Forest Ecology and Management 306 (2013) 61–67

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Full length article

Prescribed fire and mechanical thinning effects on bark beetle caused tree mortality in a mid-elevation Sierran mixed-conifer forest

Daniel T. Stark [a], David L. Wood [a], Andrew J. Storer [b], Scott L. Stephens [a,*]

[a] Department of Environmental Science, Policy, and Management, Division of Ecosystem Science, University of California, 130 Mulford Hall, Berkeley, CA 94720, USA
[b] School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931-1295, USA

ARTICLE INFO

Article history:
Received 7 March 2013
Received in revised form 4 June 2013
Accepted 10 June 2013
Available online 17 July 2013

Keywords:
Dendroctonus brevicomis
D. ponderosae
Scolytus ventralis
Bark beetles
Second order fire effects
Fire surrogates

ABSTRACT

We assessed tree mortality caused by bark beetles in a mixed-conifer forest in the central Sierra Nevada in response to fire and mechanical treatments. The treatments were: (1) no treatment, (2) prescribed fire, (3) mechanical (crown thinning-from-below followed by rotary mastication), and (4) mechanical followed by prescribed fire. Ponderosa pine (*Pinus ponderosa* Laws) mortality caused by the western pine beetle (*Dendroctonus brevicomis* LeConte), sugar pine (*Pinus lambertiana* Dougl.) mortality caused by mountain pine beetle (*D. ponderosae* Hopkins), and white fir (*Abies concolor* Gord. and Glend) mortality caused by the fir engraver beetle (*Scolytus ventralis* LeConte) was assessed pre-treatments, one-year post-treatments, and three years post-treatments. For the duration of the study, bark beetle caused mortality across all treatments for each tree species was less than 7%. Bark beetle-caused mortality of small and medium white firs increased in treatments that included fire, and bark beetle-caused mortality of medium size sugar pines was elevated in the fire only treatment compared with other treatments. Our results indicate that mechanical treatments cause little risk of mortality to residual trees from bark beetles in the short term. The higher secondary mortality in the small and medium size white firs in both fire treatments can be considered a benefit in overly dense mixed conifer forests where the understory is dominated by shade-tolerant white firs.

1. Introduction

Since the beginning of the 20th century, the suppression and intended control of fire has been at the forefront of U.S. forest management and forest policy (Biswell, 1989; Agee, 1993; Stephens and Ruth, 2005). Fire suppression has been justified over the years for many reasons other than preventing loss of human lives and structures, including protecting valuable timber resources (Show and Kotok, 1924; Show, 1926), and general aesthetic values (Berry and Hesseln, 2004). It has only been since the mid-1990s that U.S. Forest Service policy recognized fire as an important ecological process that is a critical component of forest dynamics (Stephens and Ruth, 2005). Likewise, bark beetles have been a challenge to forest managers since the importance of forest protection was recognized by federal and private owners in the western U.S. (Craighead et al., 1931), and they often affect larger areas than fire (Raffa et al., 2008). Forest insects are now commonly recognized by forest managers as an integral part of forest ecosystems (Barker, 2003; Wood and Storer, 2002; Wood and Storer, 2009).

American Indians such as the Nisenan community of the western Sierra Nevada (Kroeber, 1925, 1929; Matson, 1972) have been using fire as a management tool for nearly 2000 years prior to the arrival of European-American settlers (Cook, 1976; as in Stephens and Collins, 2004). Historically, these human-ignited, frequent, low- to moderate-intensity burning patterns, together with lightening ignited, varying intensity wildfires, created a mosaic of forest stand structures (Anderson and Moratto, 1996; Husari and McKelvey, 1996; Collins et al., 2011). As land use patterns changed, so did forest stand structure. Beginning in 1905, Euro-American-based management practices attempted to keep fire out of forests at all costs (McCullough et al., 1998). These fire suppression efforts, together with forest harvesting, contributed to dense forest regrowth of smaller diameter, fire intolerant trees (Hessburg and Agee, 2003) such as white firs (*Abies concolor* Gord. and Glend). These stands were very different from the open, park-like stands that were comprised of few, large diameter, shade intolerant pines (Agee, 1993; Skinner and Chang, 1996; Agee and Skinner, 2005; North et al. 2007) that were typically produced by American Indian management practices. It follows that as the structures of these forests changed, so did the response of bark beetles; so much so that early forest entomologists ranked insect-caused damage to the second-growth forests to be as significant as the threat of fire (Barker 2003). In 1899, motivated by the threat bark beetles posed

* Corresponding author. Tel.: +1 510 642 7304.
E-mail addresses: stark@ucanr.edu (D.T. Stark), bigwood@berkeley.edu (D.L. Wood), storer@mtu.edu (A.J. Storer), sstephens@berkeley.edu (S.L. Stephens).

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.06.018

to standing timber (Barker 2003), A.D. Hopkins traveled throughout California, Oregon, Washington, and Idaho, and recorded the extensive mortality of old growth western conifers caused by bark beetles (Wood and Storer 2002).

Prescribed fire has been used for nearly a century as a tool in forest management to reduce the severity of wildland fires (Biswell 1989), and more recently in the western U.S. to reduce hazardous fuels by restoring stand structure to an idealized previous condition, or by promoting "resiliency" (Covington et al. 1997; Keifer et al. 2000; Skinner 2005; Baker et al. 2007; Abella et al. 2007; Zhang and Ritchie 2008; Stephens et al. 2010; van Mantgem et al. 2011). Mechanical treatments (e.g. thinning from below) are often used to produce similar stand structures as fire with many similar objectives, often when prescribed burning is not a feasible option (for example, due to air quality restrictions and other public health concerns, or increased risk of structure fires)(Stephens et al. 2012). Such thinning efforts have also been federally mandated to reduce hazardous fuels (Stephens and Ruth 2005). Regardless of the management option, the overall common concern is to reduce fire hazard and minimize large tree mortality in the residual stand.

