POPULATION ECOLOGY

Bark Beetle Attacks on Ponderosa Pine Following Fire in Northern Arizona

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ABSTRACT There is little quantitative information on relationships between insect attacks and fire damage for ponderosa pine, *Pinus ponderosa* Douglas ex Lawson, in the southwestern United States. Tree mortality and insect attacks were measured on 1,367 trees for three years after a spring wildfire (4 May 1996), a summer wildfire (20 June 1996), and a fall prescribed fire (9 September 1995) in northern Arizona. Western pine beetle, *Dendroctonus brevicomis* LeConte, mountain pine beetle, *D. ponderosae* Hopkins, roundheaded pine beetle, *D. adjunctus* Blandford, red turpentine beetle, *D. valens* LeConte, *Ips* species, and wood borers in the *Buprestidae* and *Cerambycidae* families were found in fire-damaged trees. The most frequently occurring insects, listed from most to least frequent, were wood borers, red turpentine beetle, *Ips* spp., western pine beetle, roundheaded pine beetle, and mountain pine beetle. Trees attacked by *Dendroctonus* and *Ips* spp. as a group had more crown damage from fire than unattacked trees. The percentage of trees attacked by *Dendroctonus* and *Ips* species was lowest during the fall fire (11%, 25 of 222 trees), intermediate during the summer fire (19%, 154 of 833 trees), and highest during the spring fire (41%, 127 of 312 trees). More than one-half of all wood borer colonization (58%) and attacks by western pine beetle (68%), roundheaded pine beetle (56%), and *Ips* spp. (66%) occurred in the first year after the fire. Measures of tree damage from fire and insect attacks were used to develop logistic regression models of tree mortality to quantitatively investigate factors that influenced tree mortality. Tree mortality 3 yr postfire was low until crown damage by fire exceeded 70–80% for unattacked trees, 40–50% for trees with partial attacks by *Dendroctonus* and *Ips* species, and 30–40% for trees with mass attacks. We concluded that several *Dendroctonus* and *Ips* species colonize fire-damaged ponderosa pines in northern Arizona and colonization is promoted by heavy crown damage from fire.

KEY WORDS logistic regression, *Pinus ponderosa,* tree mortality, *Dendroctonus, Ips*

FOREST FIRES ARE A COMMON disturbance agent in ponderosa pine, *Pinus ponderosa* Douglas ex. Lawson, forests of the western United States, and often cause considerable tree damage and mortality. Fire can kill a tree by damage to the roots, bole, or crown. Severe damage to one of these tissues or light to moderate damage to more than one can lead to postfire tree mortality (Ryan 1990, 1998, 2000). However, tree mortality is not caused solely by the direct effects of fire; bark beetle attacks on living trees after fire have been a concern for forest managers for quite some time (e.g., Miller and Patterson 1927). Trees weakened by fire damage have been reported to be more susceptible to attack from some secondary mortality agents, such as bark beetles and fungal pathogens (Miller and Patterson 1927, Miller and Keen 1960, Furniss and Carolin 1977, Geiszler et al. 1980, Littke and Gara 1986, Thomas and Agee 1986, Amman and Ryan 1991, Agee 1993, McCullough et al. 1998, Ryan 1998, Wallin et al. 2003). Moreover, understanding of the role of fire in bark beetle populations is limited because many factors may influence bark beetle colonization and performance in fire-damaged trees (e.g., Miller and Keen 1960, McCullough et al. 1998, DeNitto et al. 2000, Wallin et al. 2003).

Models of tree mortality after fire have been developed for numerous conifer species in the western United States (Reinhardt and Ryan 1988, Ryan and Reinhardt 1988, Harrington 1993, Finney and Martin 1993, Stephens and Finney 2002). These models typically use measures of fire damage, tree size, or species-specific measures of fire resistance to predict tree mortality. Despite considerable research on quantitative modeling of tree mortality after fire (Wyant et al. 1986; Harrington 1987, 1993; Reinhardt and Ryan 1988; Ryan and Reinhardt 1988; Ryan et al. 1988; Ryan 1998; Stephens and Finney 2002), use of insect attacks in such models has been limited to a few species and regions. Peterson and Arbaugh (1986) developed a logistic regression model for Douglas-fir, *Pseudotsuga menziesii* Franco, that used crown scorch and insect

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damage to predict tree mortality after fire in the northern Rocky Mountains. Menges and Deyrup (2001) used path analysis to explore relationships among bark beetle attacks, fire characteristics, and vegetation structure in Florida slash pine, *Pinus elliottii* variety *densa.* Bradley and Tueller (2001) used logistic regression to model attacks on Jeffery pine, *Pinus jeffreyi* Grev. and Balf., by red turpentine beetle, *Dendroctonous valens* LeConte, Jeffery pine bark beetle, *Dendroctonous jeffreyi* Hopkins, and *Ips* species based on fire damage and intensity in Lake Tahoe, NV.

For ponderosa pine, previous studies have reported bark beetles in fire-damaged trees but often did not identify insect species or relate beetle attacks to levels of fire damage (Connaughton 1936, Morris and Mowat 1958, Dieterich 1979, Regelbrugge and Conard 1993). Ponderosa pines moderately damaged by fire in southern Oregon were more susceptible to attack by western pine beetle, *Dendroctonus brevicomis* LeConte, than lightly damaged trees (Miller and Patterson 1927). Miller and Keen (1960) reported that crown scorch levels above 50% increased ponderosa pine susceptibility to attack by western pine beetle after fire in California, Idaho, and southern Oregon. Wallin et al. (2003) reported that crown scorch >75% in ponderosa pine reduced resin defenses and tree resistance to attacks by *Dendroctonus* and *Ips* species compared with lower amounts of scorch in one northern Arizona wildfire. Studies of other pine species have also shown a positive relationship between tree crown damage by fire and bark beetle attacks (Amman and Ryan 1991; Ryan and Amman 1994, 1996; Rasmussen et al. 1996; Bradley and Tueller 2001; Menges and Deyrup 2001; Santoro et al. 2001; Hanula et al. 2002).

Roundheaded pine beetle, *Dendroctonus adjunctus* Blandford], western pine beetle, mountain pine beetle, *Dendroctonus ponderosae* Hopkins, red turpentine beetle, *Ips* species, and wood borers in the *Buprestidae* and *Cerambycidae* families are common subcortical insects that colonize ponderosa pine in northern Arizona. At endemic population levels, most *Ips* and *Dendroctonus* species attack highly stressed trees or felled trees, whereas at epidemic population levels, they can colonize healthy trees (e.g., Wood 1972, 1982; Raffa and Berryman 1982, 1983; Bentz et al. 1996). Wood borers in the *Buprestidae* and *Cerambycidae* families primarily use bark and xylem of dead or dying trees (Schmid and Parker 1990, Rasmussen et al. 1996, Powell et al. 2002).

