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The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine

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Abstract

Selective logging, fire suppression, forest succession and climatic changes have resulted in high fire hazards over large areas of the western USA. Federal and state hazardous fuel reduction programs have increased accordingly to reduce the risk, extent and severity of these events, particularly in the wildland–urban interface. In this study, we examined the effects of mechanical fuel reduction treatments on the activity of bark beetles in ponderosa pine, *Pinus ponderosa* Dougl ex. Laws., forests located in Arizona and California, USA. Treatments were applied in both late spring (April–May) and late summer (August–September) and included: (1) thinned biomass chipped and randomly dispersed within each 0.4 ha plot; (2) thinned biomass chipped, randomly dispersed within each plot and raked 2 m from the base of residual trees; (3) thinned biomass lopped-and-scattered (thinned trees cut into 1–2 m lengths) within each plot; (4) an untreated control. The mean percentage of residual trees attacked by bark beetles ranged from 2.0% (untreated control) to 30.2% (plots thinned in spring with all biomass chipped). A three-fold increase in the percentage of trees attacked by bark beetles was observed in chipped versus lopped-and-scattered plots. Bark beetle colonization of residual trees was higher during spring treatments, which corresponded with peak adult beetle flight periods as measured by funnel trap captures. Raking chips away from the base of residual trees did not significantly affect attack rates. Several bark beetle species were present including the roundheaded pine beetle, *Dendroctonus adjunctus* Blandford (AZ), western pine beetle, *D. brevicomis* LeConte (AZ and CA), mountain pine beetle, *D. ponderosae* Hopkins (CA), red turpentine beetle, *D. valens* LeConte (AZ and CA), Arizona fivespined ips, *Ips lecontei* Swaine (AZ), California fivespined ips, *I. paraconfusus* Lanier (CA) and pine engraver, *I. pini* (Say) (AZ). *Dendroctonus valens* was the most common bark beetle infesting residual trees. A significant correlation was found between the number of trees chipped per plot and the percentage of residual trees with *D. valens* attacks. A significantly higher percentage of residual trees was attacked by *D. brevicomis* in plots that were chipped in spring compared to the untreated control. In lopped-and-scattered treatments, engraver beetles produced substantial broods in logging debris, but few attacks were observed on standing trees. At present, no significant difference in tree mortality exists among treatments. A few trees appeared to have died solely from *D. valens* attacks, as no other scolytids were observed in the upper bole. In a laboratory study conducted to provide an explanation for the bark beetle responses observed in this study, monoterpene elution rates from chip piles declined sharply over time, but were relatively constant in lopped-and-piled treatments. The quantities of β-pinene, 3-carene, α-pinene and myrcene eluting from chips exceeded those from lopped-and-piled slash during each of 15 sample periods. These laboratory results may, in part, explain the bark beetle response observed in chipping treatments. The implications of these results to sustainable forest management are discussed.
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1. Introduction

Dendrochronological research in many western North American coniferous forests indicates a pine-dominated cover type that was open and park-like, large-tree dominated and shaped by frequent low-intensity fires prior to European settlement (Agee, 1993, 1994; Agee and Skinner, 2005; Covington and Moore, 1994; Skinner and Chang, 1996; Taylor,

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2000; Swetnam and Baisan, 2002; Stephen et al., 2003). Compared to their historical counterparts, these forests are now much denser, have more smaller trees and fewer larger trees and are dominated by more shade-tolerant and fire-intolerant tree species (Hessburg and Agee, 2003). Many areas that were previously open have become forested (Skinner, 1995; Norman and Taylor, 2005). These conditions have led to increases in competition among trees for below-ground nutrients, water and growing space, thereby increasing vulnerability of such forests to bark beetles (Coleoptera: Scolytidae) and other forest insects and diseases (Ferrell et al., 1994; Oliver, 1995; Oliver and Larson, 1996). Bark beetles are a major cause of tree mortality in ponderosa pine, *Pinus ponderosa* Dougl ex. Laws., forests (Furniss and Carolin, 1977). Extensive amounts of bark beetle-caused tree mortality may exacerbate problems associated with heavy fuel loads (Covington and Moore, 1994).

Forest fuels are generally classified into three components: ground fuels, surface fuels, and understory and overstory fuels (Agee and Skinner, 2005). Ground fuels include newly cast material (L-layer), material that has begun to degrade (F-layer) and humus consisting of largely unidentifiable organic manner (H-layer). Surface fuels include down and dead woody fuels, herbaceous vegetation, and low shrubs. This component may constitute a large fraction of the total biomass available for fire consumption. Understory (ladder) and overstory fuels include standing saplings and trees. Mechanical fuel reduction treatments and prescribed fire have functionally different effects on the fuel matrix and load within each component (Agee and Skinner, 2005), and thus on the structure and composition of forests as well as their resiliency to disturbance agents, such as bark beetle infestations.

In recent years, unusually large and catastrophic wildfires have heightened public concern. Such events emphasize the need for well-designed treatments to reduce their extent and severity. Under the National Fire Plan and Healthy Forests Restoration Act of 2003, federal and state hazardous fuel reduction programs have increased substantially (U.S. Public Law 108–148). During 2003, 1.1 million ha of federal land were treated to reduce hazardous fuels by applications of thinning (pre-commercial and commercial), prescribed fire, and/or a combination of these and other treatments (National Fire Plan, 2004). One of the key goals of this program is the reduction of hazardous fuels within the wildland–urban interface (WUI). In general terms, the WUI is defined as "the area where structures and other human developments meet or intermingle with undeveloped land" (Stewart et al., 2003). In the USA, 37% of single-family homes are located within this area (Stewart et al., 2003). The presence of housing developments significantly alters the structure and function of forest ecosystems (Theobald et al., 1997; Friesen, 1998), and the manner in which they can be managed.

The cost and complexity of conducting prescribed fires in the WUI are substantial due to concerns regarding aesthetics, air quality and structural protection (Berry and Hesseln, 2004). As a result, mechanical fuel treatments are more frequently used to manipulate stand conditions in these areas. Since sufficient markets have yet to be developed for small dimensional material (Lynch and Mackes, 2002), much of the tree biomass resulting from these treatments is not merchantable. In many areas of the western USA, this material is cut and lopped (i.e., bole severed into short lengths and limbs removed) and/or chipped, and distributed on site. The amount of total biomass on the site may be unchanged, but the torching potential (the initiation of crown fire activity) and rate of potential crown fire spread is significantly reduced. Chipping may functionally reduce the amount of biomass available for combustion, particularly on mesic sites. However, these actions result in increased amounts of host material (slash) and host volatiles (from slash and chips) that may concentrate certain bark beetle species in these areas (Renwick and Vité, 1972; Billings, 1985; Miller and Borden, 1990, 1992; Hobson et al., 1993; Six et al., 2002).

Volatiles released from cut and chipped *P. ponderosa* include monoterpenes (Schade and Goldstein, 2003), which are known to influence the physiology and behavior of bark beetles (Seybold et al., 2000, 1986). In descending order, the most abundant monoterpenes in the volatile fraction of *P. ponderosa* oleoresin from the central Sierra Nevada of California are β-pinene, 3-carene, α-pinene and myrcene (Mirov, 1961; Hobson et al., 1993; Smith, 2000). However, relative amounts may vary depending on location. For example, α-pinene comprises a greater percentage of all monoterpenes in the xylem oleoresin of *P. ponderosa* in parts of southern Arizona than elsewhere in its distribution (Smith, 2000). At high concentrations in closed containers, monoterpenes may be toxic to scolytids, but as volatiles in open airspaces they also function as attractants for some species (Seybold et al., 2000, 1986). Each of the four compounds noted above has been recorded, either alone or in combination with other semiochemicals, as an attractant for specific bark beetles associated with *P. ponderosa* forests (Skillen et al., 1997): β-pinene, 3-carene, and α-pinene – the red turpentine beetle, *Dendroctonus valens* LeConte (Hobson et al., 1993); myrcene – the western pine beetle, *D. brevicomis* LeConte (Bedard et al., 1969, 1970; Wood, 1972); 3-carene, α-pinene, and myrcene – the mountain pine beetle, *D. ponderosae* Hopkins (Pitman, 1971; Billings et al., 1976; Miller and Borden, 2000). Release of these monoterpenes into the below-canopy dispersal space of pine bark beetles during, and shortly after, mechanical fuel treatments may influence host selection and colonization behavior.