Mortality from "first-order" fire effects (i.e. direct fire effects) occurs at the time of fire or immediately afterward (Reinhardt et al., 2001), and can result from crown scorch, cambial damage, and root damage (Reinhardt et al., 2001; Kobziar et al., 2006). Such effects are often manipulated and/or mitigated depending on the desired outcome of the prescribed burn management plan. However, mortality from "second order" fire effects (i.e. indirect fire effects) such as mortality from bark beetles, can be problematic as the manifestations of these effects occur over a longer period of time (Reinhardt et al., 2001). Since bark beetles are attracted to previously stressed and weakened trees (Furniss and Carolin, 1977), any management option, whether it be prescribed fire, mechanical thinning, or fire suppression, has the potential to increase bark beetle activity and subsequent mortality (Wood et al., 1985; Fettig et al., 2007; Jenkins et al., 2008; Youngblood et al., 2009).

The objective of our study was to assess this subsequent bark beetle caused mortality from prescribed fire, mechanical harvesting (crown thinning followed by thinning-from-below), and a combination of these two treatments, as part of the Fire and Fire-Surrogate Study (FFS) (McIver et al., 2009) in the central Sierra Nevada. First order fire effects from this study site are described elsewhere (Kobziar et al., 2006; Stephens and Moghaddas, 2005).

2. Methods

2.1. Study location

The study was conducted in a mixed conifer forest in the north-central Sierra Nevada at the University of California Blodgett Forest Research Station (BFRS), approximately 20 km east of Georgetown, California. Blodgett Forest is located at latitude 38°54′45″N, longitude 120°39′27″W, between 1100 and 1410 m above sea level, and encompasses an area of 1780 ha.

Tree species in the study include sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Laws), white fir (*A. concolor* Gord. and Glend), incense-cedar (*Calocedrus decurrens* [Torr.] Floren.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), California black oak (*Quercus kelloggii* Newb.), tanoak (*Notholithocarpus densiflorus* (Hook. and Arn.) Rehder), bush chinkapin (*Chrysolepis sempervirens* (Kell.) Hjelmg.), and Pacific madrone (*Arbutus menziesii* Pursh).

Tree-killing bark beetles at BFRS and their host trees include the western pine beetle (*Dendroctonus brevicomis* LeConte) on ponderosa pine, the mountain pine beetle (*D. ponderosae* Hopkins) and red turpentine beetle (*D. valens* LeConte) on sugar and ponderosa pines, the California five-spined ips (*Ips paraconfusus* Lanier) also on ponderosa and sugar pines, the fir engraver beetle (*Scolytus ventralis* LeConte) on white fir, the Douglas-fir beetle (*D. pseudotsugae* Hopkins) on Douglas-fir, and the western cedar bark beetle (*Phloeosinus punctatus* LeConte) on incense-cedar. (See Furniss and Carolin (1977) and Wood et al. (2003) for descriptions of the biology of these species.)

Fire was a common ecosystem process in the mixed conifer forests of BFRS before the policy of fire suppression began early in the 20th century. Between 1750 and 1900, median composite fire intervals at the 9–15 ha spatial scale were 4.7 years with a fire return interval range of 4–28 years (Stephens and Collins, 2004). Forested areas at BFRS have been repeatedly harvested and subjected to fire suppression for the last 90 years reflecting a management history common to many forests in California (Laudenslayer and Darr, 1990; Stephens, 2000) and elsewhere in the Western US (Graham et al., 2004).

2.2. Treatments

The primary objective of the fuel treatments was to modify stand structure such that 80% of the dominant and co-dominant trees in the post-treatment stand would survive a wildfire modeled under 80th percentile weather conditions (Weatherspoon and McIver, 2000; McIver et al., 2009). The secondary objective was to create a stand structure that maintained or restored forest attributes and processes including, but not limited to, snag and course woody debris abundance and tree recruitment and regeneration.

Four different treatments were each randomly applied (complete randomized design) to 3 of 12 experimental units that varied in size from 14 to 29 ha. Total area for the 12 experimental units was 225 hectares. The four treatments were (1) no treatment (CONTROL); (2) prescribed fire only (FIRE); (3) mechanical only (MECH) with crown thinning followed by thinning-from-below and mastication of understory conifers and hardwoods; and (4) mechanical plus fire (MECH + FIRE) using the same mechanical

Table 1
Average pre (PRE)- and post (POST)-treatment vegetation structure (standard error) for all trees greater than 2.5 cm DBH for control (CONTROL), fire only (FIRE), mechanical only (MECH) and a combination of mechanical and fire (MECH + FIRE) treatments at Blodgett Forest Research Station, California (Stephens and Moghaddas, 2005).