The objective of our study was to examine relationships between fire damage to ponderosa pine and attacks by bark beetles and woodborers over a 3-yr period after three fires in northern Arizona forests. Logistic regression was used to evaluate the role of crown damage by fire and insect attacks in tree mortality.

Materials and Methods

Study Sites. The fall fire was a prescribed fire that was ignited 9 September 1995 and burned until 11 September 1995. The fall fire was located on the Peaks Ranger District, Coconino National Forest, ≈24 km west of Flagstaff, at a latitude of 35° 17.5′ N and a longitude of 111° 52.5′W (Fig. 1). The study site was 23.8 ha in size at an elevation range of 2225–2255 m. Aspect is generally south-southeast with slopes of 0–8%. Soils within the study area are fine, montmorillonitic Typic Argiborolls, and are gravely loams derived from residual basalt/cinder parent material (Miller et al. 1995). Vegetation at this site is a ponderosa pine-bunch grass type (USDA Forest Service 1997), with ponderosa pine as the only tree species. Ponderosa pine in the study area ranged from 7.4 cm to 44.5 cm in diameter at breast height (DBH); a few larger old-growth trees were scattered throughout the site.

The spring wildfire occurred 4 May 1996 and was located on the Peaks Ranger District, Coconino National Forest (latitude 35° 15.0′ N, longitude 111° 35.0′ W) (Fig. 1). The study site was in an 80-ha portion of the 130-ha Side wildfire at an elevation range of 2072–2195 m. Site aspect is predominately flat except where dissected by two east-west running intermittent stream courses. Soils are mixed Mollic Eutroboralfs, and are very stoney, sandy loams derived from alluvium, mixed igneous parent material (Miller et al. 1995). Vegetation at this site was a ponderosa pine-cliffrose type (USDA Forest Service 1997) with ponderosa pine as the dominant tree species. Ponderosa pine in the study area ranged in DBH between 10.2 and 91.4 cm. Unlike the fall prescribed fire, mature ponderosa pines occurred throughout the study area as scattered trees and groups of 5–20 trees.

The summer wildfire started 20 June 1996 and was located on the North Kaibab Ranger District, Kaibab National Forest, ≈32 km south-southwest of Jacob Lake, AZ at a centroid latitude of 36° 35′ N and a longitude of 111° 23′ W (Fig. 1). This fire burned until 28 June 1996, when changing weather conditions stopped its spread. The study site was 6,475 ha of the 21,449-ha Bridger-Knoll wildfire. Elevation for the area ranged between 2134 and 2255 m. All aspects were represented and slope percent ranged between 0% and 20% in bottomland areas to over 40% on ridge tops. Soils are clayey-skeletal and fine montmorillonitic, Mollic Eutroboalfs, loams and gravely loams, derived from residuum limestone parent material (Brewer et al. 1991). Vegetation at the site was a ponderosa pine-gambel oak type (USDA Forest Service 1997) with ponderosa pine the dominant tree species. DBH ranged between 22.9 and 106.2 cm.

Mean annual precipitation for the fall and spring fire areas is 57.9 cm with a mean annual snowfall of 276.4 cm (NOAA 1997), and, for the months of January and July, the mean daily minimum and maximum temperatures are −9.2°C and 5.7°C and 10.1°C and 27.7°C, respectively (NOAA 1997). Mean annual precipitation for the summer fire area is 52.5 cm with a mean annual snowfall of 267.7 cm, and for the months of January and July, the mean daily minimum and maximum temperatures are −9.1°C and 4.4°C, and 10.3°C and 26.3°C, respectively (National Climatic Data Center, station 024418, http://www.wrcc.dri.edu).

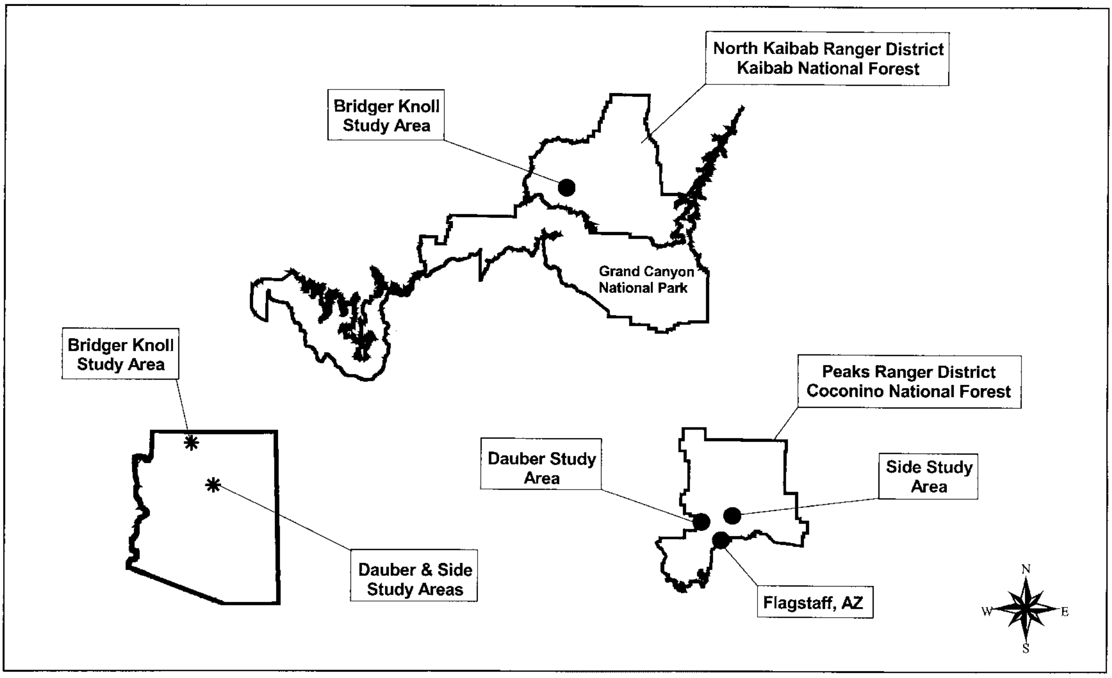

Fig. 1. Study site locations. The Side Study Area (spring wildfire) burned in the spring 1996, the Bridger Knoll Study Area (summer wildfire) burned in the summer 1996, and the Dauber Study Area (fall prescribed fire) burned in the fall 1995.

Fire Behavior and Intensity. Because of the opportunistic nature of this study, direct observations of fire behavior characteristics, such as flame length, are not available. Instead, BEHAVE version 4.4 (Andrews 1986), a fire behavior prediction model, was used to predict the possible range of fire characteristics that occurred across each site. We used BEHAVE to predict fire behavior in the flaming front based on the following inputs: Northern Forest Fire Laboratory (NFFL) fire behavior fuel models (Anderson 1982), percent fuel moisture content of the 1-, 10-, and 100-h time lag fuels (Fosberg and Deeming 1971, Rothermel 1983), midflame windspeed (Rothermel 1983), and percent slope (Table 1). Required fuel moisture and wind data for the model were obtained from USDA Forest Service records for each fire.

