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Wood-boring insect abundance in fire-injured ponderosa pine

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Abstract

1 Wood-boring larvae in the families Cerambycidae and Buprestidae are often found in high densities in burned trees after wildland fires. They play an important role in tree decomposition, often reducing the value of salvageable timber, and represent an important avian food source.

2 Three forest areas that experienced wildfires 1–3 years previously were surveyed during the summer of 2004. Ponderosa pine trees with green, scorched and consumed needles were examined for wood borer occurrence. Within each of the three needle damage categories, the mean wood borer incidence was similar between different age fires. Trees with scorched or consumed needles had significantly more wood borers than trees with green needles.

3 Larvae collected from under tree bark were identified to family; when possible, cerambycids were identified further to *Acanthocinus* spp., *Monochamus* sp., *Rhagium inquisitor* (L.) and *Stictoleptura canadensis* (LeConte), and buprestids were identified to *Chalcophora* spp. and *Chrysobothris* sp.

4 Classification tree models showed that the estimated probability of tree infestation by wood borers varied among needle damage categories. For trees with green needles, tree injury variables of high bole char height and phloem discolouration were important predictive variables. In trees where needles were consumed, tree size variables of diameter at breast height and tree height were important predictive variables.

5 More than half the dead trees examined were infested with wood borers, indicating that infestation of fire-killed ponderosa pine may represent an important food source for species such as woodpeckers and a potential problem for the utilization of infested trees.

Keywords Buprestidae, Cerambycidae, fire severity, wood-boring insects, woodpeckers.

Introduction

Wood-boring insects, such as longhorn beetles (Coleoptera: Cerambycidae) and metallic wood borers (Coleoptera: Buprestidae), are intriguing insects with diverse biological traits and life histories. Some species spend their entire life cycle in the bark of the tree, whereas other species tunnel into the wood after feeding on the outer layers of the tree. Wood borers play many important roles in forest ecosystems, having both ecological and economic significance. Ecologically, larval tunnelling contributes to wood deterioration and creates infection routes for wood-rotting fungi (Ross, 1966; Furniss & Carolin, 1977).

Wood borers are attracted to an appropriate food source as a result of changes in chemical volatiles, such as ethanol and various monoterpenes, released by trees experiencing stress (Ikeda *et al*., 1980; Kimmerer & Kozlowski, 1982; Schutz *et al*., 1999; Kelsey & Joseph, 2003; Miller, 2006). The combination of ethanol and the monoterpene α-pinene is an attractant for wood borers (Chenier & Philogene, 1989). A recent study in the Black Hills of South Dakota demonstrated that the addition of 3-carene, another monoterpene, or the *Ips* species' pheromones (ipsenol or ipsdienol) further enhanced attraction and is most likely utilized by wood borers as an indicator of a tree under stress (Costello *et al*., 2008). Several studies

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have demonstrated that some wood borer species are attracted to the pyrolysis products of trees sending a signal indicating that a tree that has been stressed by burning (Gardiner, 1957; Schmitz & Bleckmann, 1998; Schutz *et al*., 1999). Wood borers in the genus *Melanophila* (Coleoptera: Buprestidae) have specific metathoracic pit-sensing organs that detect infrared radiation in the wavelength range 2.5–4.0 μm, which is the wavelength emitted during a forest fire (Schmitz & Bleckmann, 1998). Schutz *et al*. (1999) determined that *Melanophila acuminata* (DeGeer) antennae are sensitive to 2-methoxyphenol and the monoterpenes, carene and α-pinene, which are all found in *Pinus sylvestris* smoke.

Wood borer galleries and related wood deterioration can cause economic losses by damaging wood products. Safranyik and Raske (1970) estimated that monetary losses from *Monochamus* spp. larvae (Coleoptera: Cerambycidae) in lodgepole pine could be as high as 30%. Additionally, members of the families Cerambycidae and Buprestidae can carry the pinewood nematode *Bursaphelenchus xylophilus* (Steiner and Buhrer), which causes pine wilt disease as well as mortality of native pines in Japan and ornamental pines in the U.S.A. (Linit, 1998; Yoshimura *et al*., 1999).