Resource managers are challenged to manage forests in a sustainable manner and for a variety of uses that require knowledge about the resiliency of these systems. Previous efforts have focused on providing guidelines for managing logging residues that minimize bark beetle attacks in response to these treatments (Craighead, 1927; Furniss and Carolin, 1977; Fellin, 1980). Current recommendations include generating slash during periods of adult bark beetle inactivity, limiting the size of harvested blocks, separating slash production in time and space, limiting the size and length of residual host material, and treating infested slash through solarization, burning, or direct removal from the site (Massey and Parker, 1981; Parker, 1991; Villa-Castillo and Wagner, 1996; Kegley et al., 1997). A relatively new slash management treatment is chipping. Many land managers consider this to be an ideal treatment as woody biomass is retained on site for nutrient cycling, fire hazard and soil impacts are reduced, and host material is eliminated in comparison to piled-and-burned and lopped-and-scattered treatments (Six et al., 2002).

In a preliminary study, we observed that several bark beetle species appeared to be attracted to *P. ponderosa* stands where logging residues had recently been chipped (McMillin and Anhold, unpublished data). The overall objective of this study was to determine if mechanical fuel treatments in *P. ponderosa* forests influence the susceptibility of residual trees to bark beetle attack. Specifically, the objectives were to determine the effect of: (1) chipping and lop-and-scatter treatments, and (2) seasonality of treatment on the amount of bark beetle activity in *P. ponderosa* stands. Furthermore, we describe absolute quantities of volatile monoterpenes emanating from chipped versus lopped-and-piled slash and discuss the implications of these results to forest management.

2. Materials and methods

In spring 2003, fourteen 0.4 ha square experimental plots were established within *P. ponderosa* forests at three locations (blocks): (1) the Apache-Sitgreaves National Forest, Arizona; (2) the Kaibab National Forest, Arizona; (3) the Tahoe National Forest, California, USA. At each location, one of seven treatments was assigned to experimental plots arranged in a completely randomized design. The treatments were replicated twice at each location ($N = 42$). Adjacent plots were separated by >100 m. Thinning prescriptions for hazardous fuel reduction treatments varied slightly among locations according to pre-existing stand conditions and desired post-treatment fuel loads. Thinning was conducted from below (i.e., concentrating on trees in the smaller diameter classes), which has been shown to reduce canopy bulk density, increase canopy base height, and result in a higher proportion of larger diameter trees, which collectively decrease crown fire susceptibility (Agee and Skinner, 2005). The selection of trees to cut or leave followed the same criteria on all plots in each location (see below). All tree biomass was retained within plots following felling. Treatments included: (1) an untreated control; (2) thinned biomass chipped and randomly dispersed within each plot in spring (CS); (3) thinned biomass chipped and randomly dispersed within each plot in late summer (CF); (4) thinned biomass chipped, randomly dispersed within each plot, but raked 2 m from the base of residual trees in spring (CRS); (5) thinned biomass chipped, randomly dispersed within each plot, but raked 2 m from the base of residual trees in late summer (CRF); (6) thinned biomass lopped-and-scattered within each plot in spring (LS); (7) thinned biomass lopped-and-scattered within each plot in late summer (LF). The late summer treatments (both harvesting and chipping) were applied during August and September 2003, whereas spring treatments were applied during April and May 2004. Plots were cruised by conventional methods to determine the effects of each treatment on stand structure and composition (Tables 1–3).

Table 1
Plot descriptions for the assessment of the effect of hazardous fuel reduction treatments on bark beetle activity, Lakeside Ranger District, Apache-Sitgreaves National Forest, Navajo Co., Arizona, USA, 2003–2004

Treatment[a]	Pre-treatment				Post-treatment			
	Trees[b]	BA[c]	% PP[d]	QMD[e]	Trees	BA	% PP	QMD
Untreated	202	11.9	99.5	27.4				
	298	13.6	100	24.1				
CF	223	13.2	95.5	27.4	124	10.6	91.9	33.0
	261	12.2	96.6	24.4	119	8.5	92.4	30.2
CS	292	12.5	95.9	23.4	103	7.6	88.3	30.7
	222	10.6	99.1	24.6	102	7.6	98.0	30.7
CRF	273	11.2	98.9	22.9	102	7.4	97.1	30.4
	330	14.5	98.5	23.6	147	9.6	96.6	28.9
CRS	287	10.8	95.8	21.8	116	6.6	89.7	26.9
	262	10.5	93.1	22.6	125	8.1	85.6	28.7
LF	350	13.7	98.0	22.4	123	7.4	94.3	27.7
	189	10.2	92.1	26.2	89	8.0	83.2	33.8
LS	337	12.6	98.5	21.8	148	8.0	96.6	26.2
	302	13.8	97.4	24.1	114	8.9	93.0	31.5
Means	273.4	12.2	97.1	24.1	117.7	8.2	92.2	29.9

[a] Treatments were applied to plots (0.4 ha) in late spring (S) or late summer (F): (C) thinned biomass chipped and randomly dispersed within each plot, (CR) thinned biomass chipped, randomly dispersed, and raked 2 m from the root collar of residual trees, (L) thinned biomass lopped-and-scattered within each plot, and (Untreated) control.

[b] Number of trees per plot.

[c] Basal area (m^2) per plot.

[d] % of basal area represented by *P. ponderosa*.

[e] Quadratic mean diameter (cm).

2.1. Site descriptions and treatment prescriptions

2.1.1. Apache-Sitgreaves National Forest

This block was established in 2003 on the Lakeside Ranger District, Apache-Sitgreaves National Forest, Navajo Co., Arizona, USA (34.18°N, 109.87°W; 2181 m elevation). The cover type was southwestern ponderosa pine-bunchgrass and included *P. ponderosa* var. *scopulorum*, Rocky Mountain juniper, *Juniperus scopulorum* Sarg., Utah juniper, *J. osteosperma* (Torr.) Little, oneseed juniper, *J. monosperma* (Engelm.) Sarg., alligator juniper, *J. deppeana* Steud. and Gambel oak, *Quercus gambelii* Nutt (Price, 1998). Fuel reduction treatments were conducted 26 August–16 September, 2003 (late summer treatments) and 19 April–7 May, 2004 (spring treatments). We felled by hand all *P. ponderosa* <22.9 cm diameter at breast height (d.b.h.), unless an area contained a majority of trees that were <22.9 cm d.b.h. In the later case, individual trees were cut until an average spacing of 7.6 m was achieved. Stump heights ranged from 2.5 to 15 cm.

In lopped-and-scattered treatments, all thinned trees were cut into 1–2 m lengths and randomly distributed within plot boundaries. In chipped plots, all thinned trees were cut into short lengths and manually fed through a 30.5-cm (maximum diameter material) chipper (Model 17; Wood/Chuck Chipper Corp., Shelby, NC 28151, USA) that was moved within each plot to facilitate chipping. The surface area of individual chips

Table 2
Plot descriptions for the assessment of the effect of hazardous fuel reduction treatments on bark beetle activity, Williams Ranger District, Kaibab National Forest, Coconino Co., Arizona, USA, 2003–2004

Treatment[a]	Pre-treatment				Post-treatment			
	Trees[b]	BA[c]	% PP[d]	QMD[e]	Trees	BA	% PP	QMD
Untreated	205	10.4	100	25.4				
	220	11.8	100	26.2				
CF	200	14.4	100	30.2	105	12.6	100	39.1
	210	16.4	100	31.5	148	13.9	100	34.5
CS	226	14.1	100	28.2	99	12.2	100	39.6
	270	12.6	99.6	24.4	102	10.2	99.0	35.8
CRF	224	17.2	100	31.2	159	16.5	100	36.3
	163	12.3	100	31.0	94	10.3	100	37.3
CRS	262	16.4	100	28.2	162	14.7	100	33.3
	180	13.3	100	30.7	133	12.3	100	34.3
LF	298	10.9	100	21.6	145	9.6	100	28.2
	170	11.0	100	28.7	105	9.7	100	34.3
LS	229	9.0	97.8	22.4	94	6.7	94.7	30.7
	186	12.9	100	29.7	111	10.9	100	35.3
Means	217.4	13.1	99.8	27.8	121.7	11.6	99.5	34.9

[a] Treatments were applied to plots (0.4 ha) in late spring (S) or late summer (F): (C) thinned biomass chipped and randomly dispersed within each plot, (CR) thinned biomass chipped, randomly dispersed, and raked 2 m from the root collar of residual trees, (L) thinned biomass lopped-and-scattered within each plot, and (Untreated) control.