Fireline intensity, because of its relation to flame length, is best used to express fire effects on materials affected by convective heating, such as foliage (Van Wagener 1973, Finney and Martin 1993). Agee (1993) provides ranges of fireline intensity for surface fire (0–258 kW m^{-1}), understory fire (258–2,800 kW m^{-1}), and crown fire (>2,800 kW m^{-1}). Based on these criteria, the fall fire was primarily a surface fire that reached the crowns of occasional trees, whereas the spring and summer fires varied from surface to crown fires (Table 1).

The fall fire was a prescribed burn of both natural and activity fuels (fuels generated from logging activity). Strip ignitions designed to create strip head fires were initially used to ignite the area. Later into the ignition phase, lighting patterns were changed to cause low-intensity backing fires. The 1-, 100, 100-, and 1,000-h time-lag moisture classes (Fosberg and Deeming 1971, Rothermel 1983) were within normal ranges for prescribed burning and winds were light (Table 1).

Table 1. Fuel model, fuel moisture, slope, and windspeed values used in the fire behavior model BEHAVE to predict the range of fire characteristics experienced across the study sites

Parameter	Fall prescribed fire	Spring wildfire	Summer wildfire
Fireline intensity (kW m^{-1})	44 to 234	338 to 3,726	118 to 4,132
Fuel model[a]	9,11	2,9	2,9
1-h fuel moisture content (%)	9	3	2
10-h fuel moisture content (%)	10	4	3
100-h fuel moisture content (%)	14	5	4
1,000-h fuel moisture content (%)	18	8	6
Slope (%)	5	5	5–30
Windspeed[b] (km h^{-1})	3.2–8.0	8.0–12.9	3.2–32.2

[a] Following Anderson (1982).

[b] Midflame windspeed (Rothermel 1983).

Predicted peak fireline intensity at the fall fire was lowest of all sites (Table 1).

In contrast to the fall fire, the spring fire was a human-caused wildfire ignited at ≈1430 hours; fire danger rating for the Coconino National Forest was extreme at time of ignition. Fuel moisture percentages for 1-, 10-, 100-, and 1,000-h time-lag moisture classes were extremely low (Table 1), and fire behavior was extreme. Rates of fire spread were 0.8 km per hour with spotting 0.4 km in front of the main fire. This extreme fire behavior was primarily driven by low fuel moisture content and high wind.

The summer wildfire was ignited by lightning within Grand Canyon National Park and burned onto the North Kaibab Ranger District, Kaibab National Forest, the next day. Fire danger rating for the Kaibab National Forest at the time of ignition was extreme. As with the spring fire, fuel moisture percentages for 1-, 10-, 100-, and 1,000-h time-lag fuels were extremely low (Table 1). Initial fire behavior for the summer fire was extreme with rates of spread 0.4–0.6 km per hour and spotting 0.2 km in front of the main fire. Low fuel moisture content and high wind were important drivers of the extreme fire behavior that occurred at this site.

Tree Sampling. Initial assessments of tree condition were completed in fall 1996, 5 mo postfire for the spring and summer fires and 11 mo postfire for the fall fire. Trees with no foliage (e.g., 100% consumption of foliage) were not included in the initial sampling because they were assumed to be dead immediately after the fire. Mortality was assessed for every tree (n = 1,367 total) in September 1997, 1998, and 1999. Trees were recorded as dead if no green foliage was visible on the tree.

For the fall fire, 16, 0.04-ha plots were used to collect data on 222 trees. For the the summer fire, 75 0.08-ha plots and 46 0.4-ha plots, established by Kaibab National Forest personnel, were used to collect data on 833 trees. For the fall and summer fires, plots were established on systematically located grids using a random start. At the spring fire, a total of 312 trees were measured. Of these trees, 241 were measured on 18 archaeological sites because these sites were excluded from plans for salvage logging. To increase the sample size of large trees, seven transects 20 m in width, bounded by the fire perimeter, and oriented across the primary direction of the fire were used to sample an additional 71 trees on the spring fire site.

We measured a total of 16 tree size, fire damage, and site variables on each tree (McHugh and Kolb 2003). However, in this paper we use only one measure of tree size (DBH), two measures of fire damage (crown scorch, crown consumption), and one derived measure of fire damage (total crown damage [TCD]), for brevity. We measured all variables on the fall and spring fires in all years. For the summer fire, eight U. S. Forest Service personnel measured variables after our training. We checked 80% of their year 1 measurements on the summer fire, and found them to be similar to our measurements.

Crown damage characteristics were measured on all trees on cloud-free days perpendicular to the direction of the sun. Crown scorch was estimated visually to the nearest 10% and was defined as the percentage of prefire live crown volume scorched, but not consumed by the fire (Ryan 1982, 1983; Peterson 1985; Harrington 1987). Crown consumption also was estimated visually to the nearest 10%, and was defined as the proportion of crown volume consumed by fire. Because scorch and consumption of tree crowns are often asymmetrical, measurements from four quadrants of the crown were averaged for each tree. Total crown damage was calculated by adding percent crown volume scorched and percent crown volume consumed. DBH was measured from the high ground side at 1.37 m above the forest floor to the nearest 0.10 cm.

All trees were examined once a year in the fall over the first 2 m of the bole above the ground for external evidence of attack by several taxa of subcortical insects, including presence of pitch tubes, boring dust, and woodpecker foraging. Because of the large sample sizes in our study, it was impractical to examine the entire length of the bole of each tree for insect attacks. Consequently, our estimates of the number of trees with evidence of attack by subcortical insects and colonization by wood borers are likely conservative. When signs of beetle activity were present, bark samples were removed so the insects and/or their characteristic gallery patterns could be identified (Beatty 1986). Bark sections were only removed on trees considered dead. Attacks by red turpentine beetle were assessed yearly and the number of attacked quadrants on the lower bole recorded. The presence or absence of woodborers in the *Buprestidae* and *Cerambycidae* families was established by looking for external indicators, such as emergence holes, boring dust, and woodpecker feeding, and by removing bark samples to locate characteristic larval gallery patterns.

Attacks by primary or tree-killing species of bark beetles, such as western pine beetle, mountain pine beetle, roundheaded pine beetle, and *Ips* spp., were classified using three categories: none, partial, and mass based on the following criteria. If *Dendroctonus* and *Ips* species were not present in the tree, an insect attack rating (IAR) of none (0) was assigned. If attacks by these species occupied <75% of the bole circumference, an IAR of partial attack (1) was assigned. If attacks by *Dendroctonus* and *Ips* species occupied >75% of the tree bole circumference, an IAR of mass attack (2) was assigned.