Wood borer larvae are also an important food source for many insectivores, such as woodpeckers. The hairy (*Picoides villosus* L.), downy (*P. pubescens* L.), black-backed (*P. arcticus* Swainson) and the three-toed (*P. tridactylus* L.) woodpeckers are found in the Black Hills and all feed on wood borer larvae. According to Beal (1911), approximately 75% of the black-backed and three-toed woodpeckers diets consist of wood borer larvae and a more recent study by Pechacek and Kristin (2004) reinforced the importance of cerambycid larvae in the three-toed woodpecker's diet. The black-backed and three-toed woodpeckers are classified as sensitive species in the Black Hills (Anderson, 2003) and several studies have documented an increase in abundance, nest densities or nest survival in burned areas where wood borers are abundant (Taylor & Barmore, 1980; Murphy & Lehnhausen, 1998; Dixon & Saab, 2000; Hoyt & Hannon, 2002; Saab *et al*., 2007). The black-backed and hairy woodpeckers breed in mature stands and prefer high severity burn patches (Hanson & North, 2008).

Wood borers are often found in such high concentrations after a fire that the sounds of larvae burrowing through wood can easily be heard by observers walking through a burned forest. In the Great Xing An Mountains in China, Chu *et al*. (1990) documented that almost all burned trees were infested with longhorned beetles. Previous studies indicate that the largest *Monochamus* populations were observed in moderately burned trees (Ross, 1960). Studies from burned and nonburned areas demonstrated that female *Monochamus* spp. prefer to oviposit in partial shade and that more adults emerge from larger diameter trees (Alya & Hain, 1985; Ross, 1966; Saint-Germain *et al*., 2004a, b). Despite extensive analysis of many aspects of wood borer biology and their effects on trees, few studies have examined how wood borer infestation densities are affected by multiple fire injuries to trees and time subsequent to a fire. The objectives of the present study were: (i) to compare wood borer densities within and between fires as influenced by time subsequent to a fire, tree injury and tree aspect and (ii) to determine tree characteristics or fire injury, or both, associated with the estimated probability of wood borer infestation.

Materials and methods

The Black Hills of South Dakota have experienced a total of ten wildfires, each over 2800 ha, from 1992 to 2003 resulting in extensive areas containing trees killed or stressed by fire. This has provided favourable conditions that have led to high wood borer populations across the landscape (K. Allen, personal communication). Forests in the Black Hills are dominated by ponderosa pine *Pinus ponderosa* Dougl. ex Laws. with smaller components of aspen *Populus tremuloides* Michx., bur oak *Quercus macrocarpa* Michx. and white spuce *Picea glauca* (Moench) Voss. The present study was conducted during the summer of 2004 in the Black Hills National Forest of South Dakota. Wood borer densities were measured in trees in a 1-year-old burn, the Red Point Fire, which burned in 2003; a 2-year-old burn, the Battle Creek Fire, which occurred in 2002; and a 3-year-old burn, the Rogers Shack Fire, which burned in 2001 (Table 1). The wildfires were chosen because each fire was the only fire in the Black Hills during that year large enough to produce a mixture of fire severities and damage to trees. These fires were separated by approximately 15–50 km. Tree characteristics, including diameter and tree height, were similar across all three fires and needle damage classes (Table 2).

At each of the three fire sites, we identified multiple areas burned at three different severity levels (moderate, 50% of trees with some green needles remaining; high, 100% of tree needles scorched but not consumed; severe, 100% of tree needles

Table 1 Description of fires examined for wood borer densities and tree characteristics associated with wood borer infestation, summer 2004, Black Hills, South Dakota

	1-year-old fire-Red Point fire	2-year-old fire-Battle Creek fire	3-year-old fire-Rogers Shack fire
Dates burned	24–30 July 2003	15–25 August 2002	30 July to 6 August 2001
Location (approximately central)	22 km south-east of Newcastle, Wyoming	16 km south-west of Rapid City	5 km south of Jewel Cave National Park
UTMs (approximately central)	13 T 0 579 238, 4 828 821	13 T 0 608 116, 4 891 085	13 T 0 593 487, 4 836 814
Area burned (ha)	7264	5038	4814
Unburned and low severity (%)	63	53	72
Moderate severity (%)	22	25	12
High severity (%)	15	22	16

Severities were determined by initial Landsat classification (USDA Forest Service 2001, 2002, 2003). UTM, Universal Transverse Mercator.