[b] Number of trees per plot.

[c] Basal area (m^2) per plot.

[d] % of basal area represented by *P. ponderosa*.

[e] Quadratic mean diameter (cm).

Table 3
Plot descriptions for the assessment of the effect of hazardous fuel reduction treatments on bark beetle activity, Foresthill Ranger District, Tahoe National Forest, Placer Co., California, USA, 2003–2004

Treatment[a]	Pre-treatment				Post-treatment			
	Trees[b]	BA[c]	% PP[d]	QMD[e]	Trees	BA	% PP	QMD
Untreated	230	13.6	86.1	27.4				
	320	16.8	81.5	25.9				
CF	220	11.7	97.2	25.9	180	10.3	100	26.9
	300	17.9	88.0	27.7	120	8.7	90.1	30.5
CS	290	15.1	98.8	25.7	150	9.5	93.5	28.4
	250	16.0	98.4	28.4	140	8.6	99.5	27.9
CRF	250	17.5	100	30.0	140	12.2	100	33.3
	310	20.2	85.1	29.0	160	12.8	83.2	32.0
CRS	250	14.5	95.0	27.2	120	8.8	100	30.7
	320	21.6	93.5	29.2	180	15.6	97.9	33.3
LF	280	15.8	93.2	26.9	150	11.9	96.5	31.8
	280	14.8	92.3	25.9	150	9.6	89.8	28.7
LS	230	15.5	95.3	29.2	140	11.9	93.9	33.0
	380	19.6	98.1	25.7	130	9.4	100	30.5
Means	279.3	16.5	93.0	27.4	146.7	10.8	95.4	30.6

[a] Treatments were applied to plots (0.4 ha) in late spring (S) or late summer (F): (C) thinned biomass chipped and randomly dispersed within each plot, (CR) thinned biomass chipped, randomly dispersed, and raked 2 m from the root collar of residual trees, (L) thinned biomass lopped-and-scattered within each plot, and (Untreated) control.

[b] Number of trees per plot.

[c] Basal area (m^2) per plot.

[d] % of basal area represented by *P. ponderosa*.

[e] Quadratic mean diameter (cm).

averaged 10 cm^2 in all blocks. In chipped-and-raked plots, the chips were raked manually away from the base of all pines within 48 h of chipping in all blocks.

2.1.2. Kaibab National Forest

This block was established in 2003 on the Williams Ranger District, Kaibab National Forest, Coconino Co., Arizona, USA (35.18°N, 112.02°W; 2050 m elevation). The cover type was southwestern ponderosa pine-bunchgrass and included *P. ponderosa* var. *scopulorum*, *J. osteosperma* and *Q. gambelii* (Price, 1998). Fuel reduction treatments were conducted 29–30 September, 2003 (late summer) and 19 April–7 May, 2004 (spring). Treatments were applied as described for the Apache-Sitgreaves block.

2.1.3. Tahoe National Forest

This block was established in 2003 on the Foresthill Ranger District (recently renamed the American River Ranger District), Tahoe National Forest, Placer Co., California, USA (39.13°N, 120.69°W; 1463 m elevation). The block was located within plantations established in May 1962 following a severe wildfire. Both *P. ponderosa* var. *ponderosa* (2-0) and sugar pine, *P. lambertiana* Dougl. (1-0), had been planted at 795 and 130 seedlings/ha, respectively (Price, 1998). The stand also included Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, incense cedar, *Calocedrus decurrens* (Torr.) Florin, and white fir, *Abies concolor* (Gond. and Glend.) Hildebr. in the understory. Fuel reduction treatments were conducted 10–25 August, 2003 (late summer) and 24 April–1 May, 2004 (spring). We felled by hand all conifers <30 cm d.b.h. regardless of species unless an area contained a majority of trees <30 cm d.b.h. In this case, individual trees were removed until an average spacing of 5.5 m was achieved. The best crop trees were retained without regard to species. Stump heights did not exceed 15 cm.

In lopped-and-scattered treatments, all thinned trees were delimbed, cut into 1.5–2 m lengths, and randomly distributed within plot boundaries. In chipped plots, all thinned trees were cut into acceptable lengths and manually fed through a 38-cm (maximum diameter material) diesel powered chipper (Model BC1400XL; Vermeer Equipment of Texas, Inc., Irving, TX 75062, USA) moved within each plot to facilitate chipping.

2.2. Experimental design and analyses

A 100% cruise was conducted on each plot to locate bark beetle-attacked pines during fall 2003 (late summer treatments only), spring 2004 (all treatments) and fall 2004 (all treatments). In addition, in October 2004 a 40 m wide area was surveyed for bark beetle activity around the perimeter of each plot. All pines containing successful bark beetle attacks [with oxidized phloem material (i.e., reddish-colored) present in pitch tubes] were tagged, and tree species, bark beetle species and d.b.h. were recorded. In addition, the number of *D. valens* successful attacks per tree was recorded in California. In Arizona, the number of stumps containing *D. valens* attacks was tallied and the percentage of stumps attacked was calculated. Statistical analyses of bark beetle responses were based on cumulative assessments over the 2-year period. The primary variables of interest were: (1) the mean percentage of bark beetle-attacked trees; (2) the mean number of *D. valens* attacks per tree; (3) the mean percentage of *D. brevicomis*-attacked trees; (4) the mean percentage of bark beetle-killed trees during that period. *Dendroctonus valens* and *D. brevicomis* were the only bark beetles found infesting trees in all blocks and therefore species-level analyses were limited to these species.

The experimental design was a randomized complete block with three blocks (locations), seven treatments, and two replicates/treatment/block (d.f. = 6, 21). A test of normality was performed and appropriate transformations were used when data deviated significantly from a normal distribution (Sokal and Rohlf, 1995). If a significant treatment effect was detected ($P \leq 0.05$), the Tukey's multiple comparison test (Tukey's HSD) was used for separation of treatment means (Sokal and Rohlf, 1995). The relationship between level of chipping (number of trees chipped) and *D. valens* attacks on individual trees was analyzed using Pearson's correlation coefficient (*r*) and simple linear regression (SigmaStat Version 2.0, SPSS Inc., Chicago, IL 60606, USA).

2.3. Bark beetle flight periodicity

Two (AZ) or three (CA) 12-unit multiple-funnel traps (Lindgren, 1983) were baited with commercially available lures (Phero Tech Inc., Delta, BC, Canada V4G 1E9) and used to assess the flight periodicity of *Ips* species and *D. valens* at each location [i.e., *I. pini* (Say) (Apache-Sitgreaves); Arizona fivespined ips, *I. lecontei* Swaine (Kaibab); California fivespined ips, *I. paraconfusus* Lanier (Tahoe)] (Table 4). Species were selected for monitoring based on preliminary observations concerning their responses to chipping treatments. We also modified two (AZ) or three (CA) additional 12-unit multiple-funnel traps per site to hold two 30 cm × 41 cm mesh bags (5#; Sacramento Bag Manufacturing Company, Sacramento, CA 95812, USA) containing fresh *P. ponderosa* chips to determine the relative attraction of chips to multiple bark beetle species. Traps were hung on 3-m metal poles with collection cups 50–80 cm above the ground. Traps were located approximately 0.5–2.0 km from treated areas and were separated by >100 m to avoid interference among adjacent trap treatments. A 3 × 3-cm time-released insecticidal Prozap Pest Strip (2,2-dichlorovinyl dimethyl phosphate; Loveland Industries Inc., Greely, CO 80632, USA) was placed in the collection cup to kill arriving insects and reduce loss to invertebrate predation. In general, baits were replaced every 6 weeks. Chips were placed in the traps once at the beginning of the study to mimic chip placement under field conditions. Trap catches were removed approximately biweekly and returned to the laboratory for identification of bark beetles (Wood, 1982) and tally. To determine the relative attractiveness of chips, we performed *t*-tests on the number of *D. valens* captured per trap between chip- and attractant-baited traps (SigmaStat Version 2.0, SPSS Inc.) as few other species were collected. A test of normality was performed, and square root transformations were used when the data deviated significantly from a normal distribution (Sokal and Rohlf, 1995).