Data Analysis. One-way analysis of variance (ANOVA) was performed for DBH, crown scorch, crown consumption, and TCD to test the hypothesis of no difference among fires. Pair-wise multiple comparisons were conducted to test for significant differences between group means based on Fischer's protected least significant difference (LSD) at $\alpha = 0.05$ (Ott 1992).

Two sample t-tests were conducted to test the hypothesis of no difference between live and dead trees for fire damage characteristics, IAR, and DBH within

Table 2. Summary statistics for three fires in northern Arizona for diameter breast height (DBH) and crown damage variables (means ± SEM). ANOVA was performed to test for differences in DBH and crown damage among fires

	Fall prescribed	Spring wildfire	Summer wildfire	ANOVA results		
				df	*F*	*P*
DBH (cm)	24.2a ± 0.44	40.1b ± 1.20	51.7c ± 0.57	2, 1364	256.760	≤0.001
Crown scorch (%)	45.9%a ± 2.23	55.3%b ± 1.78	27.3%c ± 1.07	2, 1364	102.952	≤0.001
Crown consumption (%)	N/A	10.3%a ± 1.17	4.4%b ± 0.55	1, 1143	26.406	≤0.001
Total crown damage (%)	45.9%a ± 2.23	65.6%b ± 1.86	31.5%c ± 1.22	2, 1364	113.367	≤0.001

Means followed by different letters are significantly different based on Fisher's protected LSD test at $\alpha = 0.05$.

each fire. Logistic regression models of tree mortality were developed for each fire using SPSS Version 8.0 (SPSS 1998). The independent variables considered for these models were DBH, crown scorch, crown consumption, TCD, and IAR. Data on IAR were pooled over all *Dendroctonus* and *Ips* species for each tree because most trees were attacked by several insect species. Also, the small number of occurrences of individual insect species made pooling over species the only feasible approach in our modeling.

For each fire, independent variables were screened for their influence on tree mortality by comparing values for dead versus live trees using two sample *t*-tests. Screening consisted of using only independent variables that differed between live and dead trees ($P \leq 0.10$), were not strongly correlated ($r \leq 0.50$) with other independent variables, and were significantly ($P \leq 0.10$) related to tree mortality. Model goodness-of-fit was assessed based on the following diagnostic statistics for each model: Studentized residual, Deviance and Cook's distance values, and a test of the model null hypothesis that all model coefficients are 0 except the constant, which is comparable to the overall *F* test for regression (Hosmer and Lemeshow 1989, Norusis 1994). The model used to predict tree mortality was:

$$P_m = 1/(1 + \exp(-(b_0 + b_1x_1 + \ldots + b_nx_n)))$$

where P_m is the probability of tree mortality, b_0, b_1, and b_n are regression coefficients, and x_1 and x_n are representative independent variables.

Receiver operating characteristic (ROC) curves were used to assess the overall accuracy for each logistic regression model (Saveland and Neuenschwander 1990, Finney and Martin 1993, Regelbrugge and Conard 1993, Finney 1999, Stephens and Finney 2002). The ROC curve is a plot of the probability of a true positive prediction, or hit rate (tree is classified as dead when it is dead), versus the probability of a false positive, or false alarm rate (type II error; tree is classified dead when it is alive) by varying the decision criterion from 0 to 1 for group membership (Saveland and Neuenschwander 1990, Bradley 1996). The ROC curve value can vary from 0.50, which is no better than chance, to 1.0, in which all predictions are correct (Saveland and Neuenschwander 1990, Swets 1996). ROC values between 0.50 and 0.70 indicate low accuracy, values between 0.70 and 0.90 indicate moderate accuracy, and values >0.90 indicate very high accuracy (Swets 1996).

Results

Tree Characteristics by Fire, Insect Attack Level, and Mortality Group. Average tree DBH was significantly smaller for the fall fire compared with the spring and summer fires (Table 2). DBH averaged over live and dead trees was similar for attacked trees (with confirmed attacks of *Dendroctonus* or *Ips* species) and unattacked trees at the fall and spring fires, whereas attacked trees were significantly larger than unattacked trees at the summer fire (Table 3). However, for dead trees (Table 4), DBH of attacked trees was significantly greater than unattacked trees at the fall fire ($t = 2.715$; df = 38; $P = 0.010$) and the summer wildfire ($t = 2.453$; df = 114; $P = 0.016$), but not at the spring wildfire ($t = 1.296$; df = 99; $P = 0.198$). For live trees (Table 4), DBH was significantly larger for attacked versus unattacked trees only at the summer fire ($t = 2.822$; df = 715; $P = 0.005$). Live unattacked trees had significantly larger DBH than dead unattacked trees at the fall and spring fires, but not at the summer fire (Table 4).

Attacked trees were divided into those that died by the end of the study and those that lived. Attacked live and dead trees had similar DBH at the fall and summer fires, whereas live attacked trees (i.e., attacked but still living at the end of the study) were marginally larger than dead attacked trees at the spring fire (Table 4). Attacked live trees were attacked only by red turpentine beetle, whereas attacked dead trees usually were attacked by primary bark beetles (e.g., western pine beetle, mountain pine beetle, roundheaded pine beetle) or *Ips* species in combination with wood borers.

Average crown scorch differed significantly among fires and was lowest on the summer fire, intermediate on the fall fire, and highest on the spring fire (Table 2). Attacked trees at all fires had significantly more crown scorch than unattacked trees (Table 3), and attacked dead trees had significantly more crown scorch than attacked live trees (Table 4). Crown scorch of unattacked dead trees was significantly higher than unattacked live trees for all fires and was nearly equal to crown scorch levels of attacked dead trees (Table 4).

Crown consumption occurred only in the spring and summer fires, and was significantly lower in the summer fire compared with the spring fire (Table 2). Crown consumption of attacked trees was significantly higher than unattacked trees for spring and summer wildfires, and crown consumption of attacked

Table 3. Means (±SEM) of tree variables by season of fire (fall, spring, summer) for attacked and unattacked ponderosa pines 3 yr postfire in northern Arizona. *P* values are results of *t*-tests between attacked versus unattacked trees. Attacked trees have attacks by *Dendroctonus* and *Ips* species, and unattacked trees do not

Season/variable	Attacked	Unattacked	*t*	*P*
Fall	*n* = 25	*n* = 197	df = 220	
DBH (cm)	25.8 ± 1.53	24.1 ± 0.46	1.280	0.202
Crown scorch (%)	58.0 ± 6.81	44.5 ± 2.35	1.927	0.055
Crown consumption (%)	0 (0)	0 (0)	N/A	N/A
Total crown damage (%)	58.0 ± 6.81	44.5 ± 2.35	1.927	0.055
Insect attack rating	1.3 (0.01)	0 (0)	39.832	≤0.001
Spring	*n* = 127	*n* = 185	df = 310	
DBH (cm)	40.6 ± 2.05	39.7 ± 1.45	0.334	0.738
Crown scorch (%)	66.2 ± 2.42	47.8 ± 2.35	5.286	≤0.001
Crown consumption (%)	18.6 ± 2.25	4.5 ± 1.03	6.274	≤0.001
Total crown damage (%)	84.8 ± 1.73	52.4 ± 2.48	9.774	≤0.001
Insect attack rating	1.4 ± 0.004	0 (0)	39.211	≤0.001
Summer	*n* = 154	*n* = 679	df = 831	
DBH (cm)	55.8 ± 1.32	50.7 ± 0.63	3.515	0.001
Crown scorch (%)	46.7 ± 2.68	22.8 ± 1.09	9.116	≤0.001
Crown consumption (%)	7.1 ± 1.54	3.7 ± 0.58	2.419	0.016
Total crown damage (%)	53.8 ± 2.91	26.5 ± 1.27	9.123	≤0.001
Insect attack rating	1.2 ± 0.003	0 (0)	82.938	≤0.001

trees in the spring fire was 2.6 times higher than attacked trees in the summer fire (Table 3). Crown consumption of dead trees was significantly greater than crown consumption of live trees regardless of attack level (Table 4).