	CONTROL	FIRE	MECH	MECH + FIRE
Basal area (m^2 ha^{-1})				
PRE	55.1 (3.1)	49.4 (2.2)	51.9 (2.0)	55.1 (1.5)
POST	56.4^a (3.0)	47.8^a (2.5)	40.9^b (0.8)	39.3^b (2.5)
Trees ha^{-1}				
PRE	1100.9 (67.3)	850.1 (16.8)	972.0 (226.2)	823.3 (187.3)
POST	1109.5^a (84.2)	441.5^b (32.1)	428.7^b (139.7)	238.9^b (20.9)
Average quadratic mean diam. (cm)				
PRE	25.3 (0.7)	27.2 (0.5)	27.3 (3.4)	30.3 (3.2)
POST	25.5^a (0.3)	37.2^{ab} (0.5)	37.7^{ab} (5.7)	46.2^b (3.5)
Tree height (m)				
PRE	15.6 (0.8)	15.8 (0.5)	16.7 (1.1)	16.5 (1.2)
POST	15.6^a (0.7)	17.8^{ab} (0.5)	22.7^{bc} (0.9)	20.4^c (0.6)
Tree height to crown base (m)				
PRE	7.6 (0.6)	6.8 (0.4)	7.9 (0.6)	7.8 (0.8)
POST	7.5^a (0.6)	7.4^{ab} (0.3)	9.5^b (0.5)	9.5^b (0.8)
Percent canopy cover				
PRE	69 (6.0)	68 (1.0)	66 (4.0)	63 (5.0)
POST	75^a (5)	65^{ab} (3)	58^b (1)	51^b (4)

In the post-treatment (POST) evaluations, mean values in a row followed by the same letter are not significantly different ($P < 0.05$).

treatment followed by prescribed fire (Stephens and Moghaddas, 2005). Mechanical harvesting was completed late summer/early fall 2001, and prescribed burning of all fire treatments occurred in October and November 2002. To reduce edge effects, data collection was restricted to a 10 ha core area in the center of each experimental unit.

2.3. Vegetation measurements

Trees were measured within twenty 0.04 ha circular plots installed in each experimental unit (240 total plots). Individual plots were placed on a 60 m grid with a random starting point. Plot centers were permanently marked with a pipe, and three witness trees were tagged to facilitate plot relocation after treatments. Tree species, diameter at breast height (DBH) (cm), total height (m), height to live crown base (m), and crown position (dominant, codominant, intermediate, suppressed) were recorded for all trees greater than 2.5 cm DBH (Stephens and Moghaddas 2005). Pre- and post-treatment vegetation structure for all trees greater than 2.5 cm DBH were summarized (Table 1; Stephens and Moghaddas, 2005).

2.4. Bark beetle-caused mortality assessments

Categorical data for external symptoms of bark beetles were collected on all recently dead or dying conifers greater than 10 cm DBH in all of the 240 plots. For each recently dead or dying tree within the plot, the entire lower 2 m of the bole was examined for pitch masses, pitch tubes, pitch streaming, and boring dust. The portion of bole above 2 m was also observed visually from the ground when branch density was low. Bark from trees with external symptoms of infestation was removed only after the tree had red foliage (completely dead) for positive identification of beetle species by verifying the characteristic galleries resulting from infestation by adults and feeding by larvae (Furniss and Carolin, 1977). Fading stage of crown (green, infested = 1, lime green = 2, yellow = 3, red = 4, old gray = 5) as well as percent canopy was recorded. Additionally, recently dead or dying trees (fading stages 2, 3, and 4) were located in a 360° scan from each plot center in each experimental unit to capture mortality outside of the plots. To account for increased visual range in the mechanical experimental units, scan distance was limited to 30 m across all experimental units, with an expanded individual plot area of approximately 0.28 ha. The azimuth, distance from plot center (m), DBH, fading stage, and bark beetle categorical data were recorded for these scan trees. The denominator in the percent mortality is total basal area per treatment unit that was extrapolated from plot level measurements.

Pretreatment data collection (PRE) was completed in summer 2001. Post-treatment data were collected in summer 2003 (POST1) and in summer 2005 (POST2). A comprehensive mortality assessment including bark dissections was conducted in summer 2004. In this assessment, the bark was removed with a hand ax or hammer and chisel and the larval galleries were identified to species where possible. When present, adults were collected for later identification.

Table 2
Pre-treatment (PRE) (2001), one year post-treatment (POST1) (2003), and three years post-treatment (POST2) (2005) mean bark beetle-caused mortality (% (SEM)) in response to control (CONTROL), fire only (FIRE), mechanical only (MECH) and a combination of mechanical and fire (MECH + FIRE) treatments at Blodgett Forest Research Station, Georgetown, CA.

Sampling round	Species	Size category	Treatment			
			CONTROL	FIRE	MECH	MECH + FIRE
PRE	White	Small	0.02 (0.02)	0.00 (0.00)	0.01 (0.01)	0.03 (0.03)
	Fir	Medium	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.03 (0.03)
		Large	0.02 (0.03)	0.02 (0.02)	0.02 (0.02)	0.09 (0.09)
	Sugar	Small	0.00 (0.00)	0.00 (0.00)	0.13 (0.13)	0.00 (0.00)
	Pine	Medium	0.11 (0.09)	0.92 (0.75)	0.00 (0.00)	0.00 (0.00)
		Large	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	Ponderosa	Small	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.09 (0.09)
	Pine	Medium	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
		Large	0.06 (0.05)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
POST1	White	Small	0.17 (0.09) *a*	4.57 (0.86) *b*	0.02 (0.02) *a*	7.08 (0.45) *b*
	Fir	Medium	0.08 (0.04) *a*	0.81 (0.35) *b*	0.00 (0.00) *a*	0.81 (0.09) *b*
		Large	0.05 (0.05)	0.27 (0.11)	0.02 (0.02)	0.35 (0.18)
	Sugar pine	Small	0.00 (0.00)	2.90 (1.50)	0.00 (0.00)	0.36 (3.6)
	Pine	Medium	0.00 (0.00)	4.77 (3.33)	0.00 (0.00)	0.13 (0.13)
		Large	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	Ponderosa	Small	0.00 (0.00)	1.80 (0.91)	0.00 (0.00)	2.81 (2.81)
	Pine	Medium	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
		Large	0.00 (0.00)	0.11 (0.11)	0.00 (0.00)	0.34 (0.24)
POST2	White	Small	0.19 (0.11)	0.62 (0.15)	0.19 (0.01)	0.11 (0.08)
	Fir	Medium	0.07 (0.04)	0.19 (0.11)	0.00 (0.00)	0.16 (0.16)
		Large	0.11 (0.10)	0.05 (0.03)	0.03 (0.03)	0.22 (0.18)
	Sugar	Small	1.08 (1.08)	1.44 (0.75)	0.00 (0.00)	0.36 (0.36)
	Pine	Medium	0.12 (0.12) *a*	5.94 (3.44) *b*	0.00 (0.00) *a*	0.00 (0.00) *a*
		Large	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.10 (0.10)
	Ponderosa	Small	0.00 (0.00)	0.20 (0.20)	0.00 (0.00)	0.00 (0.00)
	Pine	Medium	0.00 (0.00)	0.25 (0.25)	0.00 (0.00)	0.00 (0.00)
		Large	0.03 (0.03)	0.06 (0.06)	0.00 (0.00)	0.04 (0.04)