2.4. Analysis of volatile monoterpenes from chipped and lopped-and-piled slash

On 15 August 2003, 10 *P. ponderosa* (15 cm d.b.h.) from the same genetic (planting) stock were harvested from a plantation in El Dorado County, CA, and then moved to the grounds of the USDA Forest Service Institute of Forest Genetics for further manipulation. Biomass was standardized among individual trees by controlling bole length. Within 24 h of harvest, five trees were either individually chipped (treatment 1; $n = 5$) or cut into 0.8 m lengths (treatment 2; $n = 5$). In each case, the entire tree was processed and the material generated was piled

Table 4
Description of semiochemical release devices (Phero Tech Inc., Delta, BC, Canada) used in multiple-funnel traps in Arizona and California, 2003–2004

Bark beetle species	Semiochemical and enantiomeric composition[a]	Chemical purity (%)	Release rate[b] (mg/24 h)
Dendroctonus valens	(+)-α-Pinene	98	150
	(−)-β-Pinene	98	
	(+)-3-Carene	98	
Ips lecontei	Racemic ipsdienol	93	0.1–0.3
	Racemic ipsenol	97	0.1–0.3
	(−)-*cis*-Verbenol	94	1–2
I. paraconfusus	(+)-Ipsdienol	93	0.1–0.3
	Racemic ipsenol	97	0.1–0.3
	(−)-*cis*-Verbenol	94	1–2
I. pini	(−)-Ipsdienol	93	0.1–0.3
	Lanierone	98	0.1–0.3

[a] All release devices were polyvinyl chloride bubblecaps except for the *D. valens* attractant, which was a 15 ml polyethylene bottle.

[b] At 24 °C.

tightly to a height of 1 m. Each treatment pile was then covered with a 1040 l HDLP circular tank (1 m × 1.2 m external dimensions; Rotonics Manufacturing Inc., Gardena, CA 90248, USA) to create a headspace from which volatile monoterpenes were sampled. A small hole was cut into the top of each tank and a No. 11.5 rubber stopper was inserted. Teflon tubing (0.95 cm diameter PTFE; Cole-Parmer Instrument Company, Vernon Hills, IL 60055, USA) was inserted into the tank through the center of each stopper and then connected to a glass column [(2.8 cm ID/3 cm OD × 31 cm length, ground glass 24/40 joint) with constricted, open ends (0.3 cm ID/0.5 cm OD)] containing 7–8 g of Porapak-Q (50/80 mesh size; Sigma–Aldrich, St. Louis, MO 63103, USA). Porapak-Q is an absorbent resin with high affinity for organic volatiles (Bryne et al., 1975). All tubing and column junctions were sealed with Teflon tape and Parafilm M® (Pechiney Plastic Packaging, Inc., Neenah, WI 54956, USA).

Ambient air was drawn through the bottom of each tank at 4 l/min, which replaced the air within each tank ~9 times per 24 h. Flow into each tank was facilitated through the unsealed edge near the ground surface, which was elevated on bricks about 20 cm above the ground. Air was drawn from each tank and through the Porapak column for 24 h. The 10 columns were immediately sealed with Duraseal and Parafilm M®, and then stored at −80 °C prior to extraction. The study commenced on 16 August, and samples were collected daily between 17 and 23 August, every third day between 26 August and 1 September and then every fifth day between 6 and 26 September, 2003 ($N = 150$ samples). The entire sampling period lasted 41 d during which temperatures were recorded in tanks by dataloggers suspended 15 cm above treatments (HOBO Model H08-001-02; Onset Computer Corp., Bourne, MA 02532, USA).

Each Porapak-Q sample was extracted in the glass column with approx. 100 ml of pentane, and then again in some cases with approximately 100 ml of dichloromethane (Fisher Scientific, Pasadena, CA 91185, USA). Both pentane and dichloromethane extracts were collected in 100 ml brown glass sample bottles and an internal standard (80.8 μg of 4-decanone in 1 ml pentane) (99% chemical purity; Sigma–Aldrich, St. Louis, MO 63103, USA) was added to each bottle for quantitative analysis of monoterpenes (see below). The contents of each bottle were transferred to a 250 or 500 ml concentration flask with a 10 ml graduated receptacle. A boiling chip was added and the extract was concentrated to ~4 ml by Kuderna–Danish evaporative concentration (Kontes, Vineland, NJ 08361, USA) in a 50 °C water bath. The flask was then rinsed and added to the concentrate. The combined solution (total volume ~8 ml) was transferred to a sealed vial and stored at −80 °C for later quantitative analysis.

Crude extracts were analyzed for the mass of four selected monoterpenes (α-pinene, (−)-β-pinene, 3-carene and myrcene) by gas chromatography (GC) with a flame ionization detector (FID) using an Agilent 6890N gas chromatograph (Hewlett-Packard Company, Palo Alto, CA 94304, USA) equipped with a DB-Wax capillary column [60 m × 0.25 mm (ID)]. The carrier gas (He) had a flow rate of 22 cm/s and the GC was temperature programmed from 50 °C (0 min) at 2 °C/min to 220 °C (30 min). The injector and detector were set at 200 and 230 °C, respectively.

Standard α-pinene (Cat. No. 147524, Lot No. 12310BR; 94.8% chemical purity), β-pinene (Cat. No. 11208-9, Lot No. 00307LG; 98.2% chemical purity), 3-carene (Cat. No. 11577-6, Lot No. 006631KS; 90.01% chemical purity) and myrcene (Cat. No. M100005, Lot No. 22019BB; 89.5% chemical purity) were all purchased from Sigma–Aldrich and chemical purities determined by GC analysis. The four monoterpenes were quantified by comparisons to standard curves constructed for each by preparing 13 solutions of 4-decanone (80.8 μg) and the four monoterpenes in 10 ml of pentane in concentrations that were known exactly (but varied from approx. 40 ng/ml to approx. 80 mg/ml); analyzing the samples by GC; and plotting and regressing the $\log_{10}$ of the ratio of GC peak area of monoterpene to GC peak area of 4-decanone versus $\log_{10}$ mg of monoterpene ($r^2 > 0.999$, $P < 0.001$ for all regressions). The majority of the monoterpenes eluted with the pentane extract of the Porapak, but analyses of 12 and 16 dichloromethane extracts from chips and slash, respectively, showed that a range of 2.23–9.97% (chips) and 1.39–24.04 % (slash) additional monoterpene eluted with the dichloromethane (percentage depended on the species of monoterpene). Thus, for 28 samples, the masses of monoterpenes in the pentane and dichloromethane extracts were summed to give a total mass for each monoterpene trapped on the Porapak. Totals were estimated for the remaining samples using a correction factor based on analyses of the 28 dichloromethane extracts. The mass of each monoterpene was plotted as an entrapment rate (i.e., in mg/day).

The monoterpene peaks were identified initially through comparison of the unknown peaks in the samples with the retention times of the standards. The four monoterpenes were further confirmed from one of the samples of chipped *P. ponderosa* by gas chromatography–mass spectrometry (GC–MS). An Agilent 6890 GC was fitted with an HP-1MS capillary column [30 m × 0.25 mm (ID) with 0.25 μm film thickness of crosslinked methyl siloxane] and coupled with an Agilent 5973 Mass Selective Detector. Injection (220 °C) was splitless (0.7 min), the carrier gas (He) had a flow rate of 36 cm/s, and the GC was temperature programmed from 50 °C (0.7 min) to 250 °C at 6 °C/min with a final hold of 2 min. Electron impact mass spectrometry was performed using a scanning range of 40–400 at 70 eV. Compounds were identified by comparison to known spectra from an in-house library and the National Institute of Standards and Technology (NIST) library.

3. Results

3.1. Post-treatment stand structure and composition

Pre-treatment stand densities ranged from 402.6 trees/ha and 22.2 m^2/ha of basal area (Kaibab) to 938.6 trees/ha and 53.3 m^2/ha of basal area (Tahoe). On average, we removed (exclusive of untreated control) 159.6, 96.5, and 133.3 trees per plot representing 4.0, 1.8 and 5.9 m^2 of basal area on the

Apache-Sitgreaves, Kaibab and Tahoe blocks, respectively. In each case, quadratic mean diameter increased following thinning. Stand composition was relatively unchanged (Tables 1–3).