TCD was significantly different among fires and was lowest in the summer fire, intermediate in the fall fire, and greatest in the spring fire (Table 2). For all fires, TCD was significantly higher for attacked trees versus unattacked trees (Table 3). For all fires, TCD of dead trees was significantly higher than live trees regardless of attack level (Table 4).

The percentage of trees attacked by *Dendroctonus* and *Ips* species was lowest in the fall fire (11%, 25 of 222 trees), intermediate in the summer fire (19%, 154 of 833 trees), and highest in the spring fire (41%, 127 of 312 trees). The average IAR was nearly equal for all fires and ranged from a low of 1.2 in the summer fire to a high of 1.4 in the spring fire (Table 3). Dead trees had a significantly higher IAR than live trees for all fires (Table 4).

Distribution and Occurrence of Insect Taxa. Total insect occurrence pooled over all fires was lowest in all years for mountain pine beetle and roundheaded pine beetle (Fig. 2). Mountain pine beetle was not found on any trees in the fall or spring fires and on only eight trees on the summer fire 3 yr postfire. Twenty-five percent of all trees attacked by mountain pine beetle on the summer fire were attacked in the first postfire year, 1997, and attacks increased gradually in 1998 and 1999 (Fig. 2). The mean DBH for trees attacked by mountain pine beetle in the summer fire was 60.2 cm with a mean TCD of 71%. Few trees were attacked by roundheaded pine beetle for the spring (4) and summer fires (5), and no trees were attacked by this species for the fall fire 3 yr postfire. For round-

Table 4. Means (±SEM) of tree variables by season of fire (fall, spring, summer) for live and dead attacked and unattacked ponderosa pines 3 yr postfire in northern Arizona. Significance values are results of *t*-tests between live and dead trees for attacked and unattacked trees. Attacked trees have attacks by *Dendroctonus* and *Ips* species, and unattacked trees do not

Variable	Attacked				Unattacked			
	Live	Dead	*t*	*P*	Live	Dead	*t*	*P*
Fall	*n* = 14	*n* = 11	df = 23		*n* = 168	*n* = 29	df = 195	
DBH (cm)	26.4 ± 1.54	25.1 ± 2.96	0.427	0.674	25.0 ± 0.47	18.5 ± 0.10	5.397	≤0.001
Crown scorch (%)	36.4 ± 7.23	85.5 ± 5.62	5.119	≤0.001	37.6 ± 2.322	84.5 ± 2.96	8.187	≤0.001
Crown consumption (%)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Total crown damage (%)	36.4 ± 7.23	85.5 ± 5.619	5.119	≤0.001	37.6 ± 2.32	84.5 ± 2.96	8.187	≤0.001
Insect attack rating	1.0 ± 0.00	1.6 ± 0.152	4.748	0.001	N/A	N/A	N/A	N/A
Spring	*n* = 45	*n* = 82	df = 125		*n* = 166	*n* = 19	df = 183	
DBH (cm)	45.6 ± 3.44	37.8 ± 2.52	1.830	0.070	40.8 ± 1.52	30.5 ± 4.31	2.186	0.030
Crown scorch (%)	60.7 ± 3.71	69.3 ± 3.12	1.711	0.090	45.7 ± 2.44	66.8 ± 7.22	2.783	0.006
Crown consumption (%)	9.1 ± 2.29	23.8 ± 3.11	3.235	0.002	1.9 ± 0.48	26.8 ± 7.49	8.701	≤0.001
Total crown damage (%)	69.8 ± 3.28	93.1 ± 1.28	7.811	≤0.001	47.7 ± 2.51	93.7 ± 1.57	6.185	≤0.001
Insect attack rating	1.02 ± 0.002	1.7 ± 0.005	8.703	≤0.001	N/A	N/A	N/A	N/A
Summer	*n* = 98	*n* = 56	df = 152		*n* = 619	*n* = 60	df = 677	
DBH (cm)	55.9 ± 1.69	55.6 ± 2.13	0.128	0.898	52.8 ± 0.64	47.8 ± 2.35	1.461	0.144
Crown scorch (%)	35.3 ± 3.02	66.6 ± 3.91	6.300	≤0.001	19.1 ± 1.00	60.7 ± 4.44	11.859	≤0.001
Crown consumption (%)	1.4 ± 0.63	17.1 ± 3.73	5.349	≤0.001	0.695 ± 0.19	34.8 ± 4.65	21.813	≤0.001
Total crown damage (%)	36.7 ± 3.10	83.8 ± 3.09	9.953	≤0.001	19.8 ± 1.05	95.5 ± 1.15	22.365	≤0.001
Insect attack rating	1.07 ± 0.003	1.3 ± 0.006	3.990	0.001	N/A	N/A	N/A	N/A

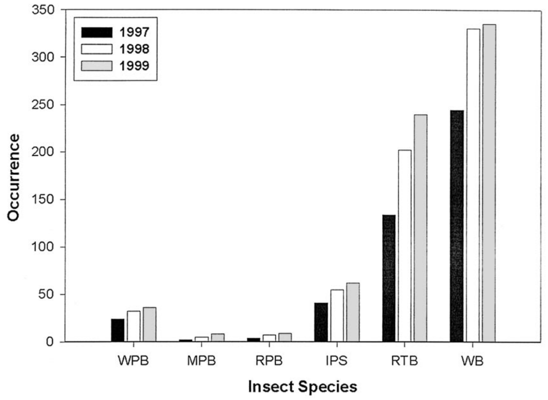

Fig. 2. Cumulative occurrence of insect taxa on ponderosa pine over three years (1997, 1998, 1999) after fire in northern Arizona. Cumulative occurrence is the number of trees attacked by each insect totaled over years. WPB = western pine beetle, MPB = mountain pine beetle, RPB = roundheaded pine beetle, IPS = *Ips* species, RTB = red turpentine beetle, WB = wood borers in the *Buprestidae* and *Cerambycidae* families. Data are pooled over fall, spring, and summer fires.

headed pine beetle, 44% of total attacks occurred in 1997 with small increases in 1998 and 1999 (Fig. 2). Mean DBH of trees attacked by roundheaded pine beetle was 50.7 cm for the spring fire and 62.0 cm for the summer fire. Mean TCD for trees attacked by roundheaded pine beetle was 82% for the spring fire and 90% for the summer fire.