Table 2 Mean ± SEM, diameter at breast height (DBH), tree height and fire injury of ponderosa pine trees in green, scorched and consumed needle damage classes for 1-year-old fire (Red Point), 2-year-old fire (Battle Creek) and 3-year-old fires (Rogers Shack Fire), Black Hills National Forest, South Dakota, 2004

	1-year-old fire			2-year-old fire			3-year-old fire		
Ponderosa pine variable	Green ($n = 199$)	Scorched ($n = 200$)	Consumed ($n = 200$)	Green ($n = 134$)	Scorched ($n = 266$)	Consumed ($n = 200$)	Green ($n = 112$)	Scorched ($n = 288$)	Consumed ($n = 199$)
DBH (cm)	27.7 ± 0.61	26.2 ± 0.66	26.4 ± 0.71	26.9 ± 0.60	22.7 ± 0.30	23.8 ± 0.55	29.9 ± 0.84	27.9 ± 0.56	27.9 ± 0.76
Height (m)	12.9 ± 0.22	12.3 ± 0.24	12.3 ± 0.24	14.7 ± 0.28	12.1 ± 0.15	12.9 ± 0.02	14.2 ± 0.36	13.7 ± 0.24	15.3 ± 0.29
Pre-fire crown ratio (%)	66 ± 0.01	56 ± 0.01	43 ± 0.01	61 ± 0.01	60 ± 0.01	41 ± 0.01	72 ± 0.02	60 ± 0.01	34 ± 0.01
Low bole char height (%)[a]	8 ± 0.01	30 ± 0.02	100 ± 0.0	5 ± 0.01	30 ± 0.02	100 ± 0.0	5 ± 0.01	32 ± 0.02	100 ± 0.0
High bole char height (%)[a]	32 ± 0.01	63 ± 0.02	100 ± 0.0	33 ± 0.01	59 ± 0.01	100 ± 0.0	19 ± 0.01	49 ± 0.02	100 ± 0.0
Phloem discolouration (%)	4 ± 0.01	51 ± 0.03	40 ± 0.02	4 ± 0.01	30 ± 0.02	18 ± 0.02	2 ± 0.01	22 ± 0.02	11 ± 0.01
Crown scorch (%)	64 ± 0.02	100 ± 0.00	100 ± 0.0	67 ± 0.01	100 ± 0.00	100 ± 0.0	51 ± 0.02	100 ± 0.0	100 ± 0.0

[a]Expressed as a percentage of total tree height.

consumed). Four 120-m linear sampling transects were established in each burn severity category in randomly selected areas throughout each fire. The beginning point of each transect was randomly selected within areas meeting burn severity characteristics. Every 5 m along each 120-m linear transect, the nearest ponderosa pine ≥13 cm in diameter at 1.37 m above the ground (diameter at breast height, DBH) was sampled. All transects contained 25 ponderosa pine trees, which were classified into three damage groups based on fire damage to needles: trees with green needles remaining, trees with needles 100% scorched and trees with needles 100% consumed. Trees were divided into three tree condition categories because it was apparent that wood borer presence was more dependent on tree condition (damage to trees) rather than transect locations within burn class. As fires aged, some of the scorched needles dropped from the trees but, even in the 3-year-old fire, it was possible to distinguish scorched trees versus consumed trees because some scorched needles remained on trees. At the time of sampling, trees with green needles remaining may have survived the fire and had healthy phloem or may have been lethally injured by fire and had dead phloem.

For every tree sampled, the information recorded comprised: DBH, tree height, pre-fire crown ratio, percentage crown scorch, low bole char height (lowest height of bole char that was observed), high bole char height and percentage ground basal char. Tree height and low and high bole char height were measured using an Impulse 200 Standard Laser (Laser Technology Inc, Centennial, Colorado). Pre-fire crown ratio was estimated to the nearest 5% as the percentage of pre-fire total height occupied by tree crown. Percentage crown scorch was obtained by estimating the percentage of green needles remaining and subtracting from 100%. Crown scorch measurements were not taken immediately or at the same time interval after each fire, which may have resulted in variable accuracy. Basal char (percentage charring of circumference at base of tree) was estimated to the nearest 5%. Low bole char and high bole char heights were converted to a percentage of the total tree height. A total of 900 trees were sampled (25 trees × 4 replicate transects × 3 burn severity levels × 3 fire sites).

Bark sections (15 × 30 cm) were removed from the north and south sides of each tree, at breast height using a hand axe. Sampling low on the tree bole was performed because previous studies indicated that a low sampling height is appropriate when estimating wood borer densities. Zhang *et al*. (1993) found that wood borer emergence was optimal at a height of 2–4 m and only slightly less at a height of 1–2 m. For each bark sample, we estimated the percentage blackened area of the outer bark surface (outer bark blackening), and the percentage blackened area under the bark (phloem discolouration). We counted egg niches, wood borer-caused perforations in the xylem, small larvae (<2.54 cm in length) and large larvae (≥2.54 cm in length). The presence of wood borer frass was also recorded for each bark section. Larvae collected from bark sections were preserved in alcohol for later identification. Cerambycid identifications were made using Craighead's (1923) larval key and verified by the Smithsonian Institute, Systematic Entomology Laboratory, where voucher specimens were deposited. Buprestid identifications were made using Burke's (1917) larval key. Bark sections determined to be live based on cambial colour and moisture were not removed, although the outer portion of a 15 × 30 cm area was examined for evidence of wood borer attack.

