thinning and burning treatment | Board feet volume per acre | | | Cubic feet volume per acre | | | Cubic meter volume per hectare | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Jeffrey pine | White fir | Combined | Jeffrey pine | White fir | Combined | Jeffrey pine | White fir | Combined |
| Initial[2] | Cut-to-length | | | | | | | | | |
| | Burned | 5370a | 1595a | 6965a | 1071.9a | 376.8a | 1448.7a | 74.96a | 26.35a | 101.31a |
| | Unburned | 8540a | 136a | 8676a | 1621.1a | 34.4a | 1655.5a | 113.36a | 2.41a | 115.77a |
| | Whole-tree | | | | | | | | | |
| | Burned | 7670a | 25a | 7695a | 1507.1a | 7.1a | 1514.2a | 105.39a | 0.50a | 105.89a |
| | Unburned | 9580a | 0a | 9580a | 1732.5a | 0.0a | 1732.5a | 121.15a | 0.00a | 121.15a |
| | Unthinned | | | | | | | | | |
| | Burned | 8750a | 305a | 9055a | 1751.4a | 75.8a | 1827.2a | 122.48a | 5.30a | 127.78a |
| | Unburned | 7140a | 2920a | 10060a | 1474.2a | 669.1a | 2143.3a | 103.09a | 46.79a | 149.88a |
| Final | Cut-to-length | | | | | | | | | |
| | Burned | 8200a | 939ab | 9139a | 1589.7a | 216.6ab | 1806.3a | 111.17a | 15.15ab | 126.32a |
| | Unburned | 13030a | 273ab | 13303a | 2379.5a | 65.2ab | 2444.7a | 166.40a | 4.56ab | 170.96a |
| | Whole-tree | | | | | | | | | |
| | Burned | 10270a | 90ab | 10360a | 1933.6a | 24.9ab | 1958.5a | 135.22a | 1.74ab | 136.96a |
| | Unburned | 13220a | 0b | 13220a | 2289.1a | 0.0b | 2289.1a | 160.07a | 0.00b | 160.07a |
| | Unthinned | | | | | | | | | |
| | Burned | 12290a | 454ab | 12744a | 2372.5a | 107.4ab | 2479.9a | 165.91a | 7.51ab | 173.42a |
| | Unburned | 11100a | 2468a | 13568a | 2207.8a | 581.2a | 2789.0a | 154.39a | 40.64a | 195.03a |
| Change in volume[3] | Cut-to-length | | | | | | | | | |
| | Burned | +2830b | –656a | +2174b | +517.8bc | –160.2a | +357.6b | +36.21bc | –11.20a | +25.01b |
| | Unburned | +4490a | +137a | +4627a | +758.4a | +30.8a | +789.2a | +53.04a | +2.15a | +55.19a |
| | Whole-tree | | | | | | | | | |
| | Burned | +2600b | +65a | +2665b | +426.5c | +17.8a | +444.3ab | +29.83c | +1.24a | +31.07ab |
| | Unburned | +3640ab | 0a | +3640ab | +556.6abc | 0.0a | +556.6ab | +38.92abc | 0.00a | +38.92ab |
| | Unthinned | | | | | | | | | |
| | Burned | +3540ab | +149a | +3689ab | +621.1abc | +31.6a | +652.7ab | +43.43abc | +2.21a | +45.64ab |
| | Unburned | +3960ab | –452a | +3508ab | +733.6ab | –87.9a | +645.7ab | +51.30ab | –6.15a | +45.15ab |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test.
[2]Prescribed underburn not yet implemented.
[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in mean values.

**TABLE 4** Biomass of a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1]

| Inventory | Thinning and burning treatment | Jeffrey pine (kg ha$^{-1}$) Foliage | Branch | Bole bark | Bole wood | Total | White fir (kg ha$^{-1}$) Foliage | Branch | Bole bark | Bole wood | Total | Combined total (kg ha$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Initial[2] | Cut-to-length | | | | | | | | | | | |
| | Burned | 3699a | 10983a | 6293a | 31032a | 52007a | 837a | 2270a | 1943a | 10755a | 15805a | 67812a |
| | Unburned | 4689a | 15565a | 8167a | 44306a | 72727a | 91a | 234a | 195a | 1097a | 1617a | 74344a |
| | Whole-tree | | | | | | | | | | | |
| | Burned | 4756a | 15100a | 8201a | 42867a | 70924a | 30a | 54a | 38a | 237a | 359a | 71283a |
| | Unburned | 4320a | 16309a | 7736a | 46813a | 75178a | 0a | 0a | 0a | 0a | 0a | 75178a |
| | Unthinned | | | | | | | | | | | |
| | Burned | 5266a | 16922a | 9121a | 48044a | 79353a | 182a | 473a | 393a | 2215a | 3263a | 82616a |
| | Unburned | 5158a | 15631a | 8818a | 44213a | 73820a | 1431a | 4028a | 3522a | 19241a | 28222a | 102041a |
| Final | Cut-to-length | | | | | | | | | | | |
| | Burned | 4652b | 14692a | 8026a | 41843a | 69213a | 473ab | 1321ab | 1152ab | 6302ab | 9248ab | 78462b |
| | Unburned | 5738ab | 20356a | 10143a | 58182a | 94419a | 149ab | 391ab | 330ab | 1841ab | 2711ab | 97130ab |
| | Whole-tree | | | | | | | | | | | |
| | Burned | 5073ab | 17027a | 8858a | 48498a | 79456a | 84ab | 172ab | 127ab | 770ab | 1153ab | 80609b |
| | Unburned | 4971ab | 19880a | 9020a | 57258a | 91128a | 0b | 0b | 0b | 0b | 0b | 91128ab |
| | Unthinned | | | | | | | | | | | |
| | Burned | 6372ab | 21423a | 11146a | 60997a | 99938a | 236ab | 665ab | 577ab | 3167ab | 4645ab | 104583ab |
| | Unburned | 6497a | 20777a | 11239a | 58971a | 97484a | 1280a | 3563a | 3082a | 16953a | 24878a | 122362a |
| Change in biomass[3] | Cut-to-length | | | | | | | | | | | |
| | Burned | +953ab | +3709ab | +1733ab | +10811ab | +17206ab | –364a | –949a | –791a | –4453a | –6557a | +10649a |
| | Unburned | +1049ab | +4791a | +1976ab | +13876a | +21692a | +58a | +157a | +135a | +744a | +1094a | +22786a |
| | Whole-tree | | | | | | | | | | | |
| | Burned | +317c | +1927b | +657c | +5631b | +8532b | +54a | +118a | +89a | +533a | +794a | +9326a |
| | Unburned | +650bc | +3571ab | +1284bc | +10445ab | +15950ab | 0a | 0a | 0a | 0a | 0a | +15950a |
| | Unthinned | | | | | | | | | | | |
| | Burned | +1106ab | +4501a | +2025ab | +12953a | +20585a | +54a | +192a | +184a | +952a | +1382a | +21967a |
| | Unburned | +1339a | +5146a | +2421a | +14758a | +23664a | –151a | –465a | –440a | –2288a | –3344a | +20320a |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test.
[2]Prescribed underburn not yet implemented.
[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in mean values.

**TABLE 5** Significant Simple Linear Regression Models Relating Tree Dimensions and Volume and Stand Volume and Biomass to Overstory Variables

| Independent variable | Dependent variable | Correlation | Model *F* test *p*-value | Model $r^2$ |
|---|---|---|---|---|
| Live crown length, initial | DBH, initial | Positive | <.0001 | .4468 |
| Live crown length, initial | Live crown length, final | Positive | <.0001 | .5866 |
| Live crown length, initial | Jeffrey pine board feet volume per acre, final | Positive | <.0001 | .4407 |
| Live crown length, initial | Jeffrey pine board feet volume per acre, change | Positive | <.0001 | .4704 |
| Live crown length, initial | Combined board feet volume per acre, final | Positive | <.0001 | .4645 |
| Live crown length, initial | Jeffrey pine cubic feet volume per acre, final | Positive | <.0001 | .4355 |
| Live crown length, initial | Jeffrey pine cubic feet volume per acre, change | Positive | .0001 | .4086 |
| Live crown length, initial | Combined cubic feet volume per acre, final | Positive | .0001 | .4205 |
| Live crown length, initial | Jeffrey pine cubic meter volume per hectare, final | Positive | <.0001 | .4355 |
| Live crown length, initial | Jeffrey pine cubic meter volume per hectare, change | Positive | .0001 | .4086 |
| Live crown length, initial | Combined cubic meter volume per hectare, final | Positive | .0001 | .4204 |
| Live crown length, initial | Jeffrey pine branch biomass, final | Positive | <.0001 | .4475 |
| Live crown length, initial | Jeffrey pine branch biomass, change | Positive | <.0001 | .4243 |
| Live crown length, initial | Jeffrey pine bole wood biomass, final | Positive | <.0001 | .4557 |
| Live crown length, initial | Jeffrey pine bole wood biomass, change | Positive | <.0001 | .4320 |
| Live crown length, initial | Jeffrey pine total biomass, final | Positive | <.0001 | .4386 |
| Live crown length, initial | Jeffrey pine total biomass, change | Positive | .0001 | .4214 |
| Live crown percent, initial | Live crown percent, final | Positive | <.0001 | .4686 |
| Live crown percent, initial | Live crown percent, change | Negative | <.0001 | .6572 |
| Live crown percent, initial | Basal area, change | Positive | <.0001 | .6062 |
| Live crown percent, initial | Jeffrey pine foliar biomass, change | Positive | <.0001 | .5652 |
| Live crown percent, initial | Jeffrey pine branch biomass, change | Positive | <.0001 | .4475 |
| Live crown percent, initial | Jeffrey pine bole bark biomass, change | Positive | <.0001 | .5483 |
| Live crown percent, initial | Jeffrey pine bole wood biomass, change | Positive | <.0001 | .4412 |
| Live crown percent, initial | Jeffrey pine total biomass, change | Positive | <.0001 | .4651 |
| Live crown percent, initial | Combined total biomass, change | Positive | .0001 | .4142 |
| Live crown length, final | Height, final | Positive | <.0001 | .5533 |
| Live crown length, final | DBH, final | Positive | <.0001 | .7077 |
| Live crown length, final | Individual Jeffrey pine board feet volume, final | Positive | <.0001 | .6232 |
| Live crown length, final | Individual Jeffrey pine board feet volume, change | Positive | <.0001 | .5094 |
| Live crown length, final | Individual Jeffrey pine cubic feet volume, final | Positive | <.0001 | .6402 |
| Live crown length, final | Individual Jeffrey pine cubic feet volume, change | Positive | <.0001 | .4549 |
| Live crown length, final | Individual Jeffrey pine cubic meter volume, final | Positive | <.0001 | .6401 |
| Live crown length, final | Individual Jeffrey pine cubic meter volume, change | Positive | <.0001 | .4588 |
| Basal area, initial | Combined board feet volume per acre, final | Positive | <.0001 | .6342 |
| Basal area, initial | Jeffrey pine cubic feet volume per acre, final | Positive | <.0001 | .4321 |
| Basal area, initial | Combined cubic feet volume per acre, final | Positive | <.0001 | .7801 |
| Basal area, initial | Jeffrey pine cubic meter volume per hectare, final | Positive | <.0001 | .4321 |
| Basal area, initial | Combined cubic meter volume per hectare, final | Positive | <.0001 | .7801 |
| Basal area, initial | Jeffrey pine foliar biomass, final | Positive | <.0001 | .5522 |
| Basal area, initial | Jeffrey pine branch biomass, final | Positive | <.0001 | .4415 |
| Basal area, initial | Jeffrey pine bole bark biomass, final | Positive | <.0001 | .5373 |
| Basal area, initial | Jeffrey pine bole wood biomass, final | Positive | <.0001 | .4302 |
| Basal area, initial | Jeffrey pine total biomass, final | Positive | <.0001 | .4557 |
| Basal area, initial | Combined total biomass, final | Positive | <.0001 | .8375 |

**TABLE 5** (*Continued*)

| Independent variable | Dependent variable | Correlation | Model *F* test *p*-value | Model $r^2$ |
|---|---|---|---|---|
| Tree count, initial | DBH, final | Negative | <.0001 | .4509 |
| Tree count, initial | Individual Jeffrey pine board feet volume, change | Negative | .0001 | .4221 |
| Tree count, initial | Individual Jeffrey pine cubic feet volume, change | Negative | .0001 | .4186 |
| Tree count, initial | Individual Jeffrey pine cubic meter volume, change | Negative | .0001 | .4161 |
| Tree count, final | DBH, final | Negative | <.0001 | .4272 |
| Tree count, final | Individual Jeffrey pine board feet volume, change | Negative | <.0001 | .4981 |
| Tree count, final | Individual Jeffrey pine cubic feet volume, change | Negative | <.0001 | .5189 |
| Tree count, final | Individual Jeffrey pine cubic meter volume, change | Negative | <.0001 | .5166 |
| Jeffrey pine foliar biomass, initial | Jeffrey pine board feet volume per acre, final | Positive | <.0001 | .6705 |
| Jeffrey pine foliar biomass, initial | Jeffrey pine cubic feet volume per acre, final | Positive | <.0001 | .7683 |
| Jeffrey pine foliar biomass, initial | Jeffrey pine cubic meter volume per hectare, final | Positive | <.0001 | .7683 |
| Jeffrey pine foliar biomass, initial | Jeffrey pine foliar biomass, final | Positive | <.0001 | .8827 |
| Jeffrey pine foliar biomass, initial | Jeffrey pine branch biomass, final | Positive | <.0001 | .8057 |
| Jeffrey pine foliar biomass, initial | Jeffrey pine bole bark biomass, final | Positive | <.0001 | .8836 |
| Jeffrey pine foliar biomass, initial | Jeffrey pine bole wood biomass, final | Positive | <.0001 | .7939 |
| Jeffrey pine foliar biomass, initial | Jeffrey pine total biomass, final | Positive | <.0001 | .8213 |
| White fir foliar biomass, initial | Individual white fir board feet volume, final | Positive | <.0001 | .4426 |
| White fir foliar biomass, initial | Individual white fir cubic feet volume, final | Positive | <.0001 | .4258 |
| White fir foliar biomass, initial | Individual white fir cubic meter volume, final | Positive | <.0001 | .4254 |
| White fir foliar biomass, initial | White fir board feet volume per acre, final | Positive | <.0001 | .9621 |
| White fir foliar biomass, initial | White fir board feet volume per acre, change | Negative | <.0001 | .7921 |
| White fir foliar biomass, initial | White fir cubic feet volume per acre, final | Positive | <.0001 | .9560 |
| White fir foliar biomass, initial | White fir cubic feet volume per acre, change | Negative | <.0001 | .7424 |
| White fir foliar biomass, initial | White fir cubic meter volume per hectare, final | Positive | <.0001 | .9560 |
| White fir foliar biomass, initial | White fir cubic meter volume per hectare, change | Negative | <.0001 | .7424 |
| White fir foliar biomass, initial | White fir foliar biomass, final | Positive | <.0001 | .9410 |
| White fir foliar biomass, initial | White fir foliar biomass, change | Negative | <.0001 | .6615 |
| White fir foliar biomass, initial | White fir branch biomass, final | Positive | <.0001 | .9525 |
| White fir foliar biomass, initial | White fir branch biomass, change | Negative | <.0001 | .7188 |
| White fir foliar biomass, initial | White fir bole bark biomass, final | Positive | <.0001 | .9575 |
| White fir foliar biomass, initial | White fir bole bark biomass, change | Negative | <.0001 | .7512 |
| White fir foliar biomass, initial | White fir bole wood biomass, final | Positive | <.0001 | .9545 |
| White fir foliar biomass, initial | White fir bole wood biomass, change | Negative | <.0001 | .7312 |
| White fir foliar biomass, initial | White fir total biomass, final | Positive | <.0001 | .9540 |
| White fir foliar biomass, initial | White fir total biomass, change | Negative | <.0001 | .7290 |
| Jeffrey pine foliar biomass, final | Jeffrey pine board feet volume per acre, final | Positive | <.0001 | .6785 |
| Jeffrey pine foliar biomass, final | Jeffrey pine board feet volume per acre, change | Positive | <.0001 | .5236 |
| Jeffrey pine foliar biomass, final | Jeffrey pine cubic feet volume per acre, final | Positive | <.0001 | .7983 |
| Jeffrey pine foliar biomass, final | Jeffrey pine cubic feet volume per acre, change | Positive | <.0001 | .4932 |
| Jeffrey pine foliar biomass, final | Jeffrey pine cubic meter volume per hectare, final | Positive | <.0001 | .7983 |
| Jeffrey pine foliar biomass, final | Jeffrey pine cubic meter volume per hectare, change | Positive | <.0001 | .4932 |
| Jeffrey pine foliar biomass, final | Jeffrey pine branch biomass, final | Positive | <.0001 | .8800 |
| Jeffrey pine foliar biomass, final | Jeffrey pine bole bark biomass, final | Positive | <.0001 | .9935 |
| Jeffrey pine foliar biomass, final | Jeffrey pine bole wood biomass, final | Positive | <.0001 | .8658 |
| Jeffrey pine foliar biomass, final | Jeffrey pine total biomass, final | Positive | <.0001 | .9009 |