3.2. *Ips* species and *D. valens* flight periodicity

In general, flight periodicity agreed with descriptions provided by other authors for similar locations (Fettig et al., 2004, 2005; Gaylord et al., 2006). There was a consistent trend among sites and species with more individuals collected in late-spring/early-summer than in late-summer/fall (Fig. 1A–C). In Arizona, peak flight activity of *D. valens*, *I. lecontei* and *I. pini* occurred from April through mid-May with a second, smaller peak occurring for *D. valens* in early to mid-July. In California, peak activity of both *D. valens* and *I. paraconfusus* occurred during June, however, *I. paraconfusus* was active throughout much of the summer (Fig. 1C). Trap catches substantially declined in all locations by late August (Fig. 1A–C); however, slash generated in late August and September 2003 was heavily colonized by *Ips* species.

Few bark beetle species, exclusive of *D. valens*, were collected in modified multiple-funnel traps baited with fresh *P. ponderosa* chips. Only one *I. paraconfusus* was collected in California and 47 *I. latidens* (LeConte) were collected in such traps at two sites in Arizona. A total of 38, 339, and 381 *D. valens* were collected in chip-baited traps at the Tahoe, Kaibab and Apache-Sitgreaves blocks, respectively. Overall, significantly more *D. valens* were collected in attractant-baited traps than chip-baited traps (19.6 ± 5.3 versus 12.6 ± 8.1; $P = 0.004$), perhaps because the chips desiccated rapidly and were attractive for a shorter period of time. For example, no significant difference was observed between trap catches when analyses were limited to the initial four sampling periods in May and June (21.3 ± 5.3 versus 32.7 ± 13.1; $P = 0.14$), which corresponds with peak flight activity for *D. valens* in California (Fettig et al., 2004). Few *D. valens* were collected in traps baited for *Ips* species.

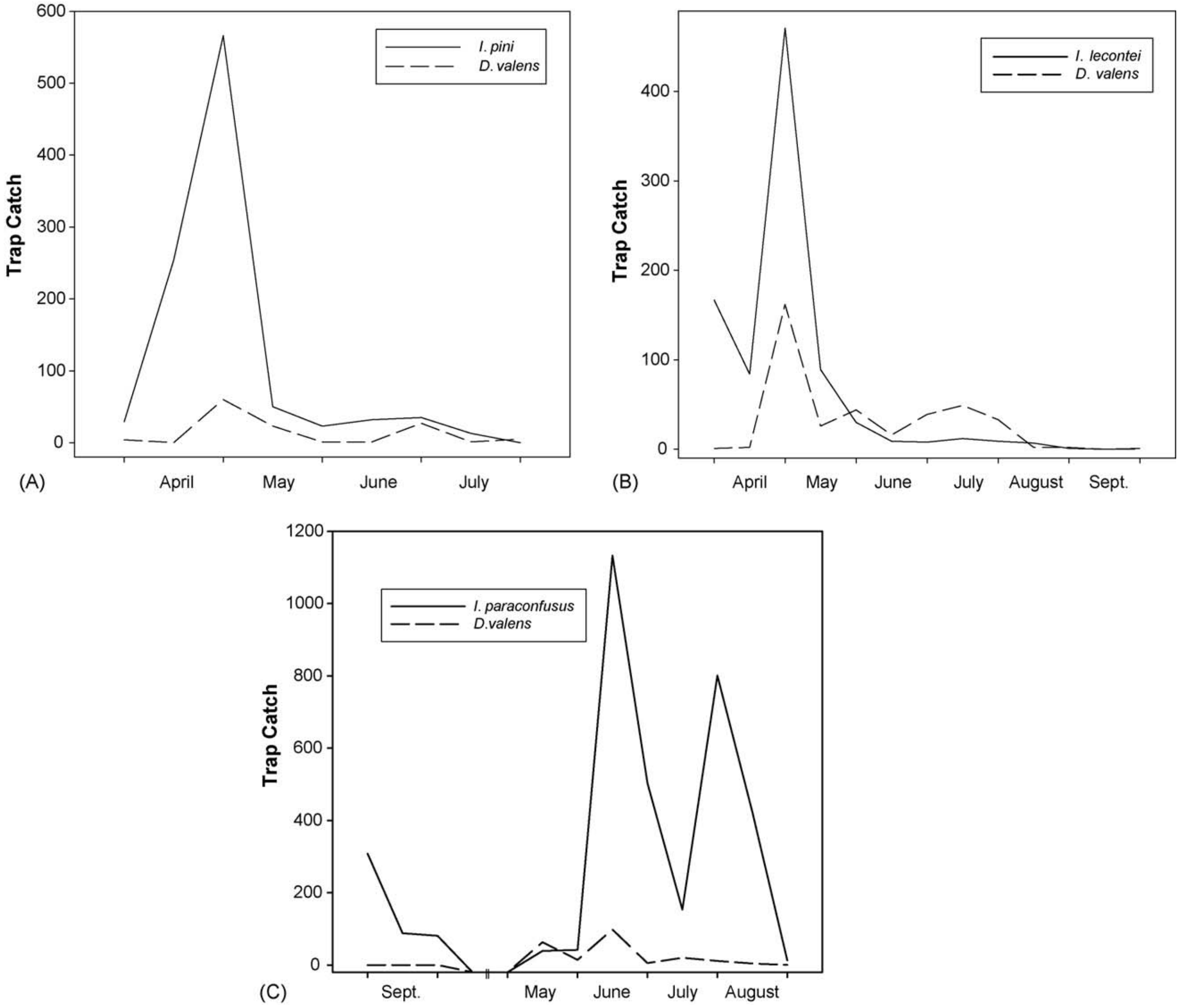

Fig. 1. Flight periodicity of selected bark beetle species based on captures in two (AZ) or three (CA) attractant-baited multiple funnel traps per block, (A) *Ips pini* and *Dendroctonus valens*, Apache-Sitgreaves National Forest, Navajo Co., Arizona, 2004, (B) *I. lecontei* and *D. valens*, Kaibab National Forest, Coconino Co., Arizona, 2004, and (C) *I. paraconfusus* and *D. valens*, Tahoe National Forest, Placer Co., California, 2003–2004.

3.3. Response by bark beetles

A significant treatment effect was observed ($F_{6,\ 21} = 12.63$; $P < 0.001$) among the percentage of residual trees attacked by bark beetles (Fig. 2). A significantly higher proportion of trees were attacked at Apache-Sitgreaves than at Kaibab or Tahoe ($F_{2,\ 21} = 15.31$; $P < 0.001$). The mean percentage of trees attacked by bark beetles ranged from 2.0% (20 trees; untreated) to 30.2% (210 trees; CS) (Fig. 2). A significantly higher percentage of *P. ponderosa* were attacked on plots chipped in spring (CS) than chipped in late summer (CF). No significant differences were observed among CRS, CF, and CRF treatments. Raking did not significantly affect the percentage of bark beetle attacks on residual trees, although we observed a 21.2 and 19.0% reduction in attacks when raking was conducted in conjunction with spring and late summer chipping treatments, respectively (Fig. 2). Chipping in spring (CS, CRS) resulted in a significant increase in the percentage of bark beetle attacks as compared to lopped-and-scattered treatments (LS and LF).

No significant differences in attacks were observed among CF, CRF, LS, LF and untreated control (Fig. 2). In LF plots, we observed a 61.3% reduction in attacks on residual trees as compared to LS, but this differences was not statistically significant (Fig. 2). In lopped-and-scattered treatments, slash was fully colonized by *Ips* species, but few residual trees (1.7 ± 0.9; $n = 6$) were attacked per plot during slash colonization or upon brood emergence. At Tahoe, most bark beetle attacks in untreated controls were limited to white pine blister rust, *Cronartium ribicola* Fisch, infected *P. lambertiana*, which were heavily represented throughout the area. In other plots, such trees were removed during thinning and thus not tallied during post-treatment assessments.

Several bark beetle species were cataloged in the treatment plots, including *D. adjunctus* (AZ), *D. brevicomis* (AZ and CA), *D. ponderosae* (CA), *D. valens* (AZ and CA), *I. lecontei* (AZ), *I. paraconfusus* (CA), and *I. pini* (AZ). Interestingly, we frequently observed *D. brevicomis* infesting slash within LS plots at Tahoe. Many of these slash sections were <15 cm in diameter. In several cases, successful brood development was documented (Dabney and Fettig, unpublished data). Both observations (colonization and brood development) are a rarely reported phenomenon for *D. brevicomis* within slash (Miller and Keen, 1960; Furniss and Carolin, 1977).