Mean values in a row followed by the same letter are not significantly different ($P < 0.05$). Where a lower case letter does not follow means, differences between treatments for a species size class on a sampling round were not significant. Analysis of variance was performed on arcsin transformed data. Mean and standard errors presented are calculated from non-transformed data. Size category small = 11.5–25.2 cm DBH; medium = 25.3–45.5 cm DBH; and large = greater than 45.6 cm DBH.

2.5. Data analyses

Tree data from the 0.04 ha plots were compiled to produce estimates of total live basal area (m^2/ha) by species and size category (small, 11.5–25.2 cm DBH; medium, 25.3–45.5 cm DBH; and large, greater than 45.6 cm DBH) in each experimental unit. Tree mortality from the expanded 0.28 ha plots was used to produce estimates of total dead basal area (m^2/ha) by species and size category in each experimental unit. Trees that were considered killed outright by fire were removed from the dataset. To determine if trees were killed outright by fire, the following criteria were used: greater than 60% crown scorch; severe bark charring (commonly 100%); bark sloughing with either no bark beetle activity or unsuccessful colonization confirmed by dissection. We acknowledge that trees with 60% scorch may also have been attacked by bark beetles, but consider mortality of trees with this level of canopy damage to be primarily fire caused (i.e. trees would have died without bark beetle colonization).

For each sample period (PRE, POST1, and POST2), bark beetle-caused mortality (%) attributed to the western pine beetle, mountain pine beetle, and the fir engraver beetle was calculated by host species and size category for all treatment units. No mortality from the California five-spined ips, red turpentine beetle, Douglas-fir beetle, or the western cedar bark beetle was observed. Also, mortality from mountain pine beetle was not observed on ponderosa pine. Data were normalized using the arcsine square root transformation (Zar 1999), and analysis of variance (ANOVA) was used to determine the significance of differences among treatments. If significant results were detected, then Tukey's All Pairs HSD was used to distinguish significant differences between pairs of treatments. Since we were interested in the changes between treatment years, we calculated the change in mortality one year after treatments (POST1-PRE), three years after treatments (POST2-PRE), and between the third and first years after treatments (POST2-POST1). Changes in percent mortality were arcsin transformed prior to calculating changes in mortality and prior to using ANOVA to test the significance of differences between treatments. If significant changes were detected, then Tukey's All Pairs HSD was used to distinguish significant differences between pairs of treatments.

3. Results

3.1. Bark beetle-caused mortality within sample periods

In the pretreatment forest (Table 2), bark beetles appeared to be at endemic levels since bark beetle-caused mortality was uniformly low or zero across all tree species and size categories, with no significant differences among the experimental units. In the POST1 sample period (Table 2), differences among treatments were significant for small sized white fir ($F_{3,8} = 73.1$, $P < 0.0001$), and for medium sized white fir ($F_{3,8} = 15.8$, $P = 0.0010$). For both small and medium white firs, each treatment that included fire (FIRE and FIRE + MECH) resulted in significantly higher mortality than did each treatment that did not include fire (CONTROL and MECH ONLY). There were no significant differences in mortality between the FIRE and MECH + FIRE or between the CONTROL and MECH ONLY treatments in any of the size categories of white fir. No other differences among treatments were detected.

In the POST2 sample period (Table 2), bark beetle-caused mortality of medium sized sugar pines differed significantly among treatments ($F_{3,8} = 9.5$, $P = 0.0051$). Mortality of medium sized sugar pine was significantly higher in the FIRE ONLY treatments when compared to each of the other treatments. Differences among treatment for other species and sizes of sugar pine were not significant.

3.2. Bark beetle-caused mortality between sample periods

Between the PRE and POST1 sample periods, differences in the change in mortality from bark beetles among treatments were significant for both small sized white firs ($F_{3,8} = 68.9$, $P < 0.0001$) and medium sized white firs ($F_{3,8} = 13.1$, $P = 0.0019$) (Table 3). For both small and medium white firs, each treatment that included fire (FIRE and FIRE + MECH) resulted in significantly greater change in mortality than did each treatment that did not include fire (CONTROL and MECH ONLY) (Table 3). Between the PRE and POST2 sample periods, differences in the change in bark beetle-caused mortality among treatments were significant for small sized white firs ($F_{3,8} = 6.7$, $P = 0.0115$) (Table 3). The change in mortality of small white firs in the FIRE treatment was significantly higher than the MECH + FIRE and the CONTROL treatments (Table 3).