**TABLE 5** (*Continued*)

| Independent variable | Dependent variable | Correlation | Model *F* test *p*-value | Model $r^2$ |
|---|---|---|---|---|
| White fir foliar biomass, final | Individual white fir board feet volume, final | Positive | <.0001 | .4728 |
| White fir foliar biomass, final | Individual white fir cubic feet volume, final | Positive | <.0001 | .4656 |
| White fir foliar biomass, final | Individual white fir cubic meter volume, final | Positive | <.0001 | .4651 |
| White fir foliar biomass, final | White fir board feet volume per acre, final | Positive | <.0001 | .9954 |
| White fir foliar biomass, final | White fir board feet volume per acre, change | Negative | <.0001 | .5789 |
| White fir foliar biomass, final | White fir cubic feet volume per acre, final | Positive | <.0001 | .9975 |
| White fir foliar biomass, final | White fir cubic feet volume per acre, change | Negative | <.0001 | .5124 |
| White fir foliar biomass, final | White fir cubic meter volume per hectare, final | Positive | <.0001 | .9975 |
| White fir foliar biomass, final | White fir cubic meter volume per hectare, change | Negative | <.0001 | .5124 |
| White fir foliar biomass, final | White fir branch biomass, final | Positive | <.0001 | .9987 |
| White fir foliar biomass, final | White fir branch biomass, change | Negative | <.0001 | .4832 |
| White fir foliar biomass, final | White fir bole bark biomass, final | Positive | <.0001 | .9973 |
| White fir foliar biomass, final | White fir bole bark biomass, change | Negative | <.0001 | .5234 |
| White fir foliar biomass, final | White fir bole wood biomass, final | Positive | <.0001 | .9982 |
| White fir foliar biomass, final | White fir bole wood biomass, change | Negative | <.0001 | .4982 |
| White fir foliar biomass, final | White fir total biomass, final | Positive | <.0001 | .9984 |
| White fir foliar biomass, final | White fir total biomass, change | Negative | <.0001 | .4955 |

**TABLE 6** Significant Simple Linear Regression Models Relating Tree Dimensions and Stand Volume and Biomass to Ground Cover Variables

| Independent variable | Dependent variable | Correlation | Model *F* test *p*-value | Model $r^2$ |
|---|---|---|---|---|
| Mahala mat cover | White fir board feet volume per acre, final | Positive | <.0001 | .6789 |
| Mahala mat cover | White fir cubic feet volume per acre, final | Positive | <.0001 | .6896 |
| Mahala mat cover | White fir cubic meter volume per hectare, final | Positive | <.0001 | .6896 |
| Mahala mat cover | White fir foliar biomass, final | Positive | <.0001 | .7064 |
| Mahala mat cover | White fir branch biomass, final | Positive | <.0001 | .6963 |
| Mahala mat cover | White fir bole bark biomass, final | Positive | <.0001 | .6899 |
| Mahala mat cover | White fir bole wood biomass, final | Positive | <.0001 | .6939 |
| Mahala mat cover | White fir total biomass, final | Positive | <.0001 | .6945 |
| Mahala mat cover | Combined total biomass, final | Positive | .0001 | .4150 |

# CHAPTER TWO

## Bark Beetle Demography in a Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescribed Fire

Roger F. Walker, Shannon L. Swim, Dale W. Johnson, Watkins W. Miller, and Robert M. Fecko

## ABSTRACT

Forest thinnings implemented with cut-to-length and whole-tree harvesting systems followed by underburning were evaluated for their effects on bark beetle prevalence in pure, uneven-aged Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) interspersed with isolated California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.). Based on pitch tube counts in a stand with a moderate bark beetle population in its pine component, the Jeffrey pine beetle (*Dendroctonus jeffreyi* Hopkins) generally preferred larger trees before treatment implementation, but after exhibiting mixed pretreatment tendencies concerning stand density demonstrated a posttreatment proclivity toward higher density. Cut-to-length thinning followed by underburning increased the pine beetle population while whole-tree thinning unaccompanied by burning reduced it. Tree mortality was induced by the bark beetle infestation but was not its sole cause. Pitch tube abundance on white fir far exceeded that on Jeffrey pine, and the greatest influence on the fir engraver (*Scolytus ventralis* LeConte) population was the prevalence of its host tree. The responses presented herein to these thinning and burning practices, which are being increasingly utilized in forest restoration efforts in the western USA, provide natural resource managers insight into potential forest health outcomes when implemented in Jeffrey pine and similar dry site forest types.

## KEYWORDS

bark beetles, stand density management, cut-to-length harvesting, whole-tree harvesting, prescription fire, *Pinus jeffreyi*, *Abies concolor*, *Dendroctonus jeffreyi*, *Scolytus ventralis*

## INTRODUCTION

Concerns are mounting that forest health in western North America is declining (Covington et al., 1994; Tkacz, Moody, & Castillo, 2007; Edmonds, Agee, & Gara, 2011) and one of the most significant indications of such has been the increase in bark beetle activity. Bark beetles (Coleoptera: Curculionidae: Scolytinae) are endemic species to the coniferous forests of North America that have traditionally functioned as natural disturbance agents by opportunistically attacking weakened host trees and thus providing necessary ecosystem functions such as the promotion of natural self-thinning and the hastening of nutrient cycling (Crookston & Stark, 1985; Christiansen, Waring, & Berryman, 1987; Logan & Powell, 2001; Fettig et al., 2007). Bark beetle outbreaks are not novel, but the magnitude of recent beetle activity has reached unprecedented levels, causing widespread mortality over vast acreages during the last decade in western North America (Goyer, Wagner, & Schowalter, 1998; Raffa et al., 2008; Bentz et al., 2009). This is compromising fiber yields, watershed integrity, wildlife habitat, and aesthetic values as well as exacerbating wildfire risk (Potts, 1984; Fettig et al., 2007; Jenkins et al., 2008; Raffa et al., 2008; Adams et al., 2012). There are several factors that have contributed to these calamities, including climatic perturbations and anthropogenic influences.

The recent bark beetle epidemics have been attributed to prolonged droughts and warmer temperatures. In point of fact, evidence amassed over several decades suggests a correlation between the timing of bark beetle outbreaks and drought episodes (Craighead, 1925a; Christiansen, Waring, & Berryman, 1987; Fettig et al., 2007; Tkacz, Moody, & Castillo, 2007; Negron et al., 2009). During severe droughts, the water stress incurred by stand constituents inhibits their ability to manufacture defense compounds, thus predisposing them to Scolytine infestations (Mattson & Haack, 1987; Raffa et al., 2008; Edmonds, Agee, & Gara, 2011). The longer growing seasons inherent in warming regional temperatures allow for an increased number of generations to emerge per year, while mild winters fail to produce temperatures low enough to induce mortality in the larval population, therefore increasing subsequent adult population densities (Waring & Six, 2005; Friedenberg et al., 2008; Waring et al., 2009). The prolonged droughts and milder winters that many western North American forests are experiencing have been attributed to climate change, which is anticipated to further exacerbate the negative effects of bark beetle activity (van Mantgem et al., 2009; Bentz et al., 2010).

High stand density is another factor that puts forests at risk for stand-replacing bark beetle attacks. Before the implementation of extensive fire suppression practices in the early 20$^{th}$ century, stand densities in many forest cover types of the western USA were much lower (Parsons & DeBenedetti, 1979; Savage, 1994; Taylor, 2004; Schwilk et at., 2006). In overstocked stands, resource competition is intensified, diminishing tree vigor and rendering them more vulnerable to attack (Savage, 1994; Fettig et al., 2007). High stand densities coupled with drought compound this effect, leading to rapidly escalating stand mortality (Savage, 1994). The propinquity of neighboring trees in dense stands may also enable bark beetles to more easily access suitable hosts. Properly implemented stand density management alleviates intense resource competition and decreases neighbor proximity, potentially enhancing resistance and resilience to attack (Fettig et al., 2007, 2012).

Fire also plays an interactive and complex role in the dynamics of bark beetle activity. Large scale beetle epidemics tend to elevate wildfire risk due to their influences on readily ignitable aerial and surface fuel accumulations. However, wildfire may also stimulate bark beetle activity (Miller & Patterson, 1927; Parker, Clancy, & Mathiasen, 2006), as the associated crown, cambial, and phloem injury to surviving trees compromises their photosynthetic capacity as well as phloem conductance of photosynthates to the roots, which eventually impairs root system development and thus water uptake (Kozlowski, Kramer, & Pallardy, 1991; Wallin et al., 2003; Walker et al., 2012). This may ultimately produce a cumulative and nearly comprehensive impairment of overall physiological functioning. Subsequently, the inability of trees thus weakened to manufacture defense compounds in sufficient quantities renders them more vulnerable to bark beetles, which increases the likelihood of further stand mortality (Miller & Patterson, 1927; Ryan & Amman, 1996; Parker, Clancy, & Mathiasen, 2006; Jenkins et al., 2008). In contrast to wildfire, prescribed fire intensities are relatively low in most instances, causing less damage to stand constituents. Nevertheless, there is documentation indicating that bark beetle activity may increase following controlled burns, contributing to subsequent stand mortality that may extend for several years after treatment implementation (Miller & Patterson, 1927; Bradley & Tueller, 2001; Ganz, Dahlsten, & Shea, 2003; McHugh, Kolb, & Wilson, 2003; Schwilk et al., 2006; Breece et al., 2008; Maloney et al., 2008; Fettig, Borys, & Dabney, 2010). However, the magnitude and duration of this effect has not been extensively investigated in many forest cover types endemic to western North America.

The study presented here examined the individual and interactive influences of stand density management and prescribed fire on bark beetle activity in a common eastern Sierra Nevada forest type. Pretreatment and posttreatment bark beetle abundance and associated tree mortality were quantified in an eastern Sierran Jeffrey pine stand over a period encompassing eleven post-thinning and ten post-burning seasons. The implications of this study may provide natural resource managers with insight into possible unintended and potentially undesirable outcomes of common forest restoration treatments in regards to subsequent bark beetle activity in dry site forest types.

## MATERIALS AND METHODS

### Study Site

The stand chosen for this study is uneven-aged, second growth, and pure Jeffrey pine with a minor representation of white fir. The site consists of 12.3 ha located on the east side of the Sierra Nevada in Nevada County, CA and is a component of the Tahoe National Forest

(39°25’45”N, 120°8’30”W). The elevation is 1800 m and the aspect is generally northeast. The soils are of the Kyburz-Trojan complex (USDA Forest Service, 1994) and are well drained with a gravelly sandy loam surface layer and an andesitic substratum. The slope varies from 3 to 12% with the majority of the site falling within 3 to 6%. Based on the 55-year average, annual precipitation is 69 cm and is predominantly snowfall. At the time of treatment installation, the stand was 105 years old based on dominant and codominant crown class trees and the site quality is $SI_{100}$21 (index height in meters) for Jeffrey pine (Fecko et al., 2008a).

Treatment Installation

In September 2000, the study site was divided into three subunits of 4.1 ha each with one of three thinning treatments randomly assigned to each subunit, specifically a cut-to-length harvesting system, a whole-tree harvesting system, or an unthinned control. As reviewed by Walker et al. (2006), cut-to-length and whole-tree systems vary greatly in their harvesting approach and site impacts. The former system utilizes two machines, one which processes the trees at the stump, thereby creating residual organic materials that it concentrates into slash mats, while the second machine self-loads the logs and forwards them to a landing. Both machines travel over the slash mats, minimizing the disturbance of mineral soil as well as its compaction, but the mats also constitute elongated surface fuel concentrations. Whole-tree harvesting systems involve two machines as well, one of which fells selected trees and bunches them for transport while the second machine skids them to a landing where further processing ensues. All organic residues created by the harvest are extracted from the stand, minimizing wildfire risk but also exposing mineral soil and increasing associated impacts. The thinning treatments were implemented concurrently over four days in October 2000 using a Timberjack 1270 processor combined with a Timberjack 1210 forwarder (Timberjack Forestry Group, Moline, IL, USA) for the cut-to-length system while the whole-tree system used a Timbco 445 feller-buncher (Timbco Hydraulics, Inc., Shawano, WI, USA) and a Caterpillar 518 grapple skidder (Caterpillar, Inc., Peoria, IL, USA). For both treatments, a free thinning approach (Nyland, 2002) was followed to release select dominant and codominant crown class trees that displayed good growth form and crown development. Trees that were removed varied in crown class but few were < 25.4 cm DBH (bole diameter 1.37 m aboveground) and those < 20.3 cm DBH were intentionally felled only when they posed an obstacle to the harvesting operation (Fecko et al., 2008b). An additional stipulation in the thinning protocol was that white fir was to be preferentially retained where available for purposes of biodiversity.

In May 2002, a prescribed underburn was implemented on one-half of each of the three subunits dedicated to the individual thinning treatments. The subunits were divided by 1.0-m-wide hand lines and one of the two portions of each subunit was randomly designated to be burned while the other was to remain unburned. For the stand portions to be burned, a strip head fire ignition pattern was applied beginning at 6:00 p.m. with the treatment of all three portions completed by 11:00 p.m. of the same day. At the time of ignition the air temperature was 16°C, relative humidity was 48%, and the wind speed was 5.5 km $hr^{-1}$, with variation over the course of the 5-hr burn period ranging from 14 to 18°C, 39 to 50%, and 4.8 to 6.6 km $hr^{-1}$, respectively. The fuel moisture content was 8% for 1-hr, 10% for 10-hr, 14% for 100-hr, and 25% for 1000-hr timelag categories. The average rate of spread of the prescribed fire was approximately 58 m $hr^{-1}$ and the average flame length was approximately .7 m.

Data Collection

During the designation of the subunits in September 2000, 30 permanent .08-ha circular plots were established for measurement of mensurational variables with 10 plots located in each of the three subunits, and within each subunit, 5 in the portion to be burned with the remaining 5 in the portion to remain unburned. At the implementation of the thinning treatments, all trees ≥ 10.2 cm DBH in every plot were measured for total height, DBH, and live crown length and then tallied by species. Subsequently, tree heights and live crown lengths were used to derive live crown percentages, and average DBH values by plot were calculated using the quadratic mean formula (Curtis & Marshall, 2000). Basal area by plot was derived from quadratic mean DBH in combination with plot stem counts (Davis et al., 2001). This inventory also included standing dead trees that were identified as those lacking any live crown, which was used to determine dead tree count and percentage. Ultimately, the stem count, basal area, and dead tree count for each plot were expanded to reflect equivalent 1.0-ha values.

To determine the prevalence of bark beetles, and therefore the severity of their attack, pitch tubes were counted on all stand constituents included in the mensurational measurements of each plot. This was accomplished by visually dividing the bole surface into vertically oriented quadrants, counting the pitch tubes in each quadrant, and then combining the counts to obtain a total for each tree. The entire bole length was included in these counts, with ocular aids used as needed. Principle bark beetle species were identified by the observation of adult and larval forms as well as pitch tube and gallery characteristics as described by Furniss and Carolin (1977). In order to also express pitch tube counts on the basis of the quantity per unit of bole surface area, tree height and DBH were used as approximations of the lateral length and base diameter, respectively, in the geometric formula for the lateral surface area of a right cone, and the counts of individual trees were then divided by their bole surface area thus approximated. Expressing abundance on the basis of the count per unit surface area compensates for the tendency of the count per tree measure to overstate attack severity simply because larger trees have more bole surface area available to colonize. For both measures of abundance, specifically total count per tree and that per unit of bole surface area by individual tree, values were averaged within and across tree species by plot. Additionally, to elucidate the influences of certain mensurational attributes, specifically diameter (DBH) and live crown percentage (LCP), on beetle prevalence, trees were segregated by species into the seven DBH and six LCP classes demarcated in Table 1.

To assess the influences of above-ground stand biomass on beetle demography, that of its individual components, specifically foliage, branch, bole bark, and bole wood, was derived from the DBH measurements of all tallied trees within each plot using the species-specific formulas of Gholz et al. (1979). For the purposes of this study, these quantities were then expressed by plot as the total of all components within species and as the combined total across species, with all plot values ultimately expanded to reflect equivalent 1.0-ha values.

A final inventory identical to that detailed above in every respect was conducted in September 2011 and all extrapolated values regarding tree dimensions, stand density and biomass, and beetle prevalence were again calculated. The availability of initial and final data permitted the calculation of those changes over the course of the study that were deemed potentially useful for revealing interactions between bark beetles and their environment as altered by the management practices examined here.