Western pine beetle was found on only three trees at the fall fire, 19 trees at the spring fire, and 13 trees on the summer fire 3 yr postfire. Sixty-eight percent of total attacks by this species occurred in 1997, with slight increases in 1998 and 1999 (Fig. 2). The mean TCD of trees attacked by western pine beetle was 92% on the spring fire and 83% on the summer fire. All three trees attacked by this species on the fall fire had 100% TCD. Average DBH of trees attacked by western pine beetle was 22.8 cm for the fall fire, 53.1 cm for the spring fire, and 56.6 cm for the summer fire.

Only three trees on the fall fire and nine trees on the summer fire were attacked by *Ips* species 3 yr postfire. However, the spring fire had 50 trees attacked by *Ips* species. For the fall fire, 100% of all *Ips* attacks occurred in the first postfire year. For the spring fire, 72% of all *Ips* attacks occurred in the first postfire year. For the summer fire, 22% of all *Ips* attacks occurred in the first postfire year (Fig. 2). Over all fires, 66% of *Ips* attacks occurred in 1997, with only slight increases in 1998 and 1999 (Fig. 2). The mean DBH of trees attacked by *Ips* was 18.4 cm for the fall fire, 23.3 cm for the spring fire, and 42.4 cm for the summer fire. The mean TCD for trees attacked by *Ips* was 80% for the fall fire, 93% for the spring fire, and 83% for the summer fire.

Red turpentine beetle was the most common species of *Dendroctonus* at all fires. In the fall and spring fires, 95% and 87% of attacks by this species occurred 1 yr postfire (1997), whereas for the summer fire only 27% of attacks occurred 1 yr postfire. Over all fires, 56% of red turpentine beetle attacks occurred in 1997, and attacks increased in 1998 and 1999 (Fig. 2).

Red turpentine beetle was present more often on live than on dead trees in the fall and summer fires. Of the 19 trees attacked by this insect in the fall fire, 14 were alive and 5 were dead 3 yr postfire. Live and dead trees attacked by red turpentine beetle in the fall fire had a similar DBH ($t = 1.154$; df = 17; $P = 0.142$), but live trees had a lower TCD (36%) than dead (90%) trees ($t = 4.300$; df = 17; $P \leq 0.001$). In the summer fire, 127 trees were attacked by red turpentine beetle, of which 87 were alive and 40 were dead 3 yr postfire. Similar to the fall fire, live and dead trees attacked by red turpentine beetle had similar DBH in the summer fire ($t = 0.018$; df = 125; $P = 0.986$), and live trees had lower TCD (39%) than dead trees (82%) ($t = 7.673$; df = 125; $P \leq 0.001$). Occurrence of red turpentine beetle on the spring fire was similar between live (45) and dead (49) trees 3 yr postfire. Again, DBH did not differ between live and dead trees attacked by red turpentine beetle on the spring fire ($t = 0.867$; df = 92; $P = 0.388$), and live trees had a lower TCD (70%) than dead (92%) trees ($t = 6.294$; df = 92; $P \leq 0.001$).

Wood borers in the *Cerambycidae* and *Buprestidae* families were the most common insect found at all fires (Fig. 2). Most colonization by wood borers occurred in the first postfire year (1997) for the fall (94% of all colonized trees) and spring (87% of all colonized trees) fires, whereas only 58% of total colonization occurred in this year for the summer fire. However, by 1998, 98% of all wood borer colonization had occurred in the summer fire. Over all fires, 73% of all trees with wood borers were colonized in 1997, and 98% in 1998 (Fig. 2). Wood borers colonized both live and dead trees; however, in live trees they were generally found in dead portions of tree cambium as a result of girdling from fire. In dead trees wood borers colonized isolated areas of dead cambium and phloem sections of the tree bole in addition to areas previously attacked by *Dendroctonus* and *Ips* species.

Mortality Models. The logistic regression model developed for the fall prescribed fire was highly significant and fit the data well based on a test of the model null hypothesis ($X^2 = 104.921$; df = 2; $P \leq 0.001$). Diagnostic statistics also indicated that overall model fit was acceptable. The ROC value of 0.93 indicates very high accuracy in model discrimination between live and dead trees. The model suggests that probability of tree mortality increased as TCD and IAR increased. Moreover, insect attacks reduced the amount of TCD associated with high levels of tree mortality (Fig. 3a). For example, for trees with a TCD of 50%, the probability of mortality was 0.02 for trees with no insect attacks, 0.14 for partial attacks, and 0.51 for mass attacks (Fig. 3a).

The logistic regression model developed for the spring prescribed fire was also highly significant and fit the data well based on a test of the model null hypothesis ($X^2 = 241.066$; df = 2; $P \leq 0.001$) and diag-