Between the POST1 and POST2 sample periods differences in the change in bark beetle-caused mortality among treatments were significant for small sized white firs ($F_{3,8} = 68.2$, $P < 0.0001$) (Table 3). Each treatment that included fire (FIRE and FIRE + MECH) resulted in significantly greater change in mortality than did each treatment that did not include fire (CONTROL and MECH) (Table 3). In some cases, mortality observed in the POST2 data collection was lower than in the POST1 data collection as indicated by the negative values (Table 3).

4. Discussion

Our results indicate that both fire and mechanical treatments resulted in minimal bark beetle-caused mortality in the residual stand when bark beetle populations are at endemic levels (Table 2), at least in the short term (three years post-treatment, 2002–2005). Overall bark beetle-caused mortality across all treatments for all trees species was below 7%. These findings are comparable to other FFS studies in western forests carried out in the Southern Cascades (Fettig et al., 2010a), and in western Montana (Six and Skov, 2009), but are higher than findings in northeastern Oregon (Youngblood et al., 2009). There have been many studies that have examined the response of bark beetles to prescribed fire (Ganz et al., 2003; McHugh et al., 2003; Breece et al., 2008; Campbell et al., 2008; Fettig et al., 2008, 2010b) and to mechanical treatments (Wood et al. 1985; Fettig et al. 2007). However, there have been very few other experimental studies, apart from those in the National FFS program, that have analyzed bark beetle caused secondary mortality in response to both prescribed fire and mechanical treatments simultaneously. Zausen et al. (2005) measured bark-beetle-caused tree mortality in response to both prescribed fire and mechanical thinning treatments, and mortality of ponderosa pine was very low in all treatments.

The greatest overall bark beetle-caused mortality across all treatments occurred in small and medium white firs in the FIRE only and MECH + FIRE treatments. These differences were significant when compared to both the MECH and CONTROL treatments in the POST1 sample period. This falls within the objectives of our study in that the density of the suppressed understory dominated by white fir was reduced, and more optimal conditions were created for shade intolerant species such as ponderosa and sugar pines (Moghaddas et al., 2008). By the POST2 sample period, mortality for white firs fell below 1%, and no differences were detected among treatments (Table 2).

Overall bark beetle-caused mortality was very low for ponderosa and sugar pines, with most of the mortality occurring in the small diameter size category (11.5–25.2 cm DBH), with the exception of medium diameter (25.3–45.5 cm DBH) sugar pines in the FIRE only treatment in the POST2 sample period (Table 2). No other

Table 3
Differences in the change in mortality (% (SEM)) from bark beetles between one year post-treatments (2003) and pre-treatments (2001)(POST1-PRE), three years post-treatments (2005) and pre-treatments (2001)(POST2-PRE), and three years post-treatments (2005) and one year post-treatments (2003)(POST2-POST1) in response to control (CONTROL), fire only (FIRE), mechanical only (MECH) and a combination of mechanical and fire (MECH + FIRE) treatments at Blodgett Forest Research Station, Georgetown, CA.

Time period	Species	Size category	Treatment			
			CONTROL	FIRE	MECH	MECH + FIRE
POST1-PRE	White	Small	0.15 (0.09) *b*	4.57 (0.86) *a*	0.01 (0.03) *b*	7.05 (0.44) *a*
	Fir	Medium	0.08 (0.04) *b*	0.81 (0.36) *a*	0.00 (0.00) *b*	0.78 (0.07) *a*
		Large	0.03 (0.03)	0.24 (0.13)	0.00 (0.04)	0.26 (0.15)
	Sugar	Small	0.00 (0.00)	2.90 (1.50)	−0.13 (0.13)	0.36 (0.36)
	Pine	Medium	−0.11 (0.11)	3.85 (4.04)	0.00 (0.00)	0.13 (0.13)
		Large	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	Ponderosa	Small	0.00 (0.00)	1.80 (0.91)	0.00 (0.00)	2.72 (2.86)
	Pine	Medium	−0.22 (0.22)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
		Large	−0.06 (0.06)	0.11 (0.11)	0.00 (0.00)	0.34 (0.24)
POST2-PRE	White	Small	0.17 (0.09) *b*	0.62 (0.15) *a*	0.19 (0.01) *ab*	0.08 (0.05) *b*
	Fir	Medium	0.07 (0.04)	0.19 (0.11)	0.00 (0.00)	0.12 (0.12)
		Large	0.09 (0.11)	0.02 (0.03)	0.01 (0.04)	0.13 (0.23)
	Sugar	Small	1.08 (1.08)	1.44 (0.75)	−0.13 (0.13)	0.36 (0.36)
	Pine	Medium	1.08 (0.01)	5.02 (3.97)	0.00 (0.00)	0.00 (0.00)
		Large	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.10 (0.10)
	Ponderosa	Small	0.00 (0.00)	0.20 (0.20)	0.00 (0.00)	−0.09 (0.09)
	Pine	Medium	−0.22 (0.22)	0.25 (0.25)	0.00 (0.00)	0.00 (0.00)
		Large	−0.04 (0.08)	0.06 (0.06)	0.00 (0.00)	0.04 (0.04)
POST2-POST1	White	Small	0.02 (0.09) *a*	−3.95 (0.80) *b*	0.17 (0.03) *a*	−6.97 (0.44) *b*
	Fir	Medium	−0.01 (0.05)	−0.62 (0.45)	0.00 (0.00)	−0.66 (0.11)
		Large	0.06 (0.13)	−0.22 (0.10)	0.00 (0.00)	−0.13 (0.17)
	Sugar	Small	1.08 (1.08)	−1.47 (0.76)	0.00 (0.00)	0.00 (0.00)
	Pine	Medium	0.12 (0.12)	1.17 (0.93)	0.00 (0.00)	−0.13 (0.13)
		Large	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.10 (0.10)
	Ponderosa	Small	0.00 (0.00)	−1.60 (0.81)	0.00 (0.00)	−2.81 (2.81)
	Pine	Medium	0.00 (0.00)	0.25 (0.25)	0.00 (0.00)	0.00 (0.00)
		Large	0.03 (0.03)	−0.15 (0.15)	0.00 (0.00)	−0.30 (0.20)