Statistical Analysis

Because field logistics involving the implementation of the thinning and prescribed fire treatments necessitated that the thinning treatments be assigned to individual subunits of the stand with the underburn then assigned to one-half of each subunit, it was necessary to test for the independence of the plots within each thinning and burning treatment combination using initial data for variables germane to this study. The chosen variables were tree height, DBH, live crown length, basal area, and stem count. For each variable, residual values were calculated, which were defined as the difference between the mean for a given variable of the five plots of each treatment combination and the values obtained from the individual plots for the selected variable. Subsequently, the residual value of one plot was designated as the independent variable and that of the immediately adjacent plot the dependent variable which was repeated sequentially within each treatment combination, yielding one value of each for each plot pair, four values of each for each of the six treatment combinations, and thus a total of 24 values of each for the entire stand.

These values were then incorporated into simple linear regression models by variable. For each regression, models were considered to be significant, signifying a lack of independence among the plots within treatments, only when $p \leq .05$ according to the $F$ test. None of the models proved to be significant, indicating that values from individual plots were not significantly influenced by those from immediately adjacent plots for any of these variables.

Excluding the changes occurring between the initial and final inventories, data pertaining to tree dimensions, stand density and biomass, and bark beetle demography were analyzed using repeated measures, mixed model analysis of variance (ANOVA) to test for effects of thinning and prescribed fire treatments, the year of inventory, and all possible interactions. This analysis incorporated both the compound symmetry covariance structure and the first-order autoregressive structure. For each variable, the covariance structure relied upon was that providing the lowest value for Akaike's Information Criterion (bias-corrected version, AICC). For changes between the initial and final inventories pertaining to the various study components, two-way ANOVA was used to test for thinning and fire treatment effects plus their interaction. In every ANOVA indicated above, main effects and their interactions were considered significant only when $p \leq .05$ according to the $F$ test. Subsequently, differences among means were evaluated using the least significant difference (LSD) test with $\alpha = .05$.

Additional statistical analysis consisted of two series of simple linear regression models used to investigate relationships between variables selected as particularly pertinent to the study, with the first series dedicated to bark beetle prevalence and the second to stand mortality. The first series was divided into three subsets, with the first consisting of models incorporating all possible combinations of tree height, DBH, and live crown length and percentage as independent variables with pitch tube counts per tree and per unit bole surface area across and within species, and within each species by DBH and LCP classes, serving as dependent variables. For every model, the values representing the independent and dependent variables were matched by inventory. The second subset of this series was configured identically to the first except that density measures, specifically basal area and tree count, constituted the independent variables rather than the tree dimensions and related live crown percentage derivative used for such in the first subset. Similarly, the third subset of the first series again relied upon the same array of dependent variables as the first two, and the independent and dependent variables were again matched by inventory, but biomass measures, specifically those of the total within species and the combined total across species, served as the independent variables. An additional stipulation regarding the third subset, however, was that the independent and dependent variables were also matched within species except that the counts for each species were paired with combined total biomass and the combined counts across species were paired with the biomass by species as well. For the second regression series, the complete array of dependent variables used in the first series was reconstituted as the independent variables while the dependent variables consisted of dead tree counts and percentages across species. As consistent with every model developed in the study, the values representing the independent and dependent variables were matched by inventory, but here the models specific to the initial and final inventories constituted the two subsets of the series. For both regression series, models were considered significant only when $p \leq .05$ according to the F test. All statistical analyses were performed using SAS (SAS Institute, Inc., Cary, NC).

## RESULTS

Tree Dimensions, Stand Density, and Mortality

When averaged across species, with the subject stand consisting of 97% Jeffrey pine and 3% white fir at the initial inventory and 95% pine and 5% fir at the final one, ANOVA revealed that total tree height was significantly influenced by the year of inventory only ($p < .0001$) while all effects on the change in this dimension were nonsignificant (Table 2). Nevertheless, the LSD test indicated that height in the unthinned but burned treatment combination significantly exceeded that in the cut-to-length and burned combination initially, and at the conclusion of the study, that in the latter was exceeded by the heights in both the whole-tree unburned and unthinned burned combinations. As for the inventory year effect, mean height increased over the course of the study within the various treatment combinations without exception. For DBH, ANOVA identified fire treatment ($p$ = .0431), year of inventory ($p$ < .0001), and the thinning × fire treatment ($p$ = .0306) and thinning treatment × inventory year ($p$ = .0114) interactions as significant, while the change in this dimension was influenced by the thinning ($p$ = .0114) treatment alone. Regarding the differences among treatment combinations in initial DBH, the LSD test disclosed that trees in the unburned portion of the whole-tree subunit and in the burned portion of the unthinned subunit were larger than those in the burned portions of the cut-to-length and whole-tree subunits. At the final inventory, however, mean DBH in the unburned portion of the whole-tree subunit exceeded those in every other treatment combination except that entailing the unthinned but burned combination. Furthermore, DBH in the latter significantly exceeded that in the cut-to-length and burned combination. The change in DBH over the course of the study indicated that this dimension increased within every treatment combination, but the LSD test revealed that the increase in the unburned portion of the whole-tree subunit surpassed those in the burned portion of the cut-to-length subunit as well as those in the unthinned subunit in its entirety.

For live crown variables, ANOVA identified significant influences of thinning ($p$ = .0026) and fire ($p$ = .0256) treatments and of the thinning treatment × year of inventory ($p$ = .0007) interaction on crown length along with a thinning effect ($p$ = .0007) on the change in length (Table 2). Initially, crown length in the unthinned subunit irrespective of fire treatment was significantly greater than those in the burned portions of the cut-to-length and whole-tree subunits according to the LSD test while it was greater in the unburned portions of these two subunits than in the burned portion of the whole-tree subunit as well. At the final inventory, crowns were larger in the unburned whole-tree combination along with those in the burned and unburned portions of the unthinned treatment than in the burned portions of the cut-to-length and whole-tree treatments. Regarding change in crown length, positive values were confined to the whole-tree subunit irrespective of fire treatment and to the burned portion of the cut-to-length subunit while losses prevailed in the three remaining treatment combinations, and the LSD test indicated that each of the three losses differed significantly from the gains within the whole-tree subunit and that the loss in the burned portion of the unthinned subunit also differed from the gain in the burned portion of the cut-to-length subunit. For live crown percentage, ANOVA revealed the influences of thinning ($p < .0001$) and fire ($p = .0019$) treatments, inventory year ($p < .0001$), and the thinning × fire treatment ($p = .0020$) and thinning treatment × year ($p < .0001$) interactions to be significant, while for the change in live percentage, thinning treatment proved to be the sole influence ($p < .0001$). According to the LSD test, the initial live percentage in the burned and unburned portions of the unthinned subunit significantly exceeded the percentages in all remaining treatments while that in the burned portion of the whole-tree treatment was exceeded by those in all other treatments. At the final inventory, the LSD test revealed a significantly greater live percentage in the unburned portion of the whole-tree treatment than in the burned portion of this treatment as well as in the cut-to-length subunit regardless of fire treatment, greater percentages in the unthinned subunit irrespective of fire treatment than in the burned portions of the cut-to-length and whole-tree treatments, and a percentage in the burned portion of the whole-tree subunit that was exceeded by those in all other treatments except that entailing the cut-to-length and burned combination. For the change in live percentage over the course of the study, increases were confined to the whole-tree subunit regardless of fire treatment while decreases prevailed elsewhere without exception, and the LSD test indicated that the former differed significantly from the latter without exception as well.

Significant effects on basal area consisted of the year of inventory and the thinning treatment × inventory year interaction (both $p < .0001$) while the change in basal area was affected by the thinning treatment alone ($p < .0001$) according to ANOVA (Table 2). The LSD test revealed that initially the basal area in the unburned portion of the cut-to-length subunit and the burned portion of the whole-tree subunit significantly exceeded those in the unthinned subunit irrespective of fire treatment while that in the cut-to-length and burned treatment combination also exceeded the basal area in the burned portion of the unthinned subunit. At the final inventory, however, the significant disparities consisted of a higher basal area in the unburned portion of the unthinned treatment than in either the cut-to-length and burned combination or the whole-tree subunit regardless of fire treatment. The changes in basal over the course of the study consisted of reductions in every subunit where thinning was implemented and increases where it was excluded, and the LSD test indicated that the former differed significantly from the latter without exception, but additionally, that the basal area in the whole-tree burned combination was exceeded by those in all of the other treatment combinations. With total tree count as the density measure, thinning treatment ($p = .0184$) and inventory year ($p < .0001$) along with the thinning × fire treatment ($p = .0277$) and thinning treatment × year ($p < .0001$) interactions influenced tree count according to ANOVA with the former also influencing the change in count ($p < .0001$). Initially, the counts in the burned portions of the cut-to-length and whole-tree treatments exceeded those in every other treatment combination except the unburned portion of the former, while those in the two portions of the unthinned treatment were exceeded by the counts in every other combination except the unburned portion of the latter. Regarding the final inventory, however, the LSD test indicated that significant disparities consisted only of a lower count in the unburned portion of the whole-tree treatment than in all remaining combinations except for the burned portion of the unthinned treatment. As for the total count change, the sole increase occurred in the burned portion of the unthinned subunit while losses prevailed in all other treatment combinations. However, the LSD test indicated that the gain in the former along with a small loss in the unburned portion of this subunit differed from the larger losses in every remaining stand portion, and additionally, that the loss in the burned portion of the whole-tree subunit exceeded that in the unburned portion.

Of the variables involved in assessment of mortality, ANOVA revealed that both the dead tree count and percentage were influenced by fire treatment ($p$ = .0187 and $p$ = .0130, respectively) and the thinning × fire treatment interaction ($p$ = .0118 and $p$ = .0281, respectively), while all effects on their changes over the course of the study were nonsignificant (Table 2). The LSD test revealed additional commonalities between these two variables regarding the disparities among treatments. Specifically, it indicated that both the dead tree count and percentage were significantly higher in the burned portion of the whole-tree subunit than in either the unburned portion of this subunit or in the burned portion of the unthinned subunit at the initial inventory. At the final inventory, however, both the count and percentage were higher in the whole-tree burned combination than in all other stand portions except the burned portion of the cut-to-length subunit. The changes occurring from the initial to the final inventories were the only instance in which a divergence was apparent between these two variables, as dead count reductions occurred in the unburned portions of the cut-to-length and unthinned subunits along with the burned portion of the whole-tree subunit, the only increase occurred in the unthinned but burned combination, and the counts were unchanged in the two remaining treatment combinations. For dead percentage, however, the reductions were limited to the unburned portions of the cut-to-length and unthinned treatments, increases occurred in the burned portions of all three thinning treatments, and only the percentage in the whole-tree unburned combination was unchanged. Nevertheless, the LSD test did not reveal any significant disparities among treatments for either dead tree count or dead percentage.

Stand Biomass

Total Jeffrey pine biomass, enumerated by treatment in the order of the cut-to-length burned, cut-to-length unburned, whole-tree burned, whole-tree unburned, unthinned burned, and unthinned unburned combinations, was 94001, 125842, 133639, 125118, 79762, and 75136 kg $ha^{-1}$ at the initial inventory and 72758, 96718, 80841, 92214, 100311, and 98068 kg $ha^{-1}$ at the final inventory. ANOVA indicated that the year of inventory and the thinning treatment × inventory year interaction (both $p < .0001$) influenced this variable, while the LSD test revealed significant differences between the whole-tree burned combination and the cut-to-length burned combination as well as the unthinned treatment irrespective of fire treatment and between the unburned portions of the cut-to-length and whole-tree treatments and the two portions of the unthinned treatment initially, but at the final inventory, all differences were nonsignificant. With the treatment order employed above for Jeffrey pine continued here for white fir, initial quantities were 18716, 3246, 548, 0, 3263, and 28222 kg $ha^{-1}$ of total biomass and final quantities were 9499, 2776, 1153, 60, 4645, and 24878 kg $ha^{-1}$. ANOVA did not divulge any significant effects for this species, and the LSD test indicated that all differences among treatments at the initial inventory were nonsignificant also. At the last inventory, however, this test revealed a significant disparity between the unburned portions of the whole-tree and unthinned subunits. With the treatment order employed above for the pine and fir again followed for combined total biomass, the initial quantities were 112717, 129088, 134187, 125118, 83025, and 103358 kg $ha^{-1}$ and those at the final inventory were 82257, 99494, 81994, 92274, 104956, and 122946 kg $ha^{-1}$. Congruent with the Jeffrey pine total biomass, significant influences identified by ANOVA for combined total biomass consisted of the year of inventory and the thinning treatment × inventory year interaction (both $p < .0001$). As for the LSD test, it disclosed significant disparities for the combined total initially between the burned portion of the unthinned treatment and both the unburned portion of the cut-to-length subunit and the burned portion of the whole-tree subunit, while at the final inventory, the disparities entailed the unburned portion of the unthinned treatment juxtaposed against the burned portions of the cut-to-length and whole-tree treatments.

Bark Beetle Demography

Based on adult and larval forms as well as pitch tube and gallery characteristics, the Jeffrey pine beetle was the principle bark beetle species infesting its namesake tree species. Using the same observational criteria, the fir engraver beetle was the only apparent species in white fir.

Regarding pitch tube counts per tree, ANOVA indicated that all effects, specifically of the thinning and fire treatments, year of inventory, and all interactions, were nonsignificant for Jeffrey pine, a result that extended to the change in counts for this species over the course of the study (Table 3). Furthermore, significant differences among treatments according to the LSD test were limited to a disparity between a higher count in the unthinned and burned treatment combination and a lower one in the cut-to-length and burned combination at the initial inventory, and thus a disparity extant before treatment implementation. For white fir, however, ANOVA revealed both thinning ($p < .0001$) and fire ($p = .0056$) treatment influences on counts per tree, and the LSD test divulged numerous significant disparities among treatments at both inventories. Specifically, the initial count was greater for the unthinned and burned combination than all other combinations where fir resided, was greater in turn in the unburned portion of the unthinned treatment than in the remaining treatment combinations, and was greater in the burned than in the unburned portion of the cut-to-length treatment. At the final inventory, the count was still greater for the unthinned and burned combination than all other combinations and was still greater in turn in the unburned portion of the unthinned treatment than in the remaining treatment combinations, but the count in the cut-to-length and burned combination now exceeded that in the whole-tree unburned combination where fir was initially absent. By way of further comparison between the two species, white fir on average had 9.5× and 8.2× the pitch tubes per tree at the first and last inventories, respectively, as that found on Jeffrey pine, while the increase over the course of the study for the former was 10.8× that for the latter. Regarding the counts per tree across the two species, ANOVA again failed to divulge any significant effects, likely reflecting that Jeffrey pine was the predominant species in stand composition. Nevertheless, the LSD test identified a significant discrepancy between treatments at each of the inventories as well as for the change in counts. Initially, this consisted of a greater count in the unburned portion of the unthinned subunit than in the burned portion of the cut-to-length subunit, but at the final inventory a greater one prevailed in the former than that in the unburned portion of the whole-tree subunit, while for the change in counts an increase in the burned portion of the cut-to-length subunit differed from a decrease in the burned portion of the unthinned subunit.

As for pitch tube counts based on bole surface area, ANOVA once again did not disclose any significant effects for Jeffrey pine, and only at the final inventory did the LSD test identify a significant difference which consisted of a greater count in the burned portion of the cut-to-length treatment than that in the unburned portion of the whole-tree treatment (Table 3). White fir, however, was affected by the thinning ($p$ = .0097) and fire ($p$ = .0218) treatments plus the thinning treatment × inventory year ($p$ = .0193) and fire treatment × inventory year ($p$ = .0373) interactions, and the change in counts per unit bole surface area was affected by the thinning ($p$ = .0235) and fire ($p$ = .0379) treatments as well. Furthermore, the LSD test identified several significant distinctions among treatments, with those at the first inventory consisting of a higher count in the unthinned but burned stand portion than in all other portions containing this species, those at the last inventory entailing a lower count in the whole-tree unburned combination than those in the cut-to-length and burned combination or in the unthinned subunit irrespective of fire treatment, and those concerning the change in counts consisting of a decrease in the unthinned but burned combination that differed from increases in all remaining treatments where fir was continually present. To further compare the two species, white fir on average had 9.8× and 10.6×

the bole surface area-based pitch tube counts at the first and last inventories, respectively, as that found on Jeffrey pine, while the increase over the course of the study for the former was 44.7× that for the latter. Again because Jeffrey pine dominated stand composition, however, significant effects as revealed by ANOVA were lacking with regard to the combined bole surface area-based counts across species, although the LSD test did identify one significant disparity between treatments at each of the inventories and for the change in counts. Specifically, the count was higher in the unburned portion of the unthinned treatment than in the unburned portion of the whole-tree treatment at each of the inventories, and an increase in the burned portion of the cut-to-length treatment differed from a decrease in the burned portion of the unthinned treatment.