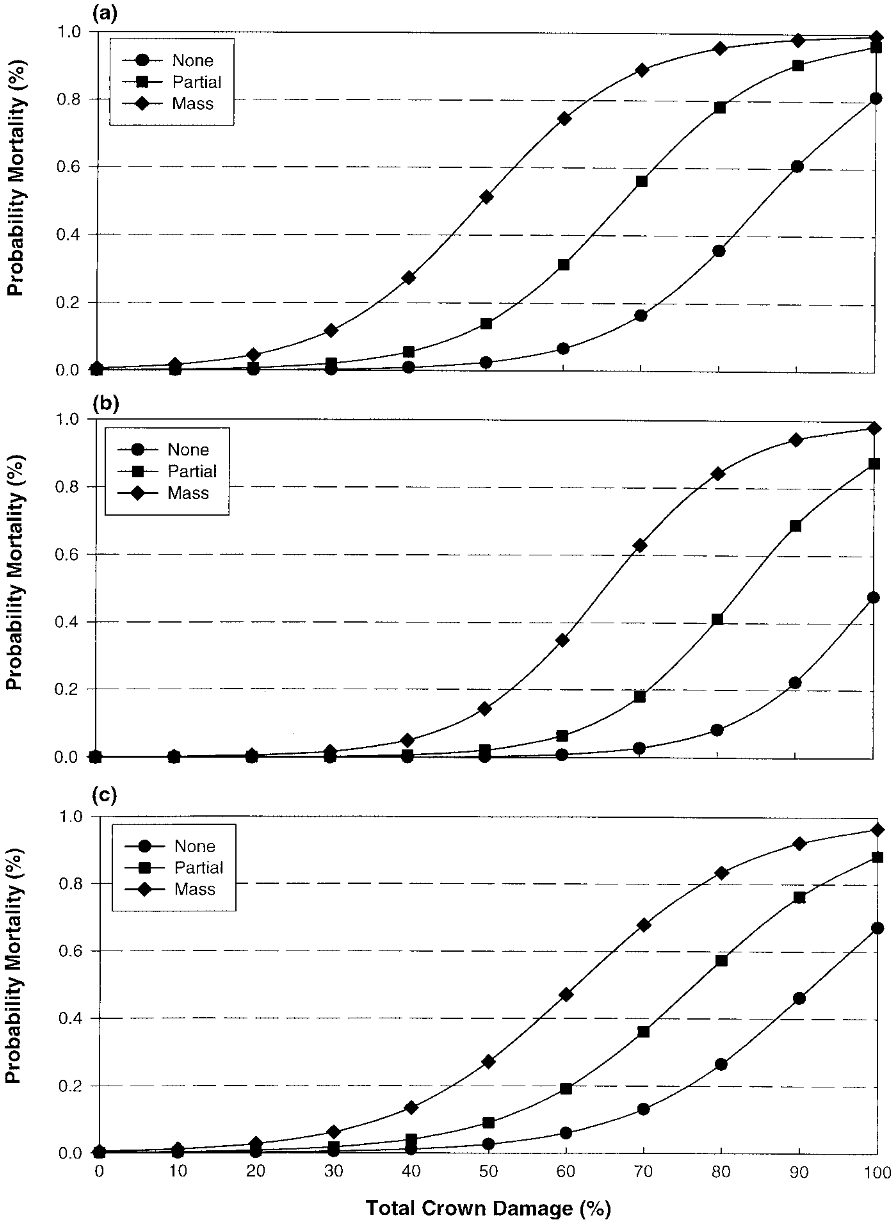

Fig. 3. Distribution of predicted probability of ponderosa pine mortality for logistic regression models using total crown damage (TCD) and insect attack rating (IAR) (none, partial, mass; *Dendroctonus* and *Ips* species) for three fires in northern Arizona. Fall prescribed fire (a), spring wildfire (b), and summer wildfire (c). See Table 5 for model equations.

nostic statistics (Table 5). Similar to the fall fire, the model for the spring fire suggests that the probability of tree mortality increased as TCD and IAR increased, and higher levels of mortality at equal TCD when insect attacks occurred (Fig. 3b). For example, for trees with 70% TCD, probability of mortality was 0.03 for trees with no attacks, 0.18 with partial attacks, and 0.63 with mass attacks (Fig. 3b).

Model results for the summer fire were similar to the fall and spring fires. The model developed for the summer prescribed fire was highly significant and fit the data well based on a test of the model null hypothesis ($X^2 = 413.577$; df = 2; $P \leq 0.001$). Diagnostic statistics also supported acceptable model fit (Table 5). For the summer fire, partial and mass attacks also increased the probability of tree mortality at a given level of TCD (Fig. 3c). For trees with partial or mass attacks, TCD was generally lower in the fall compared with the spring and summer fires (Fig. 3). For example, TCD associated with 50% mortality of trees with

Table 5. Logistic regression coefficients (±SEM), -2 log likekihood ratio statistic (-2LL), and receiver operating characteristic curve value (ROC) for selected ponderosa pine mortality prediction equations following fire in northern Arizona for a fall prescribed fire, spring wildfire, and summer wildfire. All model coefficients were significant at $\alpha = 0.05$

	Model form: $P_m = 1/[1 + exp(-(B_0 + B_1TCD + B_2IAR))]^a$				
	B_0	B_1	B_2	-2LL	ROC
Fall prescribed fire	−8.826 ± 1.4735	0.103 ± 0.0186	1.864 ± 0.5771	104.5	0.93
Spring wildfire	−11.682 ± 1.7693	0.116 ± 0.0194	2.047 ± 0.3093	151.8	0.96
Summer wildfire	−7.979 ± 0.8073	0.087 ± 0.0091	1.321 ± 0.2820	258.8	0.97

[a] Where: P_m, predicted probability of mortality; B_0, intercept, and B_n, model coefficients; TCD, total crown damage (scorch + consumption) (0–100); IAR, insect attack rating (0, none; 1, partial attack; 2, mass attack).

mass attacks was 50% for the fall fire, 65% for the spring fire, and 62% for the summer fire (Fig. 3).

Discussion

Based on precipitation data for Flagstaff, AZ (National Oceanic and Atmospheric Administration, Stations 023010/03103 and 023009/9999, http://lwf.ncdc.noaa.gov/servlets/ACS), the postfire years in our study included one extreme drought (1996), two mild droughts (1997, 1999), and one wet year (1998). Total yearly precipitation in 1996, the extreme drought, was 53% of normal. Years 1997 and 1999 were milder droughts, with similar below-average precipitation (1997: 68% of normal; 1999: 69% of normal). Precipitation during year 1998 was 20% above normal. The drought conditions following the fires in our study likely reduced postfire tree survival (Ryan 2000), and may have increased tree susceptibility to bark beetles (Furniss and Carolin 1977). Our results should not be generalized to other fires or other postfire weather conditions without further evaluation.

Mortality in fire-damaged ponderosa pine as a result of attacks by western pine beetle has been documented for parts of southern Oregon and northern California (Miller and Patterson 1927, Miller and Keen 1960). Western pine beetle can breed in old, slow-growing trees as well as in dense overstocked stands of even-aged young trees (DeMars and Roettgering 1982). These conditions existed at all our study sites, however, this insect was not a major contributor of tree mortality in our study because it occurred on only 35 trees across all fires. Average TCD of trees attacked by western pine beetle was >80%, which may have limited insect performance and spread to other trees because of associated phloem damage (Miller and Keen 1960, DeMars and Roettgering 1982). However, the more likely explanation for the low occurrence of western pine beetle in our study is that populations were low near our study sites. This is consistent with findings by Sanchez-Martinez and Wagner (2002) who reported that populations of western pine beetle were at endemic levels in the 1990s in the vicinity of our fall and spring fire study sites in northern Arizona. A review of Aerial Detection Survey (ADS) records maintained by the USDA Forest Service, Southwestern Region Entomology and Pathology, Arizona Zone Office of Entomology and Pathology located in Flagstaff, AZ for the years 1995–1999 showed isolated group clusters (five tree groups) of ponderosa pine killed by western pine beetle within 0.4 km of the summer fire. However, these records suggest that there were no large populations of western pine beetle because the next largest group cluster (20 tree groups) was 16 km from the summer fire. Important factors affecting the intensity of concentrations of western pine beetles in and around fires include the type of burn, fire timing, degree of crown injury, weather and stand conditions at the time of the fire, and, lastly, the current cycle of infestation in the area (Miller and Keen 1960). In our study, although many factors may have been ripe for an increased infestation, there was not a population available to take advantage of the habitat.