Mean values in a row followed by the same letter are not significantly different ($P < 0.05$). Where a lower case letter does not follow means, differences between treatments for a species size class on a sampling round were not significant. Negative values indicate a decrease in mortality between sample periods. Analysis of variance was performed on arcsin transformed data. Mean and standard errors presented are calculated from non-transformed data. Size category small = 11.5–25.2 cm DBH; medium = 25.3–45.5 cm DBH; and large = greater than 45.6 cm DBH.

significant differences were detected for ponderosa and sugar pines among treatments or sample periods.

Mortality in the mechanical only treatments was either extremely low (under 0.2%) or zero across all tree species. In fact, mortality in the mechanical only treatments was the same or less than in the control treatments, with few exceptions. Once again, these findings are consistent with other studies in the FFS in western forests (Fettig et al., 2010a; Six and Skov, 2009; Youngblood et al., 2009).

Considering the potential for increased risk of bark beetle infestation in the mechanical treatments (Wood et al., 1985), we were surprised by the low mortality in this treatment. Mastication of smaller diameter trees of all species in these treatment areas was carried out in the late fall 2001 and early spring 2002 post mechanical thinning, and pre-burning (October and November 2002), likely resulting in an increase in tree volatiles, such as monoterpenes, when bark beetles would be expected to be active and therefore perhaps attracted into the area (Furniss and Carolin, 1977; Wood et al., 1985; Fettig et al., 2006; Seybold et al., 2006); however our mastication prescription specified that all woody materials be processed to a maximum fuel height of 40 cm and this resulted in poor habitat for bark beetles because of relatively small woody fuel diameters that dried quickly. Fettig et al. (2006) observed increased levels of bark beetle attack following biomass chipping in either late summer or spring, but only low levels of mortality resulted. We observed higher levels of infestation by *S. ventralis* and *D. valens* across all treatments; however, only secondary mortality is reported here.

The success of any forest management plan ultimately depends on the resiliency (Holling, 1973) of the residual stand. Since trees damaged or weakened by fire are susceptible to attack by bark beetles, "second order" fire effects should be taken into consideration in any prescribed fire management plan. Likewise, the potential for increased levels of bark beetle attacks resulting from mechanical treatments should also be considered. Although mechanical treatments can be costly (but *see* Hartsough et al., 2008), our results indicate that for the short term, there appear to be fewer risks to the residual forest in the mechanical treatments from both subsequent prescribed fire and bark beetle attack when populations of bark beetles are low as was the case in this experiment.

Forest managers today are faced with a seemingly paradoxical task of protecting and restoring forests while at the same time reintroducing disturbance processes that cause mortality. While the ecological role of fire has been recognized as a critical disturbance process (Biswell, 1989), bark beetles are still commonly treated as pests by land managers (Waters et al., 1985), and the news media (Nikiforuk, 2011). However, bark beetles have played an important role in the dynamic, co-evolutionary processes that for millennia have created the successional patterns of forests that we see today (Wood and Storer, 2002; Raffa et al., 2008; Nordhaus and Bentz, 2009; Progar et al., 2009). It is reasonable to predict that as forests continue to change due to human inputs (including climate change), crucial ecological disturbance processes such as wildland fire and bark beetle caused mortality will continue to influence forest succession under these new conditions.

Acknowledgements

This is publication No. 221 of the National Fire and Fire Surrogate Study funded by the US Joint Fire Science Program. We would like to especially thank the staff at the University of California Blodgett Forest Station for their dedicated cooperation and support of the Fire Surrogate Study. We thank Andrew J. Amacher for his statistical advice. Thanks also to the U.C. Berkeley FFS Research Team and all 2001–2005 summer field assistants.

References

Abella, S.R., Covington, W.W., Fule, P.Z., Lentile, L.B., Meador, A.J.S., Morgan, P., 2007. Past, present, and future old growth in frequent-fire conifer forests of the western United States. Ecol. Soc. 12 (2), 16, http://www.ecologyandsociety.org/vol12/iss2/art16/.

Agee, J., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC.

Agee, J., Skinner, C., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211, 83–96.

Anderson, M.K., Moratto, M.J., 1996. Native American land-use practices and ecological impacts. In: Sierra Nevada Ecosystem Project: Final report to Congress. Vol. II Assessments and Scientific Basis for Management Options. Wildland Resources, University of California, Davis, pp. 187–206.

Baker, W.L., Veblen, T.T., Sherriff, R.L., 2007. Fire, fuels and restoration of ponderosa pine-Douglas fir forests in the Rocky Mountains, USA. J. Biogeogr. 34, 251–269.

Barker, J., 2003. The western pine beetle and forest health: historical approaches and contemporary consequences. Am. Entomol. 49, 142–148.

Berry, A., Hesseln, H., 2004. The effects of the wildland-urban interface on prescribed burning costs in the Pacific Northwestern United States. J. For. 102 (6), 33–37.