With pitch tube counts per tree distinguished on the basis of DBH class, ANOVA revealed significant effects for class 1 Jeffrey pine consisting of the year of inventory ($p = .0127$) and the thinning treatment × inventory year interaction ($p = .0185$), and it also revealed a significant effect of thinning treatment ($p = .0322$) on the change in these counts (Table 4). Somewhat reflective of the influences discerned by ANOVA, the LSD test did not identify any significant differences among treatments initially, but at the final inventory it revealed higher values in the unthinned subunit irrespective of fire treatment than in the unburned portion of the whole-tree subunit. Regarding the change in counts, it disclosed increases in both portions of the unthinned treatment that differed from decreases in the unburned portions of the cut-to-length and whole-tree treatments. For the remaining DBH classes, namely 2 through 7, ANOVA did not discern any significant influences on counts per tree or its change in Jeffrey pine, although the LSD test identified significant disparities among treatments in either the final inventory or in the count change for classes 2, 4, 5, and 7. In classes 2 and 7, they presided in the last inventory, with disparities in class 2 consisting of higher counts in the burned portions of the cut-to-length and whole-tree treatments than in the unburned portion of the latter, while in class 7 there was a higher count in the burned portion of the cut-to-length treatment than in all others with representatives of this class except the whole-tree unburned combination and a higher one in the latter than in the cut-to-length unburned combination. In classes 4 and 5 the significant differences involved the changes in counts, with those in the former consisting of an increase in the burned portion of the cut-to-length subunit that differed from decreases in the unthinned subunit irrespective of fire treatment, while in the latter an increase in the unburned portion of the unthinned subunit differed from a decrease in the unburned portion of the cut-to-length subunit. In comparing the seven DBH classes, initial pitch tube counts per tree for Jeffrey pine generally increased with tree size when averaged across treatments, although there was a minor discrepancy in this trend regarding classes 3 and 4, while at the final inventory counts increased with size through class 6 but that in class 7 was sharply diminished. The changes in counts were relatively erratic with both increases and decreases represented among the various classes. Nevertheless, the largest increase was observed in class 4 and the largest decrease in class 7. As for white fir, influences identified by ANOVA amounted to thinning ($p$ = .0047) and year of inventory ($p$ = .0034) effects on class 4. The LSD test revealed significant disparities among treatments in this class for the initial inventory only, however, with a higher count in the burned portion of the unthinned treatment than in either portion of the cut-to-length treatment. For the inventory year effect, the counts increased in both treatment combinations where class 4 white fir were continually present, specifically in the cut-to-length burned and unthinned unburned combinations, but the increase was especially pronounced in the former. Comparing the seven classes, there was a clear increase at both inventories in the counts per tree from class 1 to class 2 when averaged across treatments followed by another from class 3 to class 4, but thereafter evidence of continued increases was less apparent. The changes in counts clearly increased from class 2 to class 3 and then more gradually through class 5, all entailing positive values, before declining sharply to a negative value in class 6.

For pitch tube counts per unit bole surface area distinguished by DBH class, ANOVA disclosed year of inventory ($p$ = .0056) and thinning treatment × inventory year interaction ($p$ = .0230) effects for class 1 Jeffrey pine along with a thinning effect ($p$ = .0375) on the change in counts, a thinning treatment × inventory year effect ($p$ = .0337) for class 4 pine along with a thinning effect ($p$ = .0500) on the count changes, and a fire treatment × inventory year effect ($p$ = .0449) for class 7 pine (Table 5). Somewhat reflective of the influences discerned by ANOVA, the LSD test did not identify any significant differences among treatments initially for either class 1 or class 4, but at the final inventory it revealed higher values in the unthinned subunit irrespective of fire treatment than in the unburned portion of the whole-tree subunit regarding the former, while for the latter it revealed a higher count in the burned portion of the cut-to-length subunit than in either the unburned portion of this subunit or the burned portion of the unthinned subunit. For the changes in counts for these two classes, the LSD test discerned significant disparities between an increase in the unthinned but burned treatment combination and decreases in the unburned portions of the cut-to-length and whole-tree treatments in class 1, while in class 4 it discerned disparities between an increase in the cut-to-length and burned combination and decreases in both portions of the unthinned treatment. As for class 7 Jeffrey pine, the LSD test identified a significantly higher count at the last inventory in the burned portion of the cut-to-length subunit than in the unburned counterpart of this thinning treatment. Additional disparities disclosed by the LSD test for the pine involved class 2 at the final inventory and consisted of a higher count in the burned portion of the whole-tree treatment than in the unburned portion of this treatment or the burned portion of the unthinned treatment, and in turn a higher one in the burned portion of the cut-to-length subunit than in the whole-tree unburned combination. Also, differences were detected in class 5 Jeffrey pine at the final inventory and regarding the change in counts, with a higher value in the unburned portion of the unthinned treatment than in the unburned portions of either the cut-to-length or whole-tree treatments at the final inventory, while an increase in counts over the course of the study for the unthinned and unburned combination differed from a decrease in the unburned portion of the cut-to-length treatment. Comparing the DBH classes, bole surface area-based pitch tube counts at the initial inventory, when averaged across treatments, rose sharply from class 1 to class 2, thereafter remained relatively elevated through class 5 before rising further in class 6 and even more sharply in class 7, while at the final inventory these counts remained relatively static from classes 1 through 6 and then declined perceptibly in class 7. As for the count changes, general increases were evident in classes 1, 4, and 5, but most apparently in the former, while decreases prevailed in classes 2, 3, 6, and 7, but most acutely in the latter. Concerning white fir, significant influences on surface area-based counts detected by ANOVA were limited to thinning treatment ($p$ = .0364) and inventory year ($p$ = .0031) effects for class 4, but the LSD test did not disclose any significant disparities among treatments for this or any other class regarding the counts or their changes. Nevertheless, across inventories, class 4 counts were substantially higher in the unthinned than in the cut-to-length treatment, which likely accounts for the thinning effect noted above, while counts were also somewhat higher at the last inventory than at the first when averaged across treatments, which probably explains the aforementioned inventory year effect. Among the DBH classes, there was a considerable increase in the initial counts for white fir from class 1 to class 2, but thereafter they assumed intermediate values that persisted through the remaining classes, while at the last inventory the increase from class 1 to 2 was still evident but thereafter intermediate values from classes 3 through 5 were followed by sequential declines in classes 6 and 7 to averages lower than that of class 1. For the count changes, positive averages prevailed in classes 1 through 5 with no perceptible pattern therein, while class 6 was the only one with a count decrease over the course of the study.

With pitch tube counts per tree distinguished on the basis of LCP class, ANOVA revealed a significant year of inventory effect ($p$ = .0313) for class 2 Jeffrey pine and a thinning treatment × fire treatment × inventory year interaction effect ($p$ = .0210) for class 5 pine along with a thinning × fire treatment effect ($p$ = .0118) on the change in counts for the latter (Table 6). The inventory year effect for class 2 was manifested in an overall increase from the first to the last inventories. For class 5, a seemingly complex interaction according to ANOVA culminated in only a single significant disparity according to the LSD test, that between a higher initial count in the burned portion of the unthinned treatment than in the unburned portion of the cut-to-length treatment. The LSD test also identified several disparities regarding the change in counts, however, specifically between increases in the burned portions of the cut-to-length and whole-tree subunits along with another in the unburned portion of the unthinned subunit and a decrease in the burned portion of the latter, plus one between a lesser decrease in the unburned portion of the whole-tree subunit and a greater one in the burned portion of the unthinned subunit. Additional disparities according to the LSD test involved class 3 pine, and entailed a higher initial count in the unburned portion of the unthinned treatment than those in all of the other treatments. Comparisons among the six LCP classes for Jeffrey pine revealed that counts per tree at the initial inventory were highest overall in class 1, nearly negligible in class 2, and assumed intermediate values in classes 3 through 6 while at the final inventory that in class 6 was substantially lower than those in any of the others, and for the change in counts overall decreases in classes 1 and 6 contrasted sharply against increases in the remaining classes with the apex among the increases occurring in class 3 and the nadir in class 5. As for white fir, ANOVA divulged significant thinning treatment effects for class 5 ($p$ = .0243) and class 6 ($p$ = .0008) along with fire treatment ($p$ = .0064) and thinning × fire treatment interaction ($p$ = .0326) effects for the latter. Concerning class 5 fir, the LSD test discerned significant disparities at the final inventory between a higher count in the burned portion of the unthinned subunit and lower ones in all other treatments except for the unburned portion of this thinning treatment, and in turn a higher count in the latter than in the unburned portion of the whole-tree treatment. In class 6, a higher initial count in the unthinned but burned treatment combination differed from lower ones in all remaining treatments where fir of this LCP class resided. Additional disparities identified by the LSD test as significant concerned class 1, for which white fir was represented at most in two treatment combinations at either inventory. Nevertheless, a higher initial count in the unburned portion of the unthinned subunit contrasted against a lower one in the burned portion of the cut-to-length treatment. Comparisons among LCP classes for the counts per tree in this species revealed that, when averaged across treatments, such counts initially were highest overall in class 1 and lowest in class 4, while at the final inventory, they were again highest in class 1 but lowest in class 3. For the count changes, the most apparent distinction was that between a large increase in class 4 and a substantial decrease in class 5, with the latter representing the only decrease in any of the classes.

Regarding pitch tube counts per unit bole surface area distinguished by LCP class, ANOVA detected a significant thinning treatment effect ($p$ = .0070) along with thinning × fire treatment ($p$ = .0017), thinning treatment × inventory year ($p$ = .0242), and fire treatment × inventory year ($p$ = .0160) interaction effects for class 3 Jeffrey pine, and furthermore, it detected a fire treatment effect ($p$ = .0225) on the change in counts for this species and class along with thinning ($p$ = .0007) and fire ($p$ = .0086) treatment effects plus that of their interaction ($p$ = .0005) for class 5 count changes in the pine (Table 7). Despite the extensive array of significant influences for class 3 identified by ANOVA, the LSD test recognized as significant only that the initial count in the unburned portion of the unthinned treatment exceeded those in all other stand portions, although regarding the count changes, it also distinguished increases in the burned portion of every thinning treatment from a decrease in the unburned portion of the unthinned treatment. In class 5, the LSD test revealed as significant disparities between an increase in the burned portion of the whole-tree treatment and decreases in all other stand portions over the course of the study, but additionally, and despite a lack of significant influences according to

ANOVA, it revealed as significant differences at the final inventory between a higher count in the former and lower ones in every other treatment combination except that of the unthinned and unburned combination. Furthermore, and again despite the failure of ANOVA to identify pertinent influences, the LSD test detected a significant disparity for class 4 at the final inventory between a higher count in the burned portion of the cut-to-length subunit and a lower one in the unburned portion of the whole-tree subunit as well as others specific to the change in counts for this class between an increase in the burned portion of the cut-to-length treatment and decreases in the unburned portion of this treatment and the burned portion of the unthinned treatment. Concerning comparisons across classes, there was a steep decline in the initial bole surface area-based counts from class 1 to class 2 while thereafter the remaining classes exhibited intermediate values, but at the final inventory a relatively high count in class 1 ascended to an even higher one in class 2 while the remainder exhibited values that were substantially lower than either of the first two. For count changes in the pine, a steep reduction in class 1 especially but another of much less magnitude in class 6 contrasted sharply against a substantial increase in class 2, but there were also insubstantial increases in classes 3, 4, and 5. In white fir, significant influences revealed by ANOVA were limited to thinning treatment ($p$ = .0495) and year of inventory ($p$ = .0466) effects for LCP class 6. As for the LSD test, it denoted differences in class 6 between a higher initial count in the unthinned but burned combination and lower ones in the cut-to-length subunit irrespective of fire treatment as significant. It also deemed significant, however, a disparity in class 5 between a higher final count in the burned portion of the unthinned subunit and a lower one in the unburned portion of the whole-tree subunit. Through comparison among classes for the fir, it became apparent that the only obvious dissimilarity at the initial inventory entailed considerably higher counts in classes 5 and 6 than in classes 1 and 4 and the most apparent one at the final inventory involved a count in class 3 that was nearly twice that of the next highest value, while the most striking distinction regarding count changes was that class 5 alone incurred a decrease over the course of study.

Relationships of Bark Beetle Demography to Stand Attributes

The first subset of the first regression series, which was concerned with relationships between pitch tube prevalence and tree dimensions plus the related live crown percentage, produced 28 significant models (Table 8). Among these, both measures of abundance, namely pitch tubes per tree and that per unit of bole surface area, in LCP class 6 Jeffrey pine plus the count per tree in white fir overall at the first inventory were positively related to initial tree height, while the final counts by both abundance measures for DBH class 4 pine were negatively related and that per tree for pine overall as well as for the LCP class 3 pine were positively related to final height. With initial DBH as the independent variable, the dependent counterparts were the initial counts per tree for LCP class 6 pine and for fir irrespective of class, each a positive relationship, and with final DBH, they were again DBH class 4 pine at the final inventory by both abundance measures, each a negative relationship. For the above models, from nearly 15% to more than 60% of the variation in the dependent variables was explained by that in the independent variables, but models involving initial values accounted for far more of such variation than those incorporating final ones. Models focused on crown development in the independent component featured positive correlations exclusively when initial values were involved and negative correlations, also exclusively, when final ones were. These consisted of relationships between the initial pitch tube counts per tree for pine and fir combined, for each species individually, and for LCP class 3 pine and the initial live crown length, and those between DBH class 3 and class 4 pine, each by both abundance measures, and final crown length. Furthermore, the initial count per tree for LCP class 3 pine and the initial white fir counts by both measures and irrespective of class were related to initial live crown percentage, while models involving final live percentage were exclusively those of Jeffrey pine with dependent variables consisting of the final count per unit bole surface area irrespective of class plus those for DBH class 3 and LCP classes 3 and 4 along with the final counts per tree for DBH classes 2 and 3. The variation in the dependent components explained in these models ranged from nearly 15% to more than 50%, although more approximated the lower than the higher of these values, and any clear distinction between those involving the two inventories was not evident.

The second subset of the first regression series, which was concerned with relationships between pitch tube prevalence and stand density, produced 23 significant models, and all featured positive correlations (Table 8). Among these, the most prominent independent variable was basal area, to which the count per tree and that per unit bole surface area for DBH class 1 Jeffrey pine were both related within the initial inventory, while within the final inventory the dependent variables consisted of the counts by both measures for pine and fir combined, those for pine alone, the surface area-based count for DBH class 1 pine and the count per tree for LCP class 4 pine, and the counts by both measures for DBH classes 5 and 6 as well as for LCP class 3 pine. With tree count as the independent variable, all significant models involved final values exclusively, and the dependent variables were the surface area-based count for the combined species along with that for Jeffrey pine alone and for LCP class 3 pine, plus the counts by either measure for pine of DBH classes 1, 4, and 5. Generally weak correlations also prevailed in these models, although the two involving the combined species and Jeffrey pine counts per tree at the final inventory explained more than 45% of the variation in the dependent variables.

Another prolific predictor of pitch tube prevalence in this study was stand biomass, the focus of the third subset of the first regression series which also totaled 23 significant models, and among those involving the initial inventory, positive correlations prevailed throughout (Table 8). Of these, DBH class 1 Jeffrey pine counts by each of the two abundance measures were related to the total biomass of this species as was the count per tree for LCP class 6 pine while the counts by both measures for this species and class were related to combined total biomass. Furthermore, the combined pitch tube counts by each measure were related to the total biomass of white fir. For these models, the variation in the dependent variables explained ranged from more than 20% to nearly 55%, with those involving LCP class 6 pine in the dependent components the strongest overall. Of models based on the final inventory, the count per tree irrespective of class designation, the counts by both measures for DBH class 6, and the DBH class 1 count per unit bole surface area were all positively related to total biomass within Jeffrey pine. In contrast, DBH class 4 counts by both measures were negatively related to total biomass within this species. Additional models derived from the final inventory and involving pine in the dependent components featured combined total biomass as the independent variable to which the count per tree overall plus that for LCP classes 3 and 4 along with the DBH class 5 counts by both abundance measures were all positively related. Other significant models in this subset, in addition to being based on values from the final inventory, incorporated white fir biomass in the independent variables. Specifically, the combined pitch tube counts across species by both measures along with the DBH class 2 count per tree for white fir were each positively related to the total biomass of the latter. The last two significant models in the third subset of the first series paired the combined pitch tube counts by both measures with combined total biomass, all derived from the final inventory, and positive correlations prevailed in each of these. In total, models based on the last inventory explained from just over 15% to more than 90% of the variation in the dependent components, but especially strong were those focused on white fir in the independent components for which the correlations were among the highest of any regression model included in the study.