Mountain pine beetle was not found on trees at the fall or spring fires, and it occurred rarely at the summer fire, which is consistent with the view that mountain pine beetle is not attracted to fire-damaged trees (Ryan and Amman 1994, Rasmussen et al. 1996). Fire may not strongly promote population outbreaks of mountain pine beetle because it prefers fast-growing trees rather than fire-damaged, slow-growing trees (Rasmussen et al. 1996, Ryan and Amman 1996). However, another explanation for the low occurrence of mountain pine beetle in our study is low populations, because it was considered to be at an endemic population level during the 1990s in the vicinity of our fall and spring fires (Sanchez-Martinez and Wagner 2002). ADS records from the USDA Forest Service, Southwestern Region Entomology and Pathology, Arizona Zone Office of Entomology and Pathology located in Flagstaff, AZ for the years 1995–1999 indicated that several small clusters (five tree groups) of mountain pine beetle killed trees were located within 0.4 km of the summer fire, and that a large outbreak of mountain pine beetle (5,000 trees) occurred in 1997. However, this outbreak was over 32 km away and never expanded outside this area toward the summer fire.

Outbreaks of roundheaded pine beetle have caused considerable mortality of ponderosa pine in some Arizona and Utah forests (Negron 1997, Negron et al. 2000). Massey et al. (1977) reported outbreaks of roundheaded pine beetle ranging from several hundred trees to 400,000 trees over a 60,700 ha area in New Mexico. However, this beetle was rare on our study sites in northern Arizona. Most outbreaks of this species occur in slow growing, stagnated stands (Negron

1997, Negron et al. 2000). Tree diameters on the two fires in our study where it occurred (spring, summer) are within ranges reported for outbreaks of this species in trees not damaged by fire (Massey et al. 1977, Negron et al. 2000). We were unable to find published information on the relationship between roundheaded pine beetle and fire damaged trees. Low populations of this species in our study could have been caused by a weak role of fire in the population dynamics of this species, or by low populations near our study sites. Sanchez-Martinez and Wagner (2002) did not report any occurrences of this species in their study which occurred near our fall and spring fires. An evaluation of the USDA Forest Service, Southwestern Region Entomology and Pathology ADS records 1995–1999 showed no recorded observations of roundheaded pine beetle on the North Kaibab Ranger District where our summer fire study site was located.

Our measure of *Ips* populations may be an underestimate because we only examined the lower stem of trees and not the upper stem or branches (Fischer 1980). Sanchez-Martinez and Wagner (2002) reported that *Ips* attacks increased during the 1990s in the vicinity of our fall and spring study sites. In the area of the summer fire, only isolated clusters (five tree groups) of *Ips* populations were recorded in USDA Forest Service, Southwestern Region Entomology and Pathology ADS records for the years 1995–1999. The low occurrence of *Ips* in our study may be a result of negative effects of fire on host materials for brood production, or a lack of populations to take advantage of suitable habitat.

Red turpentine beetle is often found in fire-damaged trees, yet it is rarely considered to be an important cause of tree mortality (Herman 1954, Wagener 1961, Mitchell and Martin 1980). Red turpentine beetle was the most common subcortical insect except for wood borers in all fires. It occurred much more often on live trees (i.e., trees that survived for 3 yr after fire) than dead trees for the fall and summer fires. In contrast, its occurrence on the spring fire was similar between live and dead trees. Overall, our results for the fall and summer fires are similar to other studies of ponderosa pine, which concluded that attacks by this species are not related to tree mortality (Herman 1954, Wagener 1961). However, our results from the spring fire suggest that red turpentine beetle may interact with other bark beetles to influence death of fire-damaged trees on some sites.

Wood borers in the *Cerambycidae* and *Buprestidae* families were the most common insects at all sites in our study. Consistent with our observations, wood borers are known to be abundant in fire-damaged or fire-killed trees (Schmid and Parker 1990, Powell et al. 2002). While wood borers likely are not important sources of tree mortality, their economic damage can be large because of lumber degradation and introduction of wood decay fungi (Mitchell and Martin 1980, Schmid and Parker 1990). The contribution of wood borers to decay and breakdown of fire-damaged timber may be a concern to resource managers, especially if salvage operations are planned.

Trees attacked by *Dendroctonus* and *Ips* species as a group had more crown damage from fire than unattacked trees. This finding suggests that heavy crown damage by fire reduced tree carbohydrate allocation to resin defenses that repel bark beetles, as reported recently for fire-damaged ponderosa pines at one fire in northern Arizona located near our study sites (Wallin et al. 2003). Another explanation is that these insects are attracted to fire-damaged trees. Although larger trees may offer more food for beetle brood production because of thicker phloem (Amman and Pasek 1986), differences in DBH between attacked and unattacked trees were not large or consistent for all fires. Thus, we found little evidence for strong selection of specific size classes of trees for attack by *Dendroctonus* and *Ips* species as a group under our study conditions. Unfortunately, small sample sizes for some insects, and the occurrence of multiple insect species on many trees, prevented comparison of tree size between attacked and unattacked trees by individual insect species.

Our logistic regression models showed low probability of mortality over 3 yr after fire for trees not attacked by *Dendroctonus* and *Ips* species when TCD was less than $\approx$70% consistent with several other studies of ponderosa pine (Herman 1954, Dieterich 1979, Stephens and Finney 2002). At a TCD $>$70–80% (depending on the fire), the probability of mortality increased dramatically for unattacked trees. No other studies of ponderosa pine have included insect attacks in models of tree mortality after fire. We found that attacks of *Dendroctonus* and *Ips* species as a group increased the probability of mortality compared with unattacked trees. Partial attacks increased tree mortality compared with unattacked trees when TCD exceeded $\approx$50%. Mass attacks had a stronger influence, and increased tree mortality when TCD exceeded $\approx$40%. These findings suggest an important role of attacks by *Dendroctonus* and *Ips* beetles as a group in killing ponderosa pines with moderate to heavy amounts of crown damage from fire. Salvage logging operations after fire may need to consider ponderosa pines for harvest with lower levels of crown damage than previously thought in stands in which attacks by *Ips* and *Dendroctonus* species are occurring or populations are increasing.

Our results show that *Ips* and *Dendroctonus* species as a group preferred ponderosa pines that were heavily damaged by fire compared with lightly damaged trees on three fires that burned in northern Arizona in 1995 or 1996 when these insects were at an endemic population level. Such a preference may promote population increases of these insects if fire damaged trees are common. In northern Arizona, wildfires in ponderosa pine forests are currently increasing in severity and size as a result of increasing fuel loads (Covington and Moore 1994, Covington et al. 2001) and frequent droughts since 1996. Thus, current trends suggest growing numbers of fire-damaged ponderosa pines available for *Ips* and *Dendroctonus* species in northern Arizona forests. However, we have little information on fecundity and brood performance of these insects in ponderosa pines with heavy fire damage. Such information is needed to better evaluate effects of fire in ponderosa pine forests on bark beetle populations, and should be emphasized in future research.

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