Biswell, H.H., 1989. Prescribed Burning in California Wildland Vegetation Management. University of California Press, Berkeley, CA, USA, p. 255.

Breece, C.R., Kolb, T.E., Dickson, B.G., McMillin, J.D., Clancy, K.M., 2008. Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. For. Ecol. Manage. 255, 119–128.

Campbell, J.W., Hanula, J.L., Outcalt, K.W., 2008. Effects of prescribed fire and other plant community restoration treatments on tree mortality, bark beetles, and other saproxylic Coleoptera of longleaf pine, *Pinus palustris* Mill., on the coastal plain of Alabama. For. Ecol. Manage. 254, 134–144.

Collins, B.M., Everett, R.G., Stephens, S.L., 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. Ecosphere 2 (4), art51.

Cook, S.F., 1976. The Population of the California Indians, 1769–1970. University of California Press, Berkeley, California.

Covington, W.W., Fule, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., et al., 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. J. For. 95 (4), 23–29.

Craighead, F.C., Miller, J.M., Evenden, J.C., Keen, F.P., 1931. Control work against bark beetles in western forests and an appraisal of its results. J. For. 29, 1001–1018.

Fettig, C.J., McMillen, J.D., Anhold, J.A., Hamud, S.M., Borys, R.R., Dabney, C.P., Seybold, S.J., 2006. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. For. Ecol. Manage. 230, 55–68.

Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, S.A., Nebeker, T.E., Negrón, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For. Ecol. Manage. 238, 24–53.

Fettig, C.J., Borys, R.B., McKelvey, S.R., Dabney, C.P., 2008. Blacks Mountain Experimental Forest: bark beetle responses to differences in forest structure and the application of prescribed fire in interior ponderosa pine. Can. J. For. Res. 38, 924–935.

Fettig, C., Borys, R., Dabney, C., 2010a. Effects of fire and fire surrogate treatments on bark beetle-caused tree mortality in the Southern Cascades, California. For. Sci. 56, 60–73.

Fettig, C.J., McKelvey, S.R., Cluck, D.R., Smith, S.L., Otrosina, W.J., 2010b. Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in ponderosa and Jeffrey pine forests in California, USA. For. Ecol. Manage. 260, 207–218.

Furniss, R.L., Carolin, V.M., 1977. Western Forest Insects. Misc. Pub. 1339. U.S. Department of Agriculture Forest Service, Washington, DC, 654 pp..

Ganz, D.J., Dahlsten, D.L., Shea, P.J., 2003. The post-burning response of bark beetles to prescribed burning treatments. In: USDA Forest Service Proceedings RMRS-P-29, pp. 143–158.

Graham, R.T., McCaffrey, S., Jain, T.B., 2004. Science basis for changing forest structure to modify wildfire behavior and severity. In: USDA Forest Service General Technical Report, RMRS-120, Rocky Mountain Research Station, Ogden, Utah, 43 p.

Hartsough, B.R., Abrams, S., Barbour, R.J., Drews, E.S., McIver, J.D., Moghaddas, J.J., Schwilk, D.W., Stephens, S.L., 2008. The economics of alternative fuel reduction treatments in western United States dry forests: financial and policy implications from the national fire and fire surrogate study. For. Policy Econ. 10, 344–354.

Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of inland northwest United States forests, 1800–2000. For. Ecol. Manage. 178, 23–59.

Holling, C.S., 1973. Resilience and stability of ecosystems. Ann. Rev. Ecol. Syst. 4, 1–23.

Husari, S.J., McKelvey, K.S., 1996. Fire management policies and programs. In: Sierra Nevada Ecosystem Project: Final report to Congress. vol. II Assessments and Scientific Basis for Management Options. Wildland Resources, University of California, Davis, pp. 1101–1118.

Jenkins, M.J., Hebertson, E., Page, W., Jorgensen, C.A., 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For. Ecol. Manage. 254 (1), 16–34.

Keifer, M.B., Stephenson, N.L., Manley, J., 2000. Prescribed fire as the minimum tool for wilderness forest and fire regime restoration: a case study from the Sierra Nevada, California. In: Proceedings – Rocky Mountain Research Station, USDA Forest Service, RMRS-P-15, vol. 5, pp. 266–269.

Kobziar, L., Moghaddas, J., Stephens, S.L., 2006. Tree mortality patterns following prescribed fires in a mixed conifer forest. Can. J. For. Res. 36, 3222–3238.

Kroeber, A.L., 1925. Handbook of the Indians of California. No. Bulletin 78. Bureau of American Ethnology, Washington DC, USA.

Kroeber, A.L., 1929. The valley Nisenan. Univ. Calif. Publ. Am. Archaeol. Ethnol. 24, 253–290.

Laudenslayer, W.F., Darr, H.H., 1990. Historical effects of logging on forests of the Cascade and the Sierra Nevada Ranges of California. Trans. West. Sect. Wildlife Soc. 26, 12–23.

Matson, R.G., 1972. Aspects of Nisenan ecology. In: Papers on Nisenan environment and subsistence. Center for Archaeological Research Publication 3. University of California, Davis, pp. 39–41.

McCullough, D.G., Werner, R.A., Neumann, D., 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annu. Rev. Entomol. 43, 107–127.

McHugh, C.W., Kolb, T.E., Wilson, J.L., 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environ. Entomol. 32, 510–522.

McIver, J., Youngblood, A., Stephens, S.L., 2009. The National Fire and Fire Surrogate Study: ecological consequences of fuel reduction methods in seasonally dry forests. Ecol. Appl. 19, 283–284.