Relationships of Stand Mortality to Bark Beetle Demography

The second regression series, which was concerned with the relationships between tree mortality and pitch tube prevalence, generated 40 significant models, and all featured positive correlations (Table 9). For those based on the first inventory, most involved Jeffrey pine pitch tube counts in the independent variables. Of these, both the number of dead trees and the dead tree percentage were related to the overall pitch tube count per unit bole surface area, to the DBH classes 2, 3, and 7 counts by both abundance measures, and to the LCP class 1 count by both measures. Additionally, the dead tree count was related to the DBH class 4 pitch tube counts by both measures while the dead tree percentage was related to the bole surface area-based count for this class. The remaining models derived from the initial inventory consisted of relationships between dead tree percentage and both the pitch tube count per tree for DBH class 2 white fir and the combined count per unit surface area. Spanning from less than 15% to 95%, the variation in the dependent variables explained in these models varied widely, but those involving DBH class 7 and LCP class 1 pine in the independent components, along with that involving DBH class 2 fir, were among the strongest of any calculated in the study. Significant models in the second series based on the final inventory also focused heavily on pitch tube counts in pine regarding the independent variables. For these specifically, the dead tree count was related to the overall pitch tube counts, to DBH class 5 counts, and to LCP class 3 counts by both measures, the dead tree percentage was related to the overall count per unit bole surface area and to that for LCP class 3, and both the dead tree count and percentage were related to DBH class 3 and LCP class 4 counts by either measure. The sole model involving other than Jeffrey pine exclusively in the independent component entailed the combined surface area-based pitch tube count instead, to which the dead tree count was related. Ranging from nearly 15% to nearly 60%, the variation in the dependent components explained in the models of this series derived from the final inventory did not vary as widely as that prevailing for those based on the initial inventory, and for most the proportion explained was nearer the lower end than the upper end of this range.

## DISCUSSION

Because the first inventory conducted in this study was completed before the implementation of the thinning and underburning treatments, the data it provided concerning bark beetle demography was representative of the interaction of the existing beetle population with an unmanaged, second growth Jeffrey pine stand. As the subject stand was a product of natural regeneration, it featured the pronounced spatial variability concerning tree size and spacing characteristic of such stands, and thus the initial disparities among treatments and relationships between beetle prevalence and mensurational attributes may provide insight into possible proclivities of the Jeffrey pine beetle to colonize certain stand portions more so than others, ostensibly because conditions in the more heavily infested portions were better suited to an expansion of their population. With numbers of pitch tubes serving as an indicator of population density, such proclivities are perhaps best illustrated by comparing the portion to be burned within the unthinned subunit to that within the pending cut-to-length subunit, which were clearly dissimilar regarding both mensurational features and pitch tube prevalence. Distinguishable on either a statistical or numerical basis or both, the former had the tallest trees in the stand, their mean DBH was one of the two largest, and their live crown length and percentage were greatest overall, while this stand portion exhibited the lowest basal area and total stem count encountered at the initial inventory. Regarding pitch tube prevalence in the pine, it had the highest initial counts per tree and per unit bole surface area, although the latter was a numerical distinction only. Additionally, it had the highest counts by both abundance measures specifically for DBH class 6 and LCP class 5 pine, although only the count per tree for the latter entailed a statistical distinction. Perhaps coincidentally, counts by both measures of pitch tubes induced by the engraver beetle in white fir were highest there also as were those for DBH class 4 and LCP class 6, although these outcomes were based on an exceedingly small number of trees which were all of this DBH and LCP class. Nonetheless, the portion to be burned within the cut-to-length subunit had the shortest trees with the smallest DBH, bore among the smallest crowns which proportionally were intermediate within the range of values encountered, and had a moderate basal area but one of the two highest stem counts. As for pitch tube counts, that per tree on Jeffrey pine was lowest overall in this stand portion while that per unit surface area was among the lowest, although the latter was a numerical distinction only, while for LCP classes 4 and 6 it had the lowest numerical values as well. In white fir, counts by both measures fell toward the lower end of the range encountered and those per tree for DBH classes 3, 5, and 6 and per unit surface area for classes 5 and 6 along with those per tree for LCP classes 1 and 4 plus that per unit surface area for the former were the lowest found, but in large part these distinctions were numerical only and for those involving the specified classes, there was only one other mean available for comparison. Nevertheless, when considered in total, the above observations suggest an affinity of the Jeffrey pine beetle at this juncture of the study for large specimens of its namesake species with expansive crowns that were widely spaced. For the size factor, this in turn suggests a preference for trees capable of providing the resources critical to reproductive success in greatest abundance (Edmonds, Agee, & Gara, 2011), and thus the larger ones, although alternatively, or perhaps additionally, it may indicate that larger trees presented larger targets upon which to land during dispersal flights. To the extent that it is possible to draw inference from the above observations concerning the fir, the engraver beetle seemed to exhibit much the same preference regarding density but its preference concerning tree size is less certain. Based on the regression analysis, however, support for these conclusions regarding the pine was generally tepid, as there were positive correlations between initial pitch tube counts and both tree height and DBH based on both measures for the former and that per tree for the latter, but they were confined to LCP class 6. Incidentally, there were also positive relationships between the counts per tree and both height and DBH in the fir independent of any class distinctions. Regarding crown development, positive correlations were revealed between the counts per tree in pine overall and live crown length, between those per tree for LCP class 3 pine and both live length and percentage, and between the counts per tree in fir and both length and percentage plus another between the bole surface area-based count in this species and the latter. For those involving the pine, however, such relationships were exceedingly weak. Nevertheless, contrary to the above suppositions, there were positive correlations between the counts by both measures for DBH class 1 pine and initial basal area, although in addition to being confined to a narrow diameter range, these were also very weak relationships. Comparing the findings here with those of other studies conducted in the western USA, Klein, Parker, & Jensen (1978) documented an apparent preference of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) for larger diameter lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), a finding reinforced in a study by Preisler & Mitchell (1993) with another variety of this species (*P. contorta* var. *murrayana* [Grev. & Balf.] Engelm.), but the latter study also revealed their preference for higher stand densities, a finding contrary to that noted here initially regarding Jeffrey pine and its beetle. Pursuant to the mountain pine beetle but in ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.), McCambridge et al. (1982) and Negron & Popp (2004) reiterated their seeming preference for larger trees and higher densities. Specific to the latter, Mitchell, Waring, & Pitman (1983) also noted an affinity of the mountain pine beetle for higher density lodgepole pine as did Fiddler et al. (1989) for another variety of ponderosa pine (*P. ponderosa* var. *ponderosa* Dougl. ex Laws.). In all except the latter study, rapidly escalating beetle populations inducing substantial tree mortality were the focus, which may explain why their findings concerning stand density differed so markedly from that reported here, which was derived from a stand with a moderate infestation of its principal species. Regardless, another investigation of factors affecting bark beetle populations at near endemic levels in a Jeffrey pine stand again revealed their affinity for higher stand density, although most of the associated tree mortality occurred in the few white fir present as the result of attacks by the fir engraver (Fettig et al., 2012). Concerning white fir, several studies, specifically those of DeMars, Ferrell, & Otrosina (1988), Ferrell, Otrosina, & DeMars

(1994), Walker et al. (2007), and Egan et al. (2010), have reported that the more important influence of stand density on fir engraver populations was not that of the stand overall but rather of the proportional prevalence of the white fir host, with greater availability exacerbating attack severity, while the first three of these investigations noted a marginal preference of this beetle for larger fir. Thus, the finding here of a preference of the engraver beetle for lower stand density is somewhat of a divergence from those reported previously, with the disparity possibly reflecting that the stands examined in prior studies had far more fir in their compositions, while neither the present study nor its predecessors provided a compelling case of a definitive tree size-based influence on fir engraver populations.

A unique aspect of this study was the examination of possible linkages between bark beetle demography and stand biomass. Accomplished through regression analysis, several models derived from the initial data demonstrated positive relationships between pitch tube quantity by either abundance measure and biomass in aggregate. The dependent variables of two models specifically entailed DBH class 1 Jeffrey pine in which the counts by both measures were correlated with total pine biomass. Another model related the count per tree for LCP class 6 pine to that of the total biomass for this species, while two others related the counts by both measures for this class and species to combined total biomass, and overall, these models were stronger than those involving DBH class 1. The narrow diameter and live crown ranges embodied by these classes obviously preclude extrapolating relationships within them to the stand overall. Nevertheless, these models collectively provided a somewhat contrary example again of the impact of stand density on initial beetle populations if biomass is viewed as a surrogate density measure. However, DBH class 1 and LCP class 6 pine shared many constituents and both consisted primarily of young, slender stems featuring relatively thin bark and minimal self-pruning. Thus, bark and bole thickness may have been especially important to reproductive success within the limited confines of these classes specifically due to thermal insulation considerations (Rudinsky, 1962), which in essence is the finding noted here previously concerning the preference for larger trees. There were also two significant models that positively related pitch tube counts across tree species by either abundance measure to total white fir biomass. These may simply reflect that where the few fir existed within the stand, the combined counts were skewed toward higher values simply because of the exorbitant numbers found on white fir itself. Defense mechanisms of this fir provide little real protection against fir engraver attack (Ferrell, 1983; Christiansen, Waring, & Berryman, 1987; Berryman & Ferrell, 1988; Walker et al., 2007), and it has long been recognized that this tree is inferior to the pines in regard to defenses against bark beetles because of their relatively underdeveloped resin duct system (Penhallow, 1907; Lewinsohn, Gijzen, & Croteau, 1991; Trapp & Croteau, 2001). Furthermore, to the extent functional, white fir defenses are much compromised on drier sites, such as that upon which this study was conducted, as a clear lower threshold regarding precipitation, specifically 89 cm (Laacke, 1990; Edmonds, Agee, & Gara, 2011), has been established for this species to thrive in the Sierra Nevada, a minimum well above that deposited on this site annually.

Establishing a clear notion of the influence of thinning treatment on bark beetle demography in this study is severely complicated by the inclusion of the fire treatment and vice versa, and thus a simultaneous examination of these two factors is warranted. The pitch tube count per tree was not forthcoming in distinguishing either a thinning or fire treatment effect on beetle prevalence in Jeffrey pine regarding posttreatment values nor on the change in such over the course of the study for this species. Independent of treatment, however, the regression analysis offered some insight into possible influences on this abundance measure, as several models featuring positive correlations related it to either basal area or tree count or both. Specifically, the count per tree across all class designations was correlated with basal area as was that within DBH classes 5 and 6 and within LCP classes 3 and 4, while those of DBH classes 1, 4, and 5 were related to tree count. Three additional models related the count per tree to stand biomass, two featuring positive correlations also that consisted of relationships between this count irrespective of class designations plus that for DBH class 6 and total pine biomass. Moreover, the counts per tree in the pine overall and for DBH class 5 and LCP classes 3 and 4 were positively related to combined total biomass. Adding biomass to the conventional stand density measures of basal area and stem count, these models collectively infer that higher amounts of tree vegetation per unit area may have promoted an expansion of the posttreatment Jeffrey pine beetle population, although this assumption is rendered less compelling by the weakness of some of the correlations. For white fir, counts by this abundance measure were highest in the unthinned treatment and lowest in the whole-tree treatment with clear statistical distinction between the two, and in fact such a distinction was also apparent between the former and the cut-to-length treatment. Furthermore, they were numerically higher in the burned portions than in the unburned portions within each of the thinning treatments with the disparity in the unthinned subunit a statistically significant one as well. Nevertheless, in large part this outcome paralleled pretreatment differences as revealed by the initial inventory, and consequently there is little here to suggest that the implemented treatments had great influence in their aftermath on the severity of the fir engraver infestation. However, within the narrow diameter range embodied by DBH class 2, a strong regression model positively related the count per tree in white fir to total fir biomass, which again suggests that attack severity was at least somewhat a function of host tree availability. Regardless, the counts per tree across species and classes were highest throughout the study in the unthinned and unburned treatment combination, but the lowest shifted from the cut-to-length and burned combination initially to the whole-tree unburned combination at the final inventory, a transition reflecting that the largest increase in counts over the course of the study occurred in the former. In part, this increase may indicate some level of treatment influence, as it is reasonable to assume that the combustion of the slash mats created through the cut-to-length harvesting on this site, which resulted in a hotter fire of relatively prolonged duration (Walker et al., 2006) to the extent that it was probably the cause of some direct mortality in larger Jeffrey pine through elevated crown scorch (Fecko et al., 2008b), induced sufficient stress in surviving stems to compromise their defense mechanisms, a malady often linked to increases in bark beetle attack severity in western USA pines subjected to fires that consumed substantial surface fuel loads (Bradley & Tueller, 2001; McHugh, Kolb, & Wilson, 2003; Wallin et al., 2003; Waring & Six, 2005). As an aside, there was also a regression model of moderate strength that positively correlated the combined count per tree at the final inventory to combined total biomass, which again if considered a surrogate density measure suggests that higher stand density facilitated posttreatment expansion of bark beetle populations overall. Additionally, a significant model positively related the final pitch tube count per tree across species to total white fir biomass, an outcome paralleling that noted previously concerning the initial inventory. Again, these may simply reflect that where the few fir presided, the combined counts were skewed toward higher values simply because of the prodigious numbers found on white fir itself.

Somewhat more illuminating of treatment effects on Jeffrey pine specifically were pitch tube counts based on bole surface area, for which the final values were highest in the burned portion of the cut-to-length treatment and lowest in the unburned portion of the whole-tree treatment. The former may be another indication of the aforementioned increase in beetle population facilitated by compromised tree defenses associated with slash mat combustion, and if so, this result again conforms to those of the studies cited above that investigated fire-induced stress effects on such populations (Bradley & Tueller, 2001; McHugh, Kolb, & Wilson, 2003; Wallin et al., 2003; Waring & Six, 2005), although the finding here is perhaps noteworthy in that the duration of the effect was demonstrated to extend well beyond that documented in the previous studies. It may also be notable that the largest increase in counts over the course of the study occurred in the burned portion of the cut-to-length subunit, although this represented a numerical rather than a statistical distinction. The finding here of the lowest surface area-based count at the final inventory in the whole-tree unburned treatment combination may be indicative of the influence of relatively elevated tree growth on Jeffrey pine beetle demography, as this treatment combination produced the highest rate in individual stems based on several growth measures (Fecko et al., 2008a; Swim et al., 2013). Enhanced growth rates have been identified as a deterrent to bark beetle attack in other western USA pines (Mitchell, Waring, & Pitman, 1983; Fiddler et al., 1989), or alternatively, depressed growth has long been noted to amplify susceptibility (Craighead, 1925b; Person, 1928; Keen, 1936; Startwell, 1971; Larsson et al., 1983). Elevated growth is an indicator of enhanced vigor, a concept that has served as the basis for tree classification systems developed specifically for purposes of predicting susceptibility to attack (Waters, 1985; Smith et al., 1997), and vigor in turn is largely an indicator of the ability of a potential host tree to generate carbohydrates in quantities sufficient to permit allocation to the oleoresin production critical to its defense (Coulson & Witter, 1984; Kozlowski, Kramer, & Pallardy, 1991). To the extent that tree size reflects growth rate, several regression models lend credence to an assumption that elevated growth suppressed expansion of the posttreatment Jeffrey pine beetle population in this study, as in an array of negative relationships the counts per unit bole surface area at the final inventory irrespective of any class designation were correlated with live crown percentage, those within DBH class 4 pine were correlated with height, DBH, and live crown length, those within DBH class 3 were correlated with live crown length and percentage, and those within LCP classes 3 and 4 were correlated with live percentage. However, not only were most of these relationships confined to relatively narrow DBH and LCP classes but they also explained only a modest amount of the variation in the counts, and even at that they obviously represent a clear departure from the findings derived from the initial inventory concerning beetle preferences for larger trees. Several other regression models computed here may lend additional insight in the dichotomy in attack intensity between the cut-to-length burned combination and the whole-tree unburned combination, as the surface area-based count across classes in the pine was positively related to stem count as were the counts within DBH classes 1, 4, and 5 and within LCP class 3, and the final stem count in the former treatment combination greatly exceeded that in the latter. There were also positive correlations between this abundance measure within certain DBH classes and total pine biomass, but these must be evaluated with added caution not only because they were strictly limited to narrow DBH ranges but also because biomass was higher in the whole-tree unburned combination than in the cut-to-length burned combination. The bole surface area-based counts in white fir at the final inventory resembled those of the pine in that they were lowest in the unburned portion of the whole-tree subunit, but higher values in the burned portion of the cut-to-length treatment closely approximated the average within the unthinned subunit. The former cannot be interpreted with certainty because of a deficiency of pertinent stems in the whole-tree unburned treatment combination but it is possible that the high counts in the cut-to-length burned combination were another manifestation of stress induced by the burning of the slash mats, in this case specific to a species that is renowned for its poor adaptation to fire (Zouhar, 2001). However, if attack severity is considered an indication of deficient fire resistance in fir, the finding here that the only reduction in pitch tube counts between inventories occurred in the burned portion of the unthinned treatment was an anomaly for which ready explanations are lacking, but a contributing factor may have been that the post-thinning fuel loading in this treatment was far less than that in the cut-to-length treatment (Walker et al., 2006). Regarding the surface area-based counts across species, discerning a clear thinning or fire effect was questionable due to the similarities between the initial and final inventories in the disparities among treatments, with the highest and lowest counts throughout the study occurring in the unburned portions of the unthinned and whole-tree subunits, respectively. Nevertheless, significant regression models positively related the combined count at the final inventory to basal area, stem count, and combined total biomass, and the former treatment combination exhibited significantly higher values for the first two of these and a numerically higher one for the last than the latter combination. Consequently, these represent another indication that higher stand density favored increases in bark beetle populations. An additional model positively related the combined pitch tube count per unit surface area to total white fir biomass with a correlation that was among the strongest revealed in the study, and once again this may reflect that where the few fir existed within the stand, their counts were so high that they inflated the combined count. For the change in surface area-based counts across species, the burned portion of the cut-to-length treatment was again noteworthy in that the largest increase over the course of the study occurred there.