Dendroctonus valens was the most frequently observed bark beetle attacking residual trees. The percentage of residual trees attacked by *D. valens* on individual plots ranged from 0% (0 trees; untreated control and LF) to 53.4% (55 trees; CS). The mean number of *D. valens* attacks varied according to treatment ($F_{6,7} = 4.83$; $P = 0.03$), and ranged from 1.2 (untreated control) to 20.8 (CRS) attacks per tree at Tahoe (Fig. 3). In Arizona, 60.6% (CF) to 83.3% (CRS) of stumps were colonized by *D. valens*, however no significant differences were observed among treatment means ($F_{5,\ 12} = 1.72$; $P = 0.21$). A significant correlation was found between the number of trees chipped per plot (x) and percentage of residual trees with *D. valens* attacks (y) ($F_{1,\ 22} = 10.92$; $P = 0.003$; $r = 0.58$; $n = 24$). The relationship was best described by simple linear regression [percentage of residual trees attacked = −4.5 (S.E.M. = 7.4) + 0.19 (number of trees chipped) (S.E.M. = 0.06) $r^2 = 0.34$; $P = 0.003$]

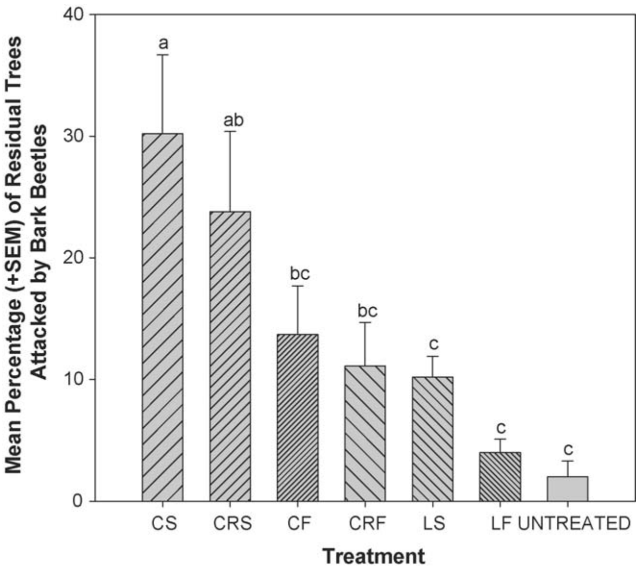

Fig. 2. Mean percentage (+S.E.M.) of residual trees attacked by bark beetles following hazardous fuel reduction treatments in Arizona and California, 2003–2004. Treatments were applied in late spring (S) and late summer (F) and included: (C) thinned biomass chipped and randomly dispersed within each plot, (CR) thinned biomass chipped, randomly dispersed, and raked 2 m from the root collar of residual trees, (L) thinned biomass lopped-and-scattered within each plot, and (Untreated) control. Means followed by the same letter are not statistically different ($P > 0.05$; Tukey's HSD).

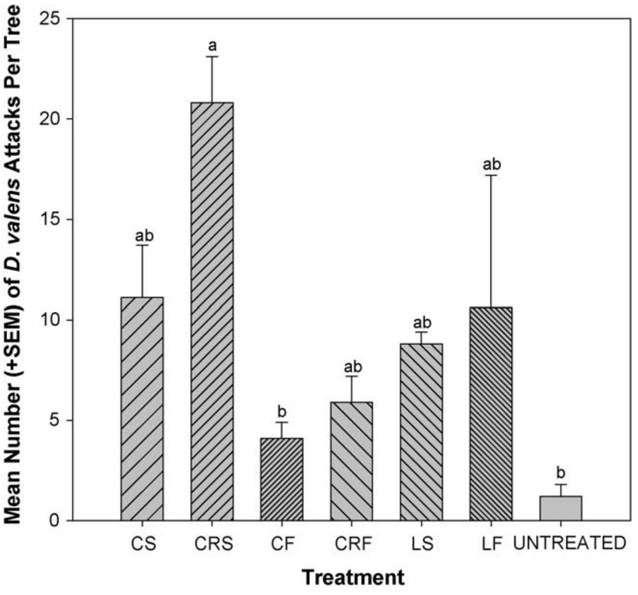

Fig. 3. Mean number (+S.E.M.) of *D. valens* attacks (by visual count of pitch tubes) per tree, Tahoe National Forest, California, 2003–2004. Treatments were applied in late spring (S) and late summer (F) and included: (C) thinned biomass chipped and randomly dispersed within each plot, (CR) thinned biomass chipped, randomly dispersed, and raked 2 m from the root collar of residual trees, (L) thinned biomass lopped-and-scattered within each plot, and (Untreated) control. Means followed by the same letter are not statistically different ($P > 0.05$; Tukey's HSD).

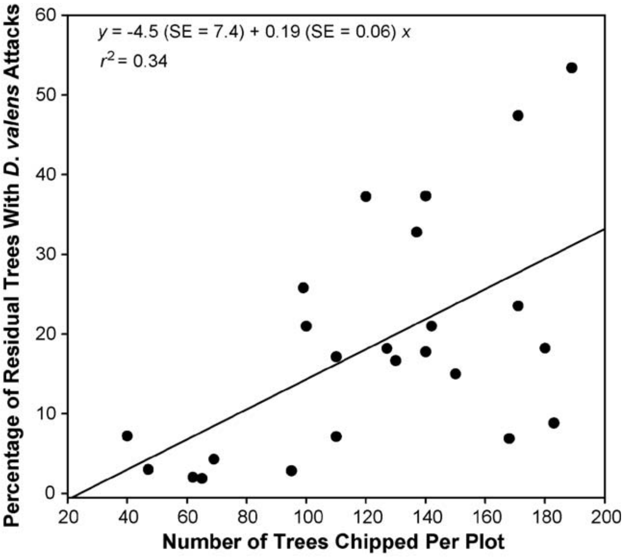

Fig. 4. Linear regression of thinning intensity (number of trees chipped) and percentage of residual trees with *D. valens* attacks ($r^2 = 0.34$; $P = 0.003$). Data points represent measurements from each of twenty-four 0.4 ha study plots.

(Fig. 4). The relationship between the amount of basal area cut and percentage of residual trees with *D. valens* attacks was not statistically significant ($F_{1,\ 22} = 1.17$; $P = 0.29$; $r = 0.23$).

The mean percentage of trees attacked by *D. brevicomis* ranged from 0.4% (5 trees; untreated) to 3.7% (28 trees; CS) (Fig. 5). Significantly more trees were attacked on CS plots than in the untreated control ($F_{6,\ 21} = 2.68$; $P < 0.04$). No other significant differences were observed among treatment means (Fig. 5).

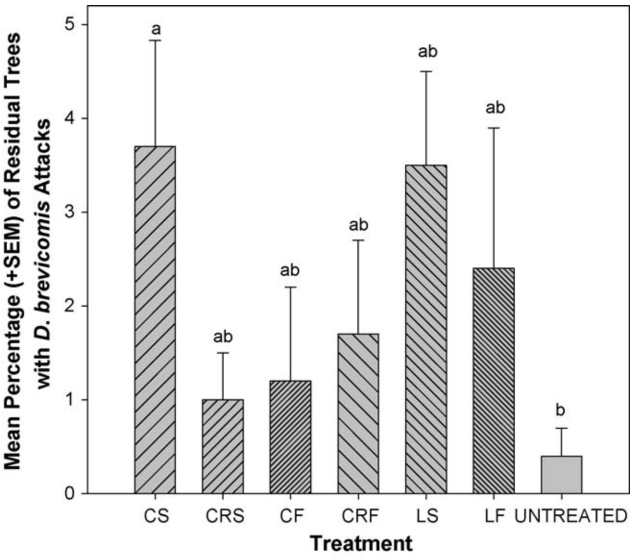

Fig. 5. Mean percentage (+S.E.M.) of residual trees attacked by *D. brevicomis* following hazardous fuel reduction treatments in Arizona and California, 2003–2004. Treatments were applied in late spring (S) and late summer (F) and included: (C) thinned biomass chipped and randomly dispersed within each plot, (CR) thinned biomass chipped, randomly dispersed, and raked 2 m from the root collar of residual trees, (L) thinned biomass lopped-and-scattered within each plot, and (Untreated) control. Means followed by the same letter are not statistically different ($P > 0.05$; Tukey's HSD).