Moghaddas, J.J., York, R.A., Stephens, S.L., 2008. Initial response of conifer and California black oak seedlings following fuel reduction activities in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. 255, 3141–3150.

Nikiforuk, A., 2011. Empire of the Beetle: How Human Folly and a Tiny Bug are Killing North America's Forests. D&M Publishers, Inc., Vancouver, Canada, 240 p..

Nordhaus, H., Bentz, B., 2009. Bark Beetle Outbreaks in Western North America: Causes and Consequences. University of Utah Press, 44 p..

North, M., Innes, J., Zald, H., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Can. J. For. Res. 37, 331–342.

Progar, R.A., Eglitis, A., Lundquist, J.E., 2009. Some ecological, economic, and social consequences of bark beetle infestations. General Technical Report – Pacific Northwest Research Station, USDA Forest Service. PNW-GTR-784, pp. 71–83.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., et al., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517.

Reinhardt, E.D., Keane, R.E., Brown, J.K., 2001. Modeling fire effects. Int. J. Wildland Fire. 10, 373–380.

Seybold, S.J., Huber, D.P.W., Lee, J.C., Graves, A.D., Bohlmann, J., 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. Phytochem. Rev. 5, 143–178.

Show, S.B., 1926. Timber growing and logging practice in the California pine region. U.S. Department of Agriculture Bulletin 1402, 75.

Show, S.B., Kotok, E.I., 1924. The role of fire in the California pine forests. USDA Bulletin no. 1294. Washington, DC, 80 pp.

Six, D.L., Skov, K., 2009. Response of bark beetles and their natural enemies to fire and fire surrogate treatments in mixed-conifer forests in western Montana. For. Ecol. Manage. 258, 761–772.

Skinner, C.N., 2005. Reintroducing fire into the Blacks Mountain research natural area: effects on fire hazard. General Technical Report – Pacific Southwest Research Station, USDA Forest Service, PSW-GTR-198, pp. 245–257.

Skinner, C.N., Chang, C., 1996. Fire regimes, past and present. In: Sierra Nevada Ecosystem Project: Final report to Congress. Vol. II Assessments and Scientific Basis for Management Options. Wildland Resources, University of California, Davis, pp. 80–91.

Stephens, S.L., 2000. Mixed conifer and red fir forest structure and uses in 1899 from the central and northern Sierra Nevada, California. Madroño. 47, 43–52.

Stephens, S.L., Collins, B.M., 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. Northwest Sci. 78, 12–23.

Stephens, S.L., Moghaddas, J.J., 2005. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. For. Ecol. Manage. 215, 21–36.

Stephens, S.L., Ruth, L., 2005. Federal forest-fire policy in the United States. Ecol. Appl. 15, 532–542.

Stephens, S.L., Millar, C.I., Collins, B.M., 2010. Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. Environ. Res. Lett. 5, 024003.

Stephens, S.L., McIver, J.D., Boerner, R.E.J., Fettig, C.J., Fontaine, J.B., Hartsough, B.R., Kennedy, P., Schwilk, D.W., 2012. Effects of forest fuel reduction treatments in the United States. Bioscience 62, 549–560.

van Mantgem, P.J., Stephenson, N.L., Knapp, E., Battles, J., Keeley, J.E., 2011. Long-term effects of prescribed fire on mixed conifer forest structure in the Sierra Nevada, California. For. Ecol. Manage. 261, 989–994.

Waters, W.E., Stark, R.W., Wood, D.L., 1985. Integrated Pest Management in Pine-Bark Beetle Ecosystems. John Wiley & Sons Inc., New York.

Weatherspoon, P.C., McIver, J., 2000. A national study of the consequences of fire and fire surrogate treatments. USDA Forest Service Pacific Southwest Research Station, Redding, CA, 114 pp. <http://www.fs.fed.us/ffs/execsumm-4-17–00 htm>.

Wood, D.L., Storer, A.J., 2002. Bark beetles infesting California's conifers. Fremontia. 30 (3-4), 19–25.

Wood, D.L., Storer, A.J., 2009. Forest habitats. In: Resh, V.H., Cardé, R.T. (Eds.), Encyclopedia of Insects, second ed. Academic Press, pp. 386–396.

Wood, D.L., Stark, R.W., Waters, W.E., Bedard, W.D., Cobbs Jr., F.W., 1985. Treatment tactics and strategies. In: Waters, W.E., Stark, R.W., Wood, D.L. (Eds.), Integrated Pest Management in Pine-Bark Beetle Ecosystems. John Wiley and Sons, Inc., New York, NY. pp. 121–139.

Wood, D.L., Koerber, T.W., Scharpf, R.F., Storer, A.J., 2003. Pests of the Native California Conifers. University of California Press, Berkeley, CA.

Youngblood, A., Grace, J.B., McIver, J.D., 2009. Delayed conifer mortality after fuel reduction treatments: interactive effects of fuel, fire intensity, and bark beetles. Ecol. Appl. 19, 321–337.

Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice Hall. Upper Saddle River, New Jersey.

Zausen, G.L., Kolb, T.E., Bailey, J.D., Wagner, M.R., 2005. Long-term impacts of thinning and prescribed burning on ponderosa pine physiology and bark beetle abundance in northern Arizona: a replicated landscape study. For. Ecol. Manage. 218, 291–305.

Zhang, J. W., Ritchie, M.W., 2008. Restoring east-side ponderosa pine ecosystems at the Blacks Mountain Experimental Forest: a case study. General Technical Report – Pacific Northwest Research Station, USDA Forest Service, PNW-GTR-733, pp. 107–116.