Separation of the trees in this study into classes on the basis of their diameter and crown development permitted an assessment of their contributions to bark beetle demography specifically focused on those aspects with the greatest implications for management, in this case regarding selection of stems for retention or removal where thinning operations are combined with subsequent underburning, where either practice is employed independently, or where neither is implemented. Proceeding on the premise that pitch tube abundance expressed on a bole surface area basis is the more accurate indicator of attack intensity of the two measures utilized, and that the initial data here obviously reflected bark beetle inclinations in an unmanaged stand, it is reasonable to assume that the change in counts over the course of the study demonstrated their proclivities under management better than final counts in and of themselves, as the latter sometimes seemed to simply reflect residual tendencies carried over from the initial inventory as has been noted previously. In this context, the finding that average surface area-based counts at the initial inventory in Jeffrey pine revealed a preference of its bark beetle for the largest DBH classes, specifically class 6 and even more so class 7, would seem to suggest that the selection of stems for retention in thinnings should favor those with smaller diameters, but the subsequent finding that these two classes displayed the largest reductions in counts while the greatest increase occurred in the smallest class leads to a conclusion that removing smaller stems, the directive of the commonly employed low thinning approach and one that best mimics the mortality inherent in natural self-thinning (Smith et al., 1997), would better promote enhanced stand health. However, this interpretation must be tempered by the propensity of overall averages to obscure the influences of individual treatments, and results here also suggest that the underburning of unthinned Jeffrey pine stands with substantial representation of class 1 stems and the burning of those with substantial quantities of the class 4 size when preceded by cut-to-length thinning will likely elevate beetle infestations as will foregoing both thinning and burning where class 5 stems are prevalent. It is also perhaps noteworthy that the cut-to-length and burned treatment combination was the only one to incur an increase in counts within every DBH class for which pertinent stems resided. For white fir, the finding that the lowest average initial count occurred in class 1 but the highest occurred in the immediately adjacent class provided a dubious indication of any proclivity of the fir engraver concerning host tree size, and the finding that the greatest count increase over the course of the study occurred in class 1 while the largest decrease occurred in class 6 was likewise of questionable predictive utility because stems of the pertinent size were found in only one treatment combination for each of these classes. Collectively, these seemingly capricious outcomes render it difficult to draw conclusions regarding management implications about fir engraver preferences where its host exists as a minor constituent in pure pine stands. Regarding LCP classes, they also provided seemingly arbitrary outcomes when initial counts and their changes are averaged across treatments, here in Jeffrey pine, as the highest initial count was found in class 1 with the lowest in class 2 while the greatest decrease between inventories occurred in the former and the largest increase occurred in the latter. As class 1 consisted of standing dead trees, an interpretation of the outcomes concerning these stems is complicated by the fact that many, if not all, of the initial class 1 constituents were no longer standing at the final inventory, which may have contributed to a deceptively large count reduction. Nevertheless, if it is assumed that the low initial counts in class 2 were a reflection of normal vacillation in beetle population levels then its large average count increase may in part reflect heightened susceptibility due to weak crown development. Despite the inconclusive results above, other LCP classes provided more definitive outcomes with clearer management implications, specifically that stands with a large component of class 3 stems as delineated here may sustain heightened attack when underburned whether preceded by thinning or not, and that large representations of class 4 and 5 stems may also elevate susceptibility when underburning is preceded by thinning using cut-to-length and whole-tree systems, respectively. Again with the caution demanded by the scarcity of white fir in this stand, the finding that the highest average surface area-based counts at the initial inventory were those in classes 5 and 6 would seem to suggest that the selection of stems for retention in thinnings should favor those with proportionally smaller crowns. Such an interpretation is rendered suspect, however, by the fact that most of the fir in the stand fell within these two LCP classes due to the propensity of this species to delay self-pruning (Zouhar, 2001), and therefore that the relatively high counts within them may simply be another manifestation of the tendency of greater host proximity to exacerbate attack intensity as noted previously, and by the finding that the only reduction in counts over the course of the study occurred in class 5.

Although it is not an entirely valid assumption that all mortality in conifer stands with endemic bark beetle populations is attributable to the lethality of the beetle itself given the myriad factors that can cause tree death, an examination of such in this Jeffrey pine stand is warranted as a component of a comprehensive investigation into beetle impacts in this forest cover type. Given that the subject stand here was overwhelmingly comprised of Jeffrey pine, its namesake beetle, which persisted at largely endemic population levels throughout the study, was the likely cause of stem mortality to the extent that such was attributable to bark beetle activity. In this study, the greatest tree mortality at the final inventory in terms of both dead tree count and percentage was found in the burned portion of the whole-tree subunit, but to attribute this outcome to the implemented treatments is illogical because the highest mortality also existed there before either of these treatments was executed. Further evidence that this result is likely another example of a pretreatment condition persisting through the end of the study was manifested in the relatively moderate pitch tube counts found in this treatment combination at both inventories, which suggests that trees died there from other causes in addition to bark beetle infestation. Perhaps tree mortality is a better indicator of attack severity in studies concerning epidemic outbreaks, which is the scenario for which it has most often been utilized (Amman & Baker, 1972; Startwell & Dolph, 1976; McCambridge et al., 1982; McCambridge & Stevens, 1982; Aukema et al., 2008), than it is where beetle population levels are persistently moderate as was the case in the present study. Nevertheless, the changes in dead stem counts here revealed numerical differences among treatments amounting to a higher mortality when assessed on an absolute count basis in the unthinned but burned treatment combination, which was the only combination to incur an increase between inventories, and a higher one in the whole-tree burned combination when expressed as a percentage, although the latter was only the highest of three in which increases occurred with each of them found in burned stand portions. There was also some evidence provided by the regression analysis establishing a probable linkage between stem mortality and pitch tube prevalence, as numerous models demonstrated positive relationships between either dead tree count or percentage, and often both, and pitch tube quantity by either one or more typically both abundance measures. Specifically, these entailed correlations between mortality and overall Jeffrey pine count as well as those for DBH classes 2, 3, 4, and 7 and LCP class 1 pine at the initial inventory, while at the final inventory significant models correlated stem mortality with overall Jeffrey pine counts along with those for DBH classes 3 and 5 plus LCP classes 3 and 4. The strength of these models differed somewhat between those derived from initial and final data, with more strength apparent in the former overall, which may infer that the implementation of the thinning and fire treatments, although perhaps more so the former, diminished bark beetle influence on tree mortality.

In summary, thinning and burning treatments increasingly utilized in forest restoration efforts in the western USA were evaluated for their long-term influences on bark beetle demography in pure, uneven-aged Jeffrey pine with a minor stand component of white fir. Quantified through pitch tube abundance in a stand with a moderate bark beetle population concerning the principal tree species, the Jeffrey pine beetle exhibited some preference for larger pine before either the thinning or fire treatments were implemented, but their proclivity regarding pretreatment stand density was unclear with some evidence for both higher and lower densities. Approximately one decade after treatment implementation, however, they demonstrated a consistent preference for higher density. There were multiple indications that the burning of the slash mats generated in the cut-to-length thinning treatment induced a marked increase in the Jeffrey pine beetle population, possibly due to the stress exerted on host trees by elevated heat loads that culminated in compromised defense mechanisms. There was also some evidence that the treatment combination most resistant to bark beetle attack in Jeffrey pine was that entailing whole-tree thinning without subsequent underburning, an outcome possibly related to the higher posttreatment vigor of the stems in this combination as demonstrated through their superior growth. A linkage was established between tree mortality and higher beetle infestation as measured through pitch tube counts, but it was also apparent that all mortality was not attributable solely to beetle activity. At both the pretreatment and posttreatment inventories, pitch tube abundance on white fir greatly exceeded that on Jeffrey pine, probably in part a reflection of the stress induced by its poor adaption to the study site. Nevertheless, results here suggest that the greatest influence on the fir engraver population both before and after treatment implementation was the prevalence of the host species. These findings advance the understanding of the likely stand health implications of density management and prescription fire in Jeffrey pine and similar dry site forest cover types.

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**TABLE 1** Seven DBH Classes and Six LCP Classes Used to Characterize Trees in a Pure, Uneven-Aged Jeffrey Pine Stand Influenced by Mechanized Thinning and Prescription Fire[1]

| Class | DBH (cm) | Live crown (%) |
|---|---|---|
| 1 | 10.2–17.7 | 0 |
| 2 | 17.8–25.3 | 1–20 |
| 3 | 25.4–32.9 | 21–40 |
| 4 | 33.0–40.5 | 41–60 |
| 5 | 40.6–48.1 | 61–80 |
| 6 | 48.2–55.7 | 81–100 |
| 7 | ≥ 55.8 | |

[1]All classes that consist of a range are inclusive of the minimum and maximum values indicated.

**TABLE 2** Mensurational Characteristics of a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1]

| Inventory | Thinning and burning treatment | Height (m) | DBH (cm) | Live crown (m) | Live crown (%) | Basal area ($m^2$ $ha^{-1}$) | Total trees (stems $ha^{-1}$) | Dead trees (stems $ha^{-1}$) | Dead trees (%) |
|---|---|---|---|---|---|---|---|---|---|
| Initial | Cut-to-length | | | | | | | | |
| | Burned | 12.4b | 27.8b | 6.4bc | 50.6b | 31.9ab | 536a | 12ab | 2.2ab |
| | Unburned | 15.3ab | 31.6ab | 8.5ab | 54.2b | 35.1a | 509ab | 12ab | 2.4ab |
| | Whole-tree | | | | | | | | |
| | Burned | 13.8ab | 28.5b | 4.9c | 33.4c | 37.9a | 605a | 27a | 4.5a |
| | Unburned | 16.2ab | 37.0a | 8.2ab | 49.4b | 30.0abc | 304bc | 0b | 0.0b |
| | Unthinned | | | | | | | | |
| | Burned | 17.0a | 36.6a | 10.8a | 64.6a | 21.4c | 203c | 0b | 0.0b |
| | Unburned | 15.7ab | 33.7ab | 10.0a | 64.2a | 25.6bc | 284c | 7ab | 2.5ab |
| Final | Cut-to-length | | | | | | | | |
| | Burned | 14.9b | 31.8c | 6.8b | 43.2cd | 21.5b | 292a | 12ab | 4.1ab |
| | Unburned | 18.2ab | 37.7bc | 8.1ab | 44.4bc | 23.7ab | 228a | 0b | 0.0b |
| | Whole-tree | | | | | | | | |
| | Burned | 17.0ab | 34.5bc | 6.6b | 35.8d | 20.6b | 220a | 25a | 11.4a |
| | Unburned | 19.3a | 45.3a | 9.7a | 52.4a | 19.3b | 121b | 0b | 0.0b |
| | Unthinned | | | | | | | | |
| | Burned | 19.4a | 39.9ab | 9.7a | 50.8ab | 25.7ab | 205ab | 5b | 2.4b |
| | Unburned | 18.2ab | 37.0bc | 9.4a | 51.2ab | 29.9a | 279a | 5b | 1.8b |
| Change in values[2] | Cut-to-length | | | | | | | | |
| | Burned | +2.5a | +4.0b | +0.4ab | –7.4b | –10.4b | –244bc | 0a | +1.9a |
| | Unburned | +2.9a | +6.1ab | –0.4bc | –9.8b | –11.4b | –281bc | –12a | –2.4a |
| | Whole-tree | | | | | | | | |
| | Burned | +3.2a | +6.0ab | +1.7a | +2.4a | –17.3c | –385c | –2a | +6.9a |
| | Unburned | +3.1a | +8.3a | +1.5a | +3.0a | –10.7b | –183b | 0a | 0.0a |
| | Unthinned | | | | | | | | |
| | Burned | +2.4a | +3.3b | –1.1c | –13.8b | +4.3a | +2a | +5a | +2.4a |
| | Unburned | +2.5a | +3.3b | –0.6bc | –13.0b | +4.3a | –5a | –2a | –0.7a |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test; each mean is based on values from five plots ($n = 5$).
[2]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in mean values.

**TABLE 3** Pitch Tube Prevalence in a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1,2]

| Inventory | Thinning and burning treatment | Counts per tree | | | Counts per $m^2$ of bole surface | | |
|---|---|---|---|---|---|---|---|
| | | Jeffrey pine | White fir | Combined | Jeffrey pine | White fir | Combined |
| Initial | Cut-to-length | | | | | | |
| | Burned | 1.72b | 10.59c | 2.32b | 0.25a | 2.56b | 0.37ab |
| | Unburned | 3.12ab | 0.00d | 3.11ab | 0.39a | 0.00b | 0.38ab |
| | Whole-tree | | | | | | |
| | Burned | 2.94ab | 5.50cd | 2.97ab | 0.40a | 1.88b | 0.42ab |
| | Unburned | 3.00ab | – | 3.00ab | 0.23a | – | 0.23b |
| | Unthinned | | | | | | |
| | Burned | 6.24a | 111.50a | 8.45ab | 0.57a | 10.88a | 0.80ab |
| | Unburned | 4.45ab | 42.29b | 10.63a | 0.53a | 4.06b | 1.09a |
| Final | Cut-to-length | | | | | | |
| | Burned | 4.34a | 30.92c | 5.72ab | 0.59a | 5.82a | 0.81ab |
| | Unburned | 4.38a | 23.67cd | 4.90ab | 0.34ab | 4.69ab | 0.44ab |
| | Whole-tree | | | | | | |
| | Burned | 4.51a | 18.50cd | 4.80ab | 0.52ab | 3.43ab | 0.58ab |
| | Unburned | 3.52a | 1.00d | 3.48b | 0.22b | 0.93b | 0.23b |
| | Unthinned | | | | | | |
| | Burned | 4.93a | 92.00a | 6.76ab | 0.36ab | 6.82a | 0.50ab |
| | Unburned | 6.18a | 62.54b | 11.49a | 0.52ab | 5.33a | 0.98a |
| Change in counts[3] | Cut-to-length | | | | | | |
| | Burned | +2.62a | +20.33a | +3.40a | +0.34a | +3.26a | +0.44a |
| | Unburned | +1.26a | +23.67a | +1.79ab | –0.05a | +4.69a | +0.06ab |
| | Whole-tree | | | | | | |
| | Burned | +1.57a | +13.00a | +1.83ab | +0.12a | +1.55a | +0.16ab |
| | Unburned | +0.52a | – | +0.48ab | –0.01a | – | 0.00ab |
| | Unthinned | | | | | | |
| | Burned | –1.31a | –19.50a | –1.69b | –0.21a | –4.06b | –0.30b |
| | Unburned | +1.73a | +20.25a | +0.86ab | –0.01a | +1.27a | –0.11ab |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test; each mean is based on values from five or fewer plots ($n \leq 5$) depending on the presence of trees of the pertinent species within individual plots.
[2]When not associated with a mean, "–" indicates an absence of trees within treatment combination.
[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in counts.