The negative binomial regression was utilized to examine the differences between fire age, needle damage class or tree aspect using the response variables of total wood borer density, egg niches or xylem perforations. Statistical analyses demonstrated several interactions including, time subsequent to a fire by needle damage class, and time subsequent to a fire by aspect, depending on the response variable analyzed. Because of these interactions, data were not pooled across time subsequent to a fire, needle damage class or aspect. The negative binomial regression was used because often no evidence of wood borers was observed. Data were analyzed in PROC GENMOD (SAS Institute Inc., 2004) with Bonferroni adjustments for comparisons ($\alpha \leq 0.0056$ when comparing fires and tree injury and $\alpha \leq 0.017$ when comparing fires and tree-facing aspect). The combined count of egg niches, wood borer-caused perforations in the xylem, small larvae and large larvae per bark section was used to represent the response variable of total wood borer densities. It was not possible to analyze the number of larvae as a result of the many zero larval counts.

We constructed classification trees to identify variables associated with wood borer infestation for each fire and needle damage category. Classification trees use recursive partitioning to develop decision rules for classifying observations into categories with a corresponding estimated probability. This approach examines every level of every variable to partition the data into the most pure membership classes at the same time as minimizing variance. The result is a binary tree with splitting rules used to classify the data points and an estimated probability. A cross-validation framework is used to determine how the resulting tree would classify another sample derived from the same population (Breiman *et al.*, 1984). All measured tree variables, including, DBH, tree height, pre-fire crown ratio, percentage crown scorch, low bole char height (lowest height of bole char that was observed), high bole char height and percentage ground basal char, were utilized in developing classification tree models. A wood borer-caused perforation in the xylem or presence of larvae was used as evidence of a successful attack in modelling the estimated probability of infestation. In the present study, the outcome was a tree where the most important variables and level, classifies and estimates the probability of wood borer infestation. Classification trees were developed with the rpart (recursive partitioning) functions within R statistical software (R Development Core Team, 2006).

Results

At all the fire sites, mean wood borer incidence (combined count of egg niches, larvae and borer perforations in the xylem) in trees with needles 100% scorched or consumed were greater than in trees with green needles (healthy, declining or dying trees with green needles) ($\chi^2 > 19.09$, d.f. $= 1$, $P < 0.001$) (Fig. 1). Mean wood borer incidence was not different in trees with scorched versus consumed needles in the 1- and 3-year-old fire ($\chi^2 = 5.06$, d.f. $= 1$, $P = 0.025$ and $\chi^2 = 1.48$, d.f. $= 1$, $P = 0.225$, respectively, Bonferroni adjustments for comparisons, alpha ≤ 0.0056 when comparing fires and tree injury), although they were higher in scorched trees than trees with consumed needles in the 2-year-old fire ($\chi^2 = 14.62$, d.f. $= 1$, $P = 0.001$) (Fig. 1).

Trees with green needles had little evidence of wood borer activity. Only two small larvae were collected from the trees with green needles in the 1-year-old fire, which translates to 0.1 small larvae/m^2 (Table 3). Some trees with green needles had viable phloem and some had dead phloem, with more wood borer activity being present in bark section with dead phloem than in trees with live phloem. Bark sections on green trees with viable phloem ($n = 402$) did not contain wood borer damage under bark and only ten sections (mean number of egg niches was 0.31 m^2) had external evidence of wood borer egg niches (Table 4). Bark sections with dead phloem were found

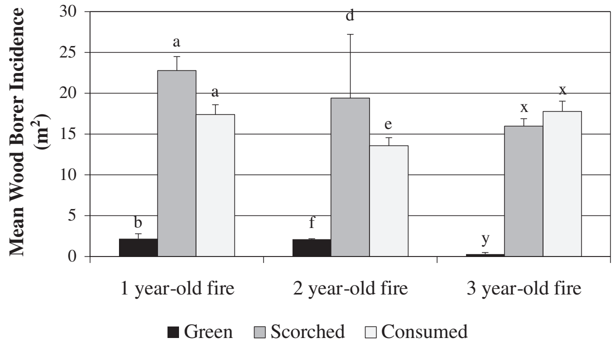

Figure 1 Mean wood borer incidence (egg niches, larvae and borer perforations in the xylem) counted in ponderosa pine trees with green, scorched, and consumed needles within the 1-, 2- and 3-year-old fires. Means labelled with the same letter are not significantly different based on effects estimated in PROC GENMOD. Fires analyzed separately, Bonferroni adjusted, $\alpha = 0.0056$, Black Hills National Forest, South Dakota, summer 2004.