3.4. Bark beetle-caused tree mortality

A significantly greater proportion of trees was killed by bark beetles at Tahoe (3.9%; 73 trees) than Kaibab (1.9%; 30 trees), and at Kaibab than Apache-Sitgreaves (0.6%; 10 trees) ($F_{2,\ 21} = 15.68$; $P < 0.001$). However, no significant differ-

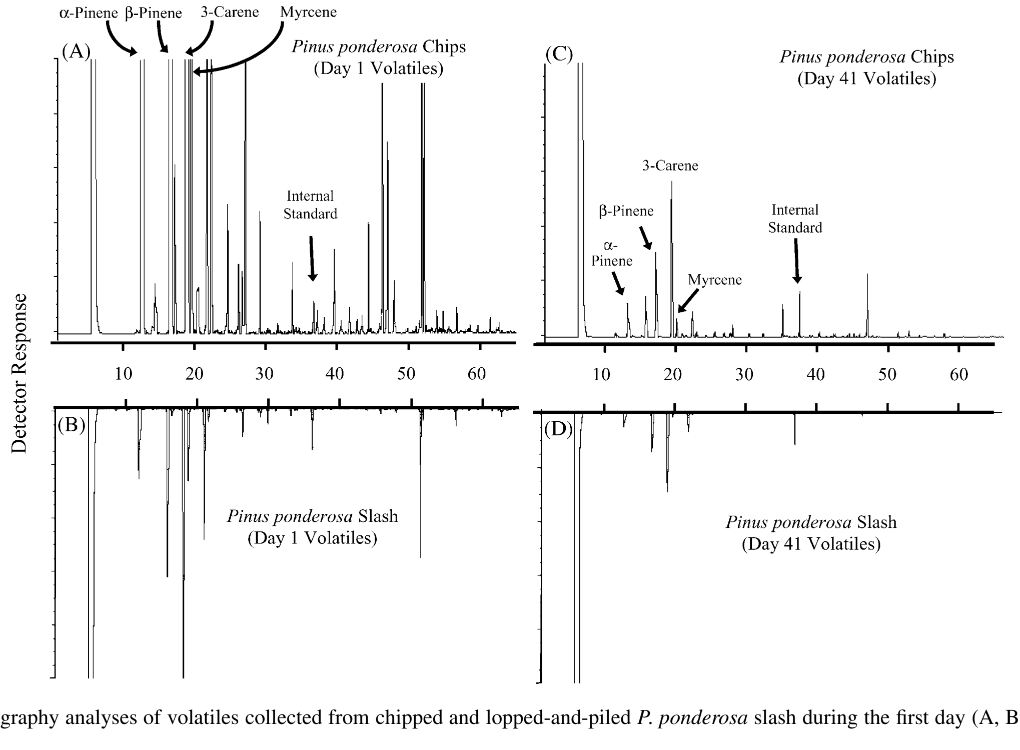

Fig. 6. Gas chromotagraphy analyses of volatiles collected from chipped and lopped-and-piled *P. ponderosa* slash during the first day (A, B) and 41st day (C, D) following cutting.

ences in the amount of bark beetle-caused tree mortality were observed among treatments ($F_{6,\ 21} = 1.63$; $P = 0.19$). Plot-level mortality rates ranged from 0% (0 trees; several treatments) to 8.1% (13 trees; CRF). Mean mortality rates ranged from 0.9% (17 trees; untreated control) to 3.1% (22 trees; CS). Mortality was primarily attributed to *Ips* and *Dendroctonus* species as confirmed by bark removal and verification of gallery patterns at 1.8 m in height on the bole. In Arizona, most trees were killed by a complex of several bark beetle species. For example, several trees were colonized by both *D. brevicomis* and *I. pini*. Five trees (two at Kaibab and three at Tahoe) appeared to have died solely from *D. valens* attacks to the lower bole (mean d.b.h. ± S.E.M. = 27.5 ± 5.2 cm). We felled one tree and confirmed the absence of other scolytids in the upper bole.

3.5. Volatile monoterpenes from chipped and lopped tree biomass

Under our chromatography conditions, retention times for α-pinene, β-pinene, 3-carene, and myrcene were 11.7, 15.7, 17.9 and 18.6 min, respectively. The retention time of the internal standard, 4-decanone, was 35.9 min. During each sample date, the quantity of α-pinene, β-pinene, 3-carene and myrcene collected from chips was greater than that from lopped-and-piled slash (Figs. 6 and 7). These differences were particularly evident early in the experiment. For example, the relative quantities of α-pinene, β-pinene, 3-carene and myrcene were 16.9, 27.9, 23.7, and 23.9 times greater, respectively, from chips than slash during day 1 (Fig. 7). At day 41, these differences were substantially reduced (approximately 2×) (Fig. 7). Monoterpene elution rates declined sharply in chipped treatments during days 1–10 (Fig. 7A), but were relatively constant in lopped-and-piled slash throughout the study (Fig. 7B). Mean temperatures (±S.E.M.) within tanks 15 cm above lopped-and-piled and chipped material were 24.8 ± 0.2 and 24.4 ± 0.1 °C, respectively. Temperatures ranged from 21.3 to 55.4 °C.

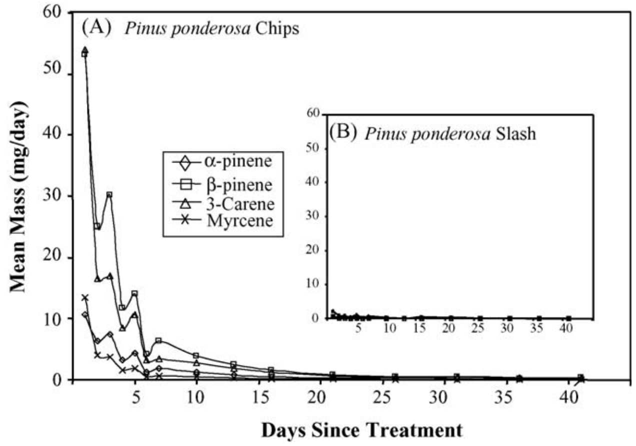

Fig. 7. Monoterpene elution rate curves based on the mass of monoterpene trapped in 24 h samples from *P. ponderosa* chips (A) and lopped-and-piled slash (B) during a 41 d interval. Each data point represents five samples, except for chips from days 3 and 7 where four replicates were analyzed.

4. Discussion

Pinus ponderosa forests throughout western North America are unhealthy and currently at risk to both stand replacement fires and large-scale bark beetle outbreaks (Samman and Logan, 2000). Treatments that reduce stand density are required to restore the long-term sustainability of these forests. This study confirms our initial observations that bark beetle attacks are exacerbated by chipping of sub- and unmerchantable trees, and other logging residues in *P. ponderosa* stands. A three-fold increase in the proportion of residual trees attacked was observed in chipped (CS, CRS) versus lopped-and-scattered (LS, LF) treatments (Fig. 2). Higher levels of attacks occurred when chipping treatments were conducted in spring (Fig. 2), which in general corresponds with peak periods of adult flight activity for several bark beetles (Fig. 1A–C). A similar temporal relationship has been demonstrated between bark beetle attacks and prescribed fire treatments (Harrington, 1993).

Ips attacks on residual trees following thinning normally occur during the initial slash colonization period (Sartwell, 1970). In late summer, the slash produced by lopped-and-scattered treatments is suitable for colonization, but *Ips* flight activity is low (Fig. 1A–C). Slash that is not colonized during early fall is usually unsuitable for colonization the following spring (Parker, 1991) or may be colonized by other competitors (Craighead, 1927). Overwintering mortality, due to prolonged periods of low temperatures, may be significant in some species (Amman, 1973), but not others (Safranyik and Linton, 1991). In California, we collected five slash bolts (15.2 cm min diameter) per plot within LF treatments and sampled these for quantification of brood production (Villa-Castillo and Wagner, 1996). *Ips paraconfusus* produced brood in each bolt and emergence was documented (32.1 ± 5.3 emergence holes per 750 cm^2), but few attacks were observed on standing trees within these plots.