**TABLE 4** Pitch Tube Prevalence by DBH Class in Terms of Counts per Tree in a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1,2]

| Inventory | Thinning and burning treatment | Class 1 | | Class 2 | | Class 3 | | Class 4 | | Class 5 | | Class 6 | | Class 7 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir |
| Initial | Cut-to-length | | | | | | | | | | | | | | |
| | Burned | 0.36a | 4.00 | 0.72a | 18.00a | 1.17a | 11.00a | 5.07a | 5.50b | 6.13a | 23.50a | 9.50a | 8.00 | – | – |
| | Unburned | 0.85a | 0.00 | 0.94a | – | 0.96a | – | 2.35a | 0.00b | 15.95a | – | 0.79a | – | 0.50a | – |
| | Whole-tree | | | | | | | | | | | | | | |
| | Burned | 0.27a | 4.00 | 2.57a | 7.00a | 9.96a | – | 3.90a | – | 2.95a | – | 12.38a | – | 53.50a | – |
| | Unburned | 0.07a | – | 0.52a | – | 7.00a | – | 0.00a | – | 1.50a | – | 5.62a | – | 4.75a | – |
| | Unthinned | | | | | | | | | | | | | | |
| | Burned | 0.00a | – | 1.58a | – | 2.53a | – | 5.47a | 111.50a | 9.35a | – | 40.00a | – | 9.00a | – |
| | Unburned | 0.00a | – | 1.39a | 36.00a | 3.75a | 18.00a | 6.37a | 56.50ab | 7.01a | 54.25a | 7.33a | 96.00 | – | 67.00 |
| Final | Cut-to-length | | | | | | | | | | | | | | |
| | Burned | 0.69ab | – | 2.23a | 24.00a | 5.55a | 27.00 | 16.13a | 38.00a | 8.27a | 66.00a | 16.50a | – | 13.00a | 51.00 |
| | Unburned | 0.60ab | 8.00 | 1.50ab | 14.00a | 1.75a | – | 2.00a | – | 4.57a | 49.00a | 8.85a | – | 2.25c | – |
| | Whole-tree | | | | | | | | | | | | | | |
| | Burned | 0.42ab | – | 2.61a | 16.00a | 5.03a | 21.00 | 6.67a | – | 9.27a | – | 6.20a | – | 4.17bc | – |
| | Unburned | 0.00b | 1.00 | 0.00b | – | 3.50a | – | 4.33a | – | 5.00a | – | 6.75a | – | 5.25ab | – |
| | Unthinned | | | | | | | | | | | | | | |
| | Burned | 1.50a | – | 1.06ab | – | 1.61a | – | 1.92a | – | 6.26a | 92.00a | 19.69a | – | 3.00bc | – |
| | Unburned | 1.50a | – | 1.55ab | 41.00a | 3.01a | – | 2.47a | 66.00a | 15.14a | 68.13a | 9.00a | 59.50 | – | – |
| Change in counts[3] | Cut-to-length | | | | | | | | | | | | | | |
| | Burned | +0.33ab | – | +1.51a | +6.00a | +4.38a | +16.00 | +11.06a | +32.50 | +2.14ab | +42.50a | +7.00a | – | – | – |
| | Unburned | –0.25b | +8.00 | +0.56a | – | +0.79a | – | –0.35ab | – | –11.38b | – | +8.06a | – | +1.75a | – |
| | Whole-tree | | | | | | | | | | | | | | |
| | Burned | +0.15ab | – | +0.04a | +9.00a | –4.93a | – | +2.77ab | – | +6.32ab | – | –6.18a | – | –49.33a | – |
| | Unburned | –0.07b | – | –0.52a | – | –3.50a | – | +4.33ab | – | +3.50ab | – | +1.13a | – | +0.50a | – |
| | Unthinned | | | | | | | | | | | | | | |
| | Burned | +1.50a | – | –0.52a | – | –0.92a | – | –3.55b | – | –3.09ab | – | –20.31a | – | –6.00a | – |
| | Unburned | +1.50a | – | +0.16a | +5.00a | –0.74a | – | –3.90b | +9.50 | +8.13a | +13.88a | +1.67a | –36.50 | – | – |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test; each mean is based on values from five or fewer plots ($n \leq 5$) depending on the presence of trees of the pertinent species and/or class within individual plots, and means without letters indicate that available values were insufficient to perform the LSD test.

[2]When not associated with a mean, "–" indicates an absence of trees within DBH class.

[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in counts.

**TABLE 5** Pitch Tube Prevalence by DBH Class in Terms of Counts per Unit ($m^2$) of Bole Surface Area in a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1,2]

| Inventory | Thinning and burning treatment | Class 1 | | Class 2 | | Class 3 | | Class 4 | | Class 5 | | Class 6 | | Class 7 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir |
| Initial | Cut-to-length | | | | | | | | | | | | | | |
| | Burned | 0.17a | 3.32 | 0.28a | 4.08a | 0.19a | 2.81a | 0.52a | 0.47a | 0.41a | 1.73a | 0.42a | 0.47 | – | – |
| | Unburned | 0.43a | 0.00 | 0.29a | – | 0.16a | – | 0.19a | 0.00a | 1.14a | – | 0.05a | – | 0.02a | – |
| | Whole-tree | | | | | | | | | | | | | | |
| | Burned | 0.17a | 1.56 | 0.54a | 2.20a | 1.23a | – | 0.48a | – | 0.18a | – | 0.60a | – | 4.28a | – |
| | Unburned | 0.04a | – | 0.14a | – | 1.08a | – | 0.00a | – | 0.09a | – | 0.29a | – | 0.19a | – |
| | Unthinned | | | | | | | | | | | | | | |
| | Burned | 0.00a | – | 0.57a | – | 0.38a | – | 0.52a | 10.88a | 0.64a | – | 2.86a | – | 0.37a | – |
| | Unburned | 0.00a | – | 0.37a | 11.94a | 0.54a | 2.62a | 0.67a | 5.38a | 0.49a | 4.19a | 0.39a | 4.99 | – | 2.57 |
| Final | Cut-to-length | | | | | | | | | | | | | | |
| | Burned | 0.35ab | – | 0.51ab | 8.31a | 0.88a | 7.34 | 1.26a | 3.97a | 0.61ab | 4.06a | 0.80a | – | 0.43a | 2.33 |
| | Unburned | 0.47ab | 6.64 | 0.35abc | 4.10a | 0.25a | – | 0.15b | – | 0.29b | 3.33a | 0.44a | – | 0.08b | – |
| | Whole-tree | | | | | | | | | | | | | | |
| | Burned | 0.34ab | – | 0.64a | 3.65a | 0.65a | 3.21 | 0.57ab | – | 0.58ab | – | 0.30a | – | 0.18ab | – |
| | Unburned | 0.00b | 0.93 | 0.00c | – | 0.47a | – | 0.38ab | – | 0.29b | – | 0.30a | – | 0.18ab | – |
| | Unthinned | | | | | | | | | | | | | | |
| | Burned | 1.03a | – | 0.26bc | – | 0.22a | – | 0.17b | – | 0.43ab | 6.82a | 1.02a | – | 0.11ab | – |
| | Unburned | 0.90a | – | 0.34abc | 11.09a | 0.36a | – | 0.24ab | 6.30a | 1.10a | 4.72a | 0.48a | 3.53 | – | – |
| Change in counts[3] | Cut-to-length | | | | | | | | | | | | | | |
| | Burned | +0.18ab | – | +0.23a | +4.23a | +0.69a | +4.53 | +0.74a | +3.50 | +0.20ab | +2.33a | +0.38a | – | – | – |
| | Unburned | –0.04b | +6.64 | –0.06a | – | +0.09a | – | –0.04ab | – | –0.85b | – | +0.39a | – | +0.06a | – |
| | Whole-tree | | | | | | | | | | | | | | |
| | Burned | +0.17ab | – | +0.10a | +1.45a | –0.58a | – | –0.09ab | – | +0.40ab | – | –0.30a | – | –4.10a | – |
| | Unburned | –0.04b | – | –0.14a | – | –0.61a | – | +0.38ab | – | +0.20ab | – | +0.01a | – | –0.01a | – |
| | Unthinned | | | | | | | | | | | | | | |
| | Burned | +1.03a | – | –0.31a | – | –0.16a | – | –0.35b | – | –0.21ab | – | –1.84a | – | –0.26a | – |
| | Unburned | +0.90ab | – | –0.03a | –0.85a | –0.18a | – | –0.43b | +0.92 | +0.61a | +0.53a | +0.09a | –1.46 | – | – |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test; each mean is based on values from five or fewer plots ($n \leq 5$) depending on the presence of trees of the pertinent species and/or class within individual plots, and means without letters indicate that available values were insufficient to perform the LSD test.
[2]When not associated with a mean, "–" indicates an absence of trees within DBH class.
[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in counts.

**TABLE 6** Pitch Tube Prevalence by LCP Class in Terms of Counts per Tree in a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1,2]

| Inventory | Thinning and burning treatment | Class 1 | | Class 2 | | Class 3 | | Class 4 | | Class 5 | | Class 6 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir |
| Initial | Cut-to-length | | | | | | | | | | | | |
| | Burned | 3.00a | 11.17b | 0.00a | – | 0.55b | – | 1.64a | 4.00 | 3.33ab | 13.00 | 0.00a | 11.37b |
| | Unburned | 2.75a | – | 0.00a | – | 0.33b | – | 5.57a | – | 1.23b | – | – | 0.00b |
| | Whole-tree | | | | | | | | | | | | |
| | Burned | 15.17a | – | 0.08a | – | 0.91b | – | 3.33a | – | 2.00ab | 5.50 | 1.00a | – |
| | Unburned | – | – | 0.00a | – | 1.27b | – | 3.98a | – | 4.85ab | – | 7.00a | – |
| | Unthinned | | | | | | | | | | | | |
| | Burned | – | – | – | – | 2.00b | – | 4.73a | – | 7.34a | – | 6.00a | 111.50a |
| | Unburned | 0.00a | 81.50a | – | – | 6.50a | – | 3.64a | 34.00 | 5.11ab | 86.00 | 1.56a | 36.06b |
| Final | Cut-to-length | | | | | | | | | | | | |
| | Burned | 4.34a | – | 2.25a | – | 3.72a | 28.00 | 5.74a | 66.00 | 5.88a | 29.00bc | – | 39.00a |
| | Unburned | – | – | 0.00a | – | 4.16a | – | 5.40a | 8.00 | 0.67a | 31.50bc | – | – |
| | Whole-tree | | | | | | | | | | | | |
| | Burned | 1.52a | – | 5.50a | – | 5.23a | – | 4.43a | 18.50 | 6.50a | – | – | – |
| | Unburned | – | – | – | – | 4.67a | – | 3.23a | – | 4.80a | 1.00c | – | – |
| | Unthinned | | | | | | | | | | | | |
| | Burned | 7.00a | – | – | – | 6.06a | – | 3.87a | – | 1.89a | 92.00a | 1.00 | – |
| | Unburned | – | 84.50 | – | – | 4.75a | – | 7.12a | 80.00 | 6.73a | 53.80ab | – | 58.67a |
| Change in counts[3] | Cut-to-length | | | | | | | | | | | | |
| | Burned | +1.34a | – | +2.25a | – | +3.17a | – | +4.10a | +62.00 | +2.55a | +16.00 | – | +27.63a |
| | Unburned | – | – | 0.00a | – | +3.83a | – | –0.17a | – | –0.56ab | – | – | – |
| | Whole-tree | | | | | | | | | | | | |
| | Burned | –13.65a | – | +5.42a | – | +4.32a | – | +1.10a | – | +4.50a | – | – | – |
| | Unburned | – | – | – | – | +3.40a | – | –0.75a | – | –0.05a | – | – | – |
| | Unthinned | | | | | | | | | | | | |
| | Burned | – | – | – | – | +4.06a | – | –0.86a | – | –5.45b | – | –5.00 | – |
| | Unburned | – | +3.00 | – | – | +1.75a | – | +3.48a | +46.00 | +1.62a | –32.20 | – | +22.61a |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test; each mean is based on values from five or fewer plots ($n \leq 5$) depending on the presence of trees of the pertinent species and/or class within individual plots, and means without letters indicate that available values were insufficient to perform the LSD test.
[2]When not associated with a mean, "–" indicates an absence of trees within LCP class.
[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in counts.

**TABLE 7** Pitch Tube Prevalence by LCP Class in Terms of Counts per Unit ($m^2$) of Bole Surface Area in a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1,2]

| Inventory | Thinning and burning treatment | Class 1 | | Class 2 | | Class 3 | | Class 4 | | Class 5 | | Class 6 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir | Jeffrey pine | White fir |
| Initial | Cut-to-length | | | | | | | | | | | | |
| | Burned | 1.04a | 1.20a | 0.00a | – | 0.19b | – | 0.19a | 3.32 | 0.52a | 4.20 | 0.00a | 2.40b |
| | Unburned | 1.18a | – | 0.00a | – | 0.08b | – | 0.56a | – | 0.26a | – | – | 0.00b |
| | Whole-tree | | | | | | | | | | | | |
| | Burned | 2.37a | – | 0.08a | – | 0.17b | – | 0.25a | – | 0.15a | 1.88 | 0.10a | – |
| | Unburned | – | – | 0.00a | – | 0.11b | – | 0.30a | – | 0.39a | – | 0.80a | – |
| | Unthinned | | | | | | | | | | | | |
| | Burned | – | – | – | – | 0.15b | – | 0.50a | – | 0.63a | – | 0.47a | 10.88a |
| | Unburned | 0.00a | 3.78a | – | – | 1.41a | – | 0.44a | 2.34 | 0.57a | 7.63 | 0.27a | 4.51ab |
| Final | Cut-to-length | | | | | | | | | | | | |
| | Burned | 0.59a | – | 1.41a | – | 0.62a | 12.12 | 0.64a | 4.06 | 0.33b | 4.24ab | – | 4.83a |
| | Unburned | – | – | 0.00a | – | 0.26a | – | 0.42ab | 6.65 | 0.14b | 3.72ab | – | – |
| | Whole-tree | | | | | | | | | | | | |
| | Burned | 0.48a | – | 1.12a | – | 0.52a | – | 0.37ab | 3.43 | 1.30a | – | – | – |
| | Unburned | – | – | – | – | 0.22a | – | 0.22b | – | 0.26b | 0.93b | – | – |
| | Unthinned | | | | | | | | | | | | |
| | Burned | 1.00a | – | – | – | 0.39a | – | 0.28ab | – | 0.25b | 6.82a | 0.42 | – |
| | Unburned | – | 5.57 | – | – | 0.45a | – | 0.56ab | 5.63 | 0.53ab | 4.06ab | – | 7.41a |
| Change in counts[3] | Cut-to-length | | | | | | | | | | | | |
| | Burned | –0.45a | – | +1.41a | – | +0.43a | – | +0.45a | +0.74 | –0.19b | +0.04 | – | +2.43a |
| | Unburned | – | – | 0.00a | – | +0.18ab | – | –0.14b | – | –0.12b | – | – | – |
| | Whole-tree | | | | | | | | | | | | |
| | Burned | –1.89a | – | +1.04a | – | +0.35a | – | +0.12ab | – | +1.15a | – | – | – |
| | Unburned | – | – | – | – | +0.11ab | – | –0.08ab | – | –0.13b | – | – | – |
| | Unthinned | | | | | | | | | | | | |
| | Burned | – | – | – | – | +0.24a | – | –0.22b | – | –0.38b | – | –0.05 | – |
| | Unburned | – | +1.79 | – | – | –0.96b | – | +0.12ab | +3.29 | –0.04b | –3.57 | – | +2.90a |

[1]Within each table component, means sharing a common letter do not differ significantly at $\alpha = .05$ according to the LSD test; each mean is based on values from five or fewer plots ($n \leq 5$) depending on the presence of trees of the pertinent species and/or class within individual plots, and means without letters indicate that available values were insufficient to perform the LSD test.
[2]When not associated with a mean, "–" indicates an absence of trees within LCP class.
[3]Means preceded by "+" indicate increases while those preceded by "–" indicate reductions in counts.

**TABLE 8** Significant Simple Linear Regression Models Relating Pitch Tube Prevalence to Mensurational, Stand Density, and Biomass Variables in a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1]

| Independent variable | Dependent variable | Correlation | Model *F* test *p*-value | Model $r^2$ |
|---|---|---|---|---|
| Tree dimensions subset: | | | | |
| Height, initial | Jeffrey pine LCP class 6 pitch tube count per tree, initial | Positive | .0131 | .6087 |
| Height, initial | Jeffrey pine LCP class 6 pitch tube count per $m^2$, initial | Positive | .0471 | .4524 |
| Height, initial | White fir pitch tube count per tree, initial | Positive | .0434 | .3799 |
| Height, final | Jeffrey pine pitch tube count per tree, final | Positive | .0376 | .1454 |
| Height, final | Jeffrey pine DBH class 4 pitch tube count per tree, final | Negative | .0241 | .2023 |
| Height, final | Jeffrey pine DBH class 4 pitch tube count per $m^2$, final | Negative | .0219 | .2082 |
| Height, final | Jeffrey pine LCP class 3 pitch tube count per tree, final | Positive | .0455 | .1353 |
| DBH, initial | Jeffrey pine LCP class 6 pitch tube count per tree, initial | Positive | .0233 | .5442 |
| DBH, initial | White fir pitch tube count per tree, initial | Positive | .0146 | .5023 |
| DBH, final | Jeffrey pine DBH class 4 pitch tube count per tree, final | Negative | .0396 | .1715 |
| DBH, final | Jeffrey pine DBH class 4 pitch tube count per $m^2$, final | Negative | .0458 | .1624 |
| Live crown length, initial | Combined pitch tube count per tree, initial | Positive | .0461 | .1346 |
| Live crown length, initial | Jeffrey pine pitch tube count per tree, initial | Positive | .0239 | .1694 |
| Live crown length, initial | Jeffrey pine LCP class 3 pitch tube count per tree, initial | Positive | .0238 | .2529 |
| Live crown length, initial | White fir pitch tube count per tree, initial | Positive | .0125 | .5180 |
| Live crown length, final | Jeffrey pine DBH class 3 pitch tube count per tree, final | Negative | .0115 | .2379 |
| Live crown length, final | Jeffrey pine DBH class 3 pitch tube count per $m^2$, final | Negative | .0149 | .2229 |
| Live crown length, final | Jeffrey pine DBH class 4 pitch tube count per tree, final | Negative | .0284 | .1921 |
| Live crown length, final | Jeffrey pine DBH class 4 pitch tube count per $m^2$, final | Negative | .0258 | .1981 |
| Live crown percentage, initial | Jeffrey pine LCP class 3 pitch tube count per tree, initial | Positive | .0282 | .2404 |
| Live crown percentage, initial | White fir pitch tube count per tree, initial | Positive | .0435 | .3798 |
| Live crown percentage, initial | White fir pitch tube count per $m^2$, initial | Positive | .0473 | .3694 |
| Live crown percentage, final | Jeffrey pine pitch tube count per $m^2$, final | Negative | .0073 | .2301 |
| Live crown percentage, final | Jeffrey pine DBH class 2 pitch tube count per tree, final | Negative | .0318 | .1929 |
| Live crown percentage, final | Jeffrey pine DBH class 3 pitch tube count per tree, final | Negative | .0036 | .3020 |
| Live crown percentage, final | Jeffrey pine DBH class 3 pitch tube count per $m^2$, final | Negative | .0057 | .2773 |
| Live crown percentage, final | Jeffrey pine LCP class 3 pitch tube count per $m^2$, final | Negative | .0098 | .2154 |
| Live crown percentage, final | Jeffrey pine LCP class 4 pitch tube count per $m^2$, final | Negative | .0379 | .1450 |
| Stand density subset: | | | | |
| Basal area, initial | Jeffrey pine DBH class 1 pitch tube count per tree, initial | Positive | .0378 | .1743 |
| Basal area, initial | Jeffrey pine DBH class 1 pitch tube count per $m^2$, initial | Positive | .0326 | .1835 |
| Basal area, final | Combined pitch tube count per tree, final | Positive | <.0001 | .4606 |
| Basal area, final | Combined pitch tube count per $m^2$, final | Positive | .0030 | .2733 |
| Basal area, final | Jeffrey pine pitch tube count per tree, final | Positive | <.0001 | .4574 |
| Basal area, final | Jeffrey pine pitch tube count per $m^2$, final | Positive | .0204 | .1775 |
| Basal area, final | Jeffrey pine DBH class 1 pitch tube count per $m^2$, final | Positive | .0221 | .2253 |
| Basal area, final | Jeffrey pine DBH class 5 pitch tube count per tree, final | Positive | .0043 | .2830 |
| Basal area, final | Jeffrey pine DBH class 5 pitch tube count per $m^2$, final | Positive | .0130 | .2224 |
| Basal area, final | Jeffrey pine DBH class 6 pitch tube count per tree, final | Positive | .0154 | .2387 |
| Basal area, final | Jeffrey pine DBH class 6 pitch tube count per $m^2$, final | Positive | .0171 | .2323 |
| Basal area, final | Jeffrey pine LCP class 3 pitch tube count per tree, final | Positive | .0199 | .1788 |
| Basal area, final | Jeffrey pine LCP class 3 pitch tube count per $m^2$, final | Positive | .0392 | .1432 |
| Basal area, final | Jeffrey pine LCP class 4 pitch tube count per tree, final | Positive | .0011 | .3214 |
| Tree count, final | Combined pitch tube count per $m^2$, final | Positive | .0019 | .2968 |
| Tree count, final | Jeffrey pine pitch tube count per $m^2$, final | Positive | .0077 | .2278 |
| Tree count, final | Jeffrey pine DBH class 1 pitch tube count per tree, final | Positive | .0098 | .2778 |

**TABLE 8** (*Continued*)

| Independent variable | Dependent variable | Correlation | Model *F* test *p*-value | Model $r^2$ |
|---|---|---|---|---|
| Tree count, final | Jeffrey pine DBH class 1 pitch tube count per $m^2$, final | Positive | .0401 | .1857 |
| Tree count, final | Jeffrey pine DBH class 4 pitch tube count per tree, final | Positive | .0313 | .1861 |
| Tree count, final | Jeffrey pine DBH class 4 pitch tube count per $m^2$, final | Positive | .0411 | .1691 |
| Tree count, final | Jeffrey pine DBH class 5 pitch tube count per tree, final | Positive | .0121 | .2266 |
| Tree count, final | Jeffrey pine DBH class 5 pitch tube count per $m^2$, final | Positive | .0282 | .1783 |
| Tree count, final | Jeffrey pine LCP class 3 pitch tube count per $m^2$, final | Positive | .0032 | .2711 |
| Stand biomass subset: | | | | |
| Jeffrey pine total biomass, initial | Jeffrey pine DBH class 1 pitch tube count per tree, initial | Positive | .0176 | .2214 |
| Jeffrey pine total biomass, initial | Jeffrey pine DBH class 1 pitch tube count per $m^2$, initial | Positive | .0144 | .2334 |
| Jeffrey pine total biomass, initial | Jeffrey pine LCP class 6 pitch tube count per tree, initial | Positive | .0352 | .4923 |
| Combined total biomass, initial | Jeffrey pine LCP class 6 pitch tube count per tree, initial | Positive | .0241 | .5400 |
| Combined total biomass, initial | Jeffrey pine LCP class 6 pitch tube count per $m^2$, initial | Positive | .0362 | .4883 |
| White fir total biomass, initial | Combined pitch tube count per tree, initial | Positive | <.0001 | .4359 |
| White fir total biomass, initial | Combined pitch tube count per $m^2$, initial | Positive | .0002 | .3860 |
| Jeffrey pine total biomass, final | Jeffrey pine pitch tube count per tree, final | Positive | .0206 | .1771 |
| Jeffrey pine total biomass, final | Jeffrey pine DBH class 1 pitch tube count per $m^2$, final | Positive | .0494 | .1715 |
| Jeffrey pine total biomass, final | Jeffrey pine DBH class 4 pitch tube count per tree, final | Negative | .0418 | .1681 |
| Jeffrey pine total biomass, final | Jeffrey pine DBH class 4 pitch tube count per $m^2$, final | Negative | .0344 | .1803 |
| Jeffrey pine total biomass, final | Jeffrey pine DBH class 6 pitch tube count per tree, final | Positive | .0036 | .3258 |
| Jeffrey pine total biomass, final | Jeffrey pine DBH class 6 pitch tube count per $m^2$, final | Positive | .0077 | .2808 |
| Combined total biomass, final | Jeffrey pine pitch tube count per tree, final | Positive | <.0001 | .4971 |
| Combined total biomass, final | Jeffrey pine DBH class 5 pitch tube count per tree, final | Positive | .0084 | .2469 |
| Combined total biomass, final | Jeffrey pine DBH class 5 pitch tube count per $m^2$, final | Positive | .0256 | .1839 |
| Combined total biomass, final | Jeffrey pine LCP class 3 pitch tube count per tree, final | Positive | .0175 | .1854 |
| Combined total biomass, final | Jeffrey pine LCP class 4 pitch tube count per tree, final | Positive | .0002 | .3975 |
| White fir total biomass, final | Combined pitch tube count per tree, final | Positive | <.0001 | .7746 |
| White fir total biomass, final | Combined pitch tube count per $m^2$, final | Positive | <.0001 | .8186 |
| White fir total biomass, final | White fir DBH class 2 pitch tube count per tree, final | Positive | .0126 | .9061 |
| Combined total biomass, final | Combined pitch tube count per tree, final | Positive | <.0001 | .5182 |
| Combined total biomass, final | Combined pitch tube count per $m^2$, final | Positive | .0034 | .2675 |

[1]Each model is based on values from 30 or fewer plots ($n \leq 30$) depending on the presence of trees of the pertinent species and/or class within individual plots.

**TABLE 9** Significant Simple Linear Regression Models Relating Tree Mortality to Pitch Tube Prevalence in a Pure, Uneven-Aged Jeffrey Pine Stand as Influenced by Mechanized Thinning and Prescription Fire[1]

| Independent variable | Dependent variable | Correlation | Model $F$ test $p$-value | Model $r^2$ |
|---|---|---|---|---|
| Initial inventory subset: | | | | |
| Jeffrey pine pitch tube count per $m^2$, initial | Dead tree count, initial | Positive | .0474 | .1331 |
| Jeffrey pine pitch tube count per $m^2$, initial | Dead tree percentage, initial | Positive | .0216 | .1746 |
| Jeffrey pine DBH class 2 pitch tube count per tree, initial | Dead tree count, initial | Positive | .0002 | .4220 |
| Jeffrey pine DBH class 2 pitch tube count per tree, initial | Dead tree percentage, initial | Positive | <.0001 | .4961 |
| Jeffrey pine DBH class 2 pitch tube count per $m^2$, initial | Dead tree count, initial | Positive | .0071 | .2558 |
| Jeffrey pine DBH class 2 pitch tube count per $m^2$, initial | Dead tree percentage, initial | Positive | .0034 | .2946 |
| Jeffrey pine DBH class 3 pitch tube count per tree, initial | Dead tree count, initial | Positive | .0026 | .3193 |
| Jeffrey pine DBH class 3 pitch tube count per tree, initial | Dead tree percentage, initial | Positive | .0004 | .4103 |
| Jeffrey pine DBH class 3 pitch tube count per $m^2$, initial | Dead tree count, initial | Positive | .0076 | .2613 |
| Jeffrey pine DBH class 3 pitch tube count per $m^2$, initial | Dead tree percentage, initial | Positive | .0017 | .3435 |
| Jeffrey pine DBH class 4 pitch tube count per tree, initial | Dead tree count, initial | Positive | .0214 | .1941 |
| Jeffrey pine DBH class 4 pitch tube count per $m^2$, initial | Dead tree count, initial | Positive | .0047 | .2781 |
| Jeffrey pine DBH class 4 pitch tube count per $m^2$, initial | Dead tree percentage, initial | Positive | .0136 | .2198 |
| Jeffrey pine DBH class 7 pitch tube count per tree, initial | Dead tree count, initial | Positive | .0001 | .8548 |
| Jeffrey pine DBH class 7 pitch tube count per tree, initial | Dead tree percentage, initial | Positive | <.0001 | .9319 |
| Jeffrey pine DBH class 7 pitch tube count per $m^2$, initial | Dead tree count, initial | Positive | <.0001 | .8763 |
| Jeffrey pine DBH class 7 pitch tube count per $m^2$, initial | Dead tree percentage, initial | Positive | <.0001 | .9495 |
| Jeffrey pine LCP class 1 pitch tube count per tree, initial | Dead tree count, initial | Positive | .0107 | .6892 |
| Jeffrey pine LCP class 1 pitch tube count per tree, initial | Dead tree percentage, initial | Positive | .0010 | .8533 |
| Jeffrey pine LCP class 1 pitch tube count per $m^2$, initial | Dead tree count, initial | Positive | .0080 | .7170 |
| Jeffrey pine LCP class 1 pitch tube count per $m^2$, initial | Dead tree percentage, initial | Positive | .0074 | .7242 |
| White fir DBH class 2 pitch tube count per tree, initial | Dead tree percentage, initial | Positive | .0374 | .9265 |
| Combined pitch tube count per $m^2$, initial | Dead tree percentage, initial | Positive | .0191 | .1810 |
| Final inventory subset: | | | | |
| Jeffrey pine pitch tube count per tree, final | Dead tree count, final | Positive | .0164 | .1890 |
| Jeffrey pine pitch tube count per $m^2$, final | Dead tree count, final | Positive | .0006 | .3452 |
| Jeffrey pine pitch tube count per $m^2$, final | Dead tree percentage, final | Positive | .0032 | .2714 |
| Jeffrey pine DBH class 3 pitch tube count per tree, final | Dead tree count, final | Positive | .0005 | .4065 |
| Jeffrey pine DBH class 3 pitch tube count per tree, final | Dead tree percentage, final | Positive | <.0001 | .5930 |
| Jeffrey pine DBH class 3 pitch tube count per $m^2$, final | Dead tree count, final | Positive | .0013 | .3575 |
| Jeffrey pine DBH class 3 pitch tube count per $m^2$, final | Dead tree percentage, final | Positive | <.0001 | .5897 |
| Jeffrey pine DBH class 5 pitch tube count per tree, final | Dead tree count, final | Positive | .0264 | .1822 |
| Jeffrey pine DBH class 5 pitch tube count per $m^2$, final | Dead tree count, final | Positive | .0291 | .1765 |
| Jeffrey pine LCP class 3 pitch tube count per tree, final | Dead tree count, final | Positive | .0206 | .1770 |
| Jeffrey pine LCP class 3 pitch tube count per $m^2$, final | Dead tree count, final | Positive | .0048 | .2515 |
| Jeffrey pine LCP class 3 pitch tube count per $m^2$, final | Dead tree percentage, final | Positive | .0335 | .1515 |
| Jeffrey pine LCP class 4 pitch tube count per tree, final | Dead tree count, final | Positive | .0135 | .1988 |
| Jeffrey pine LCP class 4 pitch tube count per tree, final | Dead tree percentage, final | Positive | .0224 | .1727 |
| Jeffrey pine LCP class 4 pitch tube count per $m^2$, final | Dead tree count, final | Positive | .0024 | .2853 |
| Jeffrey pine LCP class 4 pitch tube count per $m^2$, final | Dead tree percentage, final | Positive | .0012 | .3170 |
| Combined pitch tube count per $m^2$, final | Dead tree count, final | Positive | .0416 | .1400 |

[1]Each model is based on values from 30 or fewer plots ($n \leq 30$) depending on the presence of trees of the pertinent species and/or class within individual plots.

## OVERALL CONCLUSIONS

Thinning and burning treatments increasingly utilized in forest restoration efforts in the western USA were evaluated for their long-term influences on individual tree and stand level growth measures as well as bark beetle prevalence in pure, uneven-aged Jeffrey pine with a minor stand component of white fir. Concerning their effects on tree growth, individual trees in the stand subunit subjected to whole-tree thinning exhibited the greatest evidence of a subsequent stimulatory effect apparent in both dimension and volume measures, although it was largely confined to the unburned portion. However, at the stand level, a diminished volume growth response occurred in the whole-tree subunit, especially in the burned portion, mostly attributable to exaggerated stocking losses, while a superior response in the unburned portion of a subunit in which cut-to-length thinning was implemented likely reflected not only the absence of detrimental fire impacts but also benefits of on-site slash retention. Regarding stand level biomass, diminished growth in the whole-tree subunit was again evident, with that in the burned portion again most pronounced, while biomass accrual in the unburned cut-to-length treatment combination was generally comparable to that in the unthinned control. As for bark beetle demography, the Jeffrey pine beetle exhibited some preference for larger pine before either the thinning or fire treatments were implemented, but their proclivity regarding pretreatment stand density was unclear with some evidence for both higher and lower densities. Approximately one decade after treatment implementation, however, they demonstrated a consistent preference for higher density. There were multiple indications that the burning of the slash mats generated in the cut-to-length thinning treatment induced a marked increase in the Jeffrey pine beetle population, possibly due to the stress exerted on host trees by elevated heat loads that culminated in compromised defense mechanisms. There was also some evidence that the treatment combination most resistant to bark beetle attack in Jeffrey pine was that entailing whole-tree thinning without subsequent underburning, an outcome possibly related to the higher posttreatment vigor of the stems in this combination as demonstrated through their superior growth.  A linkage was established between tree mortality and higher beetle infestation as measured through pitch tube counts, but it was also apparent that all mortality was not attributable solely to beetle activity.  At both the pretreatment and posttreatment inventories, pitch tube abundance on white fir greatly exceeded that on Jeffrey pine, probably in part a reflection of the stress induced by its poor adaption to the study site.  Nevertheless, results here suggest that the greatest influence on the fir engraver population both before and after treatment implementation was the prevalence of the host species.

Collectively, these studies indicate that the long-term cumulative effects of stress from thinning and underburning implemented in concert may inadvertently lead to abated growth and increased susceptibility to bark beetle attacks in dry site forest types regardless of the thinning approach utilized.  Thus, these practices may diminish forest health and potentially elevate the risk of wildfire for at least a decade following treatment implementation.  Given that Jeffrey pine forests of the eastern Sierra Nevada are considered outside of their historical range of variability concerning structural attributes and fuels accumulations, one-time treatments may not be sufficient to reestablish natural successional patterns and restore historic stand characteristics. Therefore, subsequent maintenance treatments, perhaps most especially underburning, may be required to fully achieve the goal of restoration, as mortality and stem damage would likely diminish with repeated management entries.