It is likely that the benefit of conducting chipping treatments in late summer (CF) arises, in part, from the relative inactivity of certain *Ips* species and *D. valens* during this time (Fig. 1A–C). In this study, we demonstrated that *D. valens* is attracted to multiple-funnel traps baited with fresh *P. ponderosa* chips. Following chipping, relatively large quantities of monoterpenes, such as α-pinene, β-pinene, 3-carene and myrcene, are present for relatively short periods of time (Figs. 6 and 7). In a similar forest type, monoterpene fluxes increased tenfold during a thinning operation (Schade and Goldstein, 2003). The response of bark beetles to the high concentrations of volatiles released from chips would presumably be most significant when a large segment of the beetle population is most active.

Bark beetles often colonize a few closely related tree species (Wood, 1982). Volatile stimuli associated with host trees are important in mediating behavioral responses in some species (Byers, 1995). Some scolytid species (e.g., *D. valens*) appear to use only host kairomones, whereas others are believed to use a combination of aggregation pheromones and host co-attractants to locate suitable host material (Seybold et al., 1986). For example, *D. brevicomis* produces (+)-*exo*-brevicomin and frontalin, and both pheromone compounds elicit an aggregation response (Browne et al., 1979). Myrcene enhances the response of *D. brevicomis* to its aggregation pheromone (Bedard et al., 1969). In the literature, there is little evidence that *Dendroctonus* and *Ips* species are attracted to monoterpenes in the absence of their aggregation pheromone with the exception of *D. valens* (Hobson et al., 1993), *D. terebrans* (Fatzinger et al., 1987) *I. latidens* (Miller and Borden, 1990, 1992) and perhaps others (Seybold et al., 1986). However, the relatively high levels of monoterpenes produced by chipping may be sufficient to initially elicit a positive response by *D. brevicomis*, and other bark beetles, in order to explain the responses observed in this study. A significantly higher percentage of *D. brevicomis*-attacked trees were observed on chipped (CS) than untreated control plots.

In general, removing chips from the base of residual trees resulted in a 19.3% (CRF) and 21.2% (CRS) reduction in bark beetle attacks, but these differences were not statistically significant (Fig. 2). Removal of chips from the base of residual trees may reduce a strong monoterpene odor source from the basal bole area (Fig. 7), thereby reducing the probability of successful host finding and subsequent colonization by some bark beetle species. However, the potential benefits of raking may be offset if raking injures fine roots that must be rebuilt (Wilson, 1970), and are of higher priority for allocation of photosynthate than insect and disease resistance mechanisms in most conifers (Oliver and Larson, 1996). Mechanical root damage may create an additional monoterpene source or further weaken trees rendering them susceptible to other biotic agents, such as root weevils and pathogens (Sullivan et al., 2003). Based on monoterpene degradation curves (Fig. 7), raking should occur immediately after chipping to achieve maximum effect. In our study, raking was delayed for up to 48 h following chipping and the large amount of monoterpenes released during this time could have reduced the effectiveness of this treatment. At Tahoe, *D. valens* was observed initiating fresh attacks on residual trees while chipping was being conducted. The practice of raking fuels away from the boles of trees to reduced scorch during prescribed fires is common (Jerman et al., 2004), but to our knowledge raking has not been used operationally to remove chips away from the base of residual trees.

Dendroctonus valens is a common bark beetle species found throughout much of North America (Furniss and Carolin, 1977). (−)-β-Pinene is highly attractive to both sexes and the effect increases with release rate (Hobson et al., 1993). Hobson et al. (1993) also reported significant increases in *D. valens* trap catch attributable to 3-carene and (+)-α-pinene. Combinations of these three monoterpenes are a highly effective bait in multiple-funnel traps (Fettig et al., 2004). In our study, initial quantities of α-pinene, β-pinene, 3-carene and myrcene eluting from chips were 16.9, 27.9, 23.7 and 23.9 times greater, respectively, than lopped-and-piled slash (Fig. 7), which likely explains the response of *D. valens* to freshly chipped sites (Figs. 3 and 4), and to chip-baited traps. It is possible that delaying the chipping of sub- and unmerchantable trees after felling for several weeks could result in monoterpene degradation curves similar to those described for lopped-and-piled slash (Fig. 7). Such monoterpene levels may not elicit the *D. valens* response observed in our plots.

Attacks by *D. valens* are usually confined to basal portions of fire-damaged, stressed, weakened, or dead and dying trees (Furniss and Carolin, 1977). Significant tree mortality has been attributed to *D. valens* in a 17-year-old *P. ponderosa* plantation in northern California (Rappaport et al., 2001), and in *P. tabuliformis* Carriere forests in China (Sun et al., 2004; Yan et al., 2005). Overall, much uncertainty exists as to whether *D. valens* is a primary mortality agent. It is known to vector a rather virulent strain of the ophiostomoid fungus, *Leptographium terebrantis* Barras and Perry (Owen et al., 1987). In our study, mortality was defined as the presence of crown fading, an irreversible symptom of pending tree mortality. It is possible that trees have been attacked at sufficient densities to cause tree mortality, but have not yet faded (Furniss and Carolin, 1977). The negative effects of prolonged and large numbers of *D. valens* attacks on individual tree health may not be realized for some time. We caution the reader that the mortality rates reported here are likely conservative. In the future, we hope to re-assess these plots on an annual basis to determine if bark beetle attack and mortality patterns progress. The effect of *D. valens* as a predisposing factor to subsequent attacks by more aggressive congenerics, and other species, can not be isolated in our study.

Our estimates of tree mortality were confined within plot boundaries, but treatment effects may actually influence a larger area. Data collected adjacent to the boundary of chipped plots revealed large numbers of freshly-attacked trees. In addition, we observed that many *D. brevicomis* and *D. ponderosae* attacks occurred immediately within the perimeter of the chipped area. Bark beetle outbreaks have been associated with high stand densities, presumably because below ground competition for nutrients and water lead to reductions in host vigor (Mitchell et al., 1983; McGregor et al., 1987; Amman et al., 1988; Fiddler et al., 1989). Thinning not only affects the vigor of residual trees by increasing growing space (Larsson et al., 1983; Mitchell et al., 1983), but the physical environment around individual trees. For example, phloem and outer bark temperatures increase after thinning (Amman, 1989), and may accelerate the development of certain bark beetles rendering them more susceptible to freezing when overwintering (Amman, 1973). The environment created by our chipping treatments likely increased plot risk in the short-term by the production of large amounts of attractive monoterpenes, but simultaneously decreased hazard by increasing the amount of growing space allocated to each residual tree, and by influencing the dispersal of volatile compounds with these stands. Untreated areas immediately adjacent to freshly chipped plots do not benefit from the positive effects of thinning (i.e., growing space), but suffer a similar level of risk associated with high levels of monoterpenes present beneath the forest canopy. Monoterpenes emitted during forestry operations may also give rise to high levels of photo-oxidants that may present another form of stress on trees in and around the area of operation (Strömvall and Petersson, 1991; Schade and Goldstein, 2003).

Nitrogen is the most common limiting nutrient for tree and microorganism growth (Oliver and Larson, 1996). The presence of large quantities of chips on the forest floor alters the C:N ratio, and could result in soils and trees becoming nitrogen deficient for some period of time (Bulmer, 2000). The effects of nitrogen deficiency on tree vigor and growth have been well defined (Oliver and Larson, 1996), and could also impact long-term tree susceptibility to bark beetle attack.

Our study has demonstrated that bark beetle attacks are exacerbated by chipping of sub- and unmerchantable trees during the spring within *P. ponderosa* stands and has important implications to forest management. Managers should conduct chipping during periods of relative bark beetle inactivity (e.g., late summer through winter) to reduce attacks on residual trees. Reasonable effort should be made to limit large quantities of chips from directly contacting residual trees. Treatments that promote the desiccation of slash and rapid decay of monoterpenes prior to chipping should be considered. The percentage of *D. valens* attacked trees was positively correlated with the number of trees chipped (Fig. 4), suggesting that the response of this species will increase with thinning (and chipping) intensity. Treatment units should be designed to minimize the amount of edge per unit area as chipping may influence bark beetle attacks beyond the spatial scale of treatments. Trees attacked in adjacent areas may increase bark beetle populations on a localized basis and threaten neighboring treated areas. This may be of particular importance in the WUI where large amounts of boundary exist per unit area; where bark beetle-caused tree mortality would increase fuel loads in areas likely not to be re-treated for many years; and where residual trees are of generally higher value.

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