Table 4 Mean ± SEM of under bark wood borer activity in viable ($n = 402$) and dead ($n = 1396$) phloem sections in ponderosa pine trees sampled in three fires [1-year-old fire (Red Point), 2-year-old fire (Battle Creek) and 3-year-old fire (Rogers Shack Fire)], Black Hills, South Dakota, 2004

	Viable phloem	Dead pholem
Egg niches (m^2)	0.31 ± 0.12	10.0 ± 0.35
Small larvae (m^2)	0.00 ± 0.00	0.53 ± 0.07
Large larvae (m^2)	0.00 ± 0.00	0.15 ± 0.03
Xylem perforations (m^2)	0.00 ± 0.00	6.8 ± 0.24
Containing live larvae or xylem perforations (%)	0 ± 0	54 ± 1
Containing Frass (%)	0 ± 0	76 ± 8

Table 3 Mean ± SEM wood borer counts for 1-year-old fire (Red Point), 2-year-old fire (Battle Creek) and 3-year-old fires (Rogers Shack Fire), in ponderosa pine trees with green, scorched and consumed needles, Black Hills, South Dakota, 2004

	1-year-old fire			2-year-old fire			3-year-old fire		
	Green ($n = 199$)	Scorched ($n = 200$)	Consumed ($n = 200$)	Green ($n = 134$)	Scorched ($n = 266$)	Consumed ($n = 200$)	Green ($n = 112$)	Scorched ($n = 288$)	Consumed ($n = 199$)
Egg niches (m^2)	1.6 ± 0.45b[a]	13.7 ± 1.25a	10.2 ± 0.91a	1.4 ± 0.04e	11.4 ± 4.57d	5.6 ± 0.66e	0.2 ± 0.14y	10.5 ± 0.69x	8.5 ± 0.96xy
Small larvae (m^2)[b]	0.1 ± 0.05	1.3 ± 0.33	1.3 ± 0.29	0.0 ± 0.00	0.4 ± 0.15	0.3 ± 0.12	0.0 ± 0.00	0.1 ± 0.06	0.0 ± 0.03
Large larve (m^2)[b]	0.0 ± 0.03	0.8 ± 0.15	0.2 ± 0.10	0.0 ± 0.00	0.0 ± 0.01	0.0 ± 0.03	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
Borer perforations in the xylem (m^2)	0.4 ± 0.16b	7.1 ± 0.67a	5.6 ± 0.55a	0.7 ± 0.03e	7.6 ± 3.08d	7.6 ± 0.59d	0.1 ± 0.06y	5.1 ± 0.46y	9.2 ± 0.87x

[a]Means followed by the same lowercase letters within a row are not significantly different based on effects estimated in PROC GENMOD. Fires analyzed separately, Bonferroni adjusted, $\alpha = 0.0056$.
[b]No statistics presented as a result of only a few counts.

on 41 trees with green needles across all fires. Out of these 41 trees, 27 contained wood borer evidence either in the form of egg niches, small larvae, large larvae, borer perforations in the xylem or frass.

Within the bark sections with dead phloem (n = 1396), the mean number of egg niches and borer perforations in the xylem were 10.0/m^2 and 6.8/m^2, respectively, across all fires and needle damage classes (Table 4). Over half of the trees examined containing bark sections with dead phloem were infested with wood borers; 54% had larvae or borer perforations in the xylem and 76% contained frass. In total, 112 small larvae and 32 large larvae were collected, yielding 0.53 small larvae/m^2 and 0.15 large larvae/m^2 (total 0.68 larvae/m^2).

Across needle damage classes (green, scorched, consumed), the number of wood borer indicators (total number of egg niches, larvae and borer perforations in the xylem) counted on trees with green or consumed needles were not statistically different between different age fires ($\chi^2 \leq 5.07$, d.f. = 1, $P \geq 0.024$) (Fig. 2). For trees with scorched needles, more wood borer indicators were counted in trees in the 1- and 2-year-old fires than the 3-year-old fire ($\chi^2 = 9.23$, d.f. = 1, $P = 0.002$) (Fig. 2).

More egg niches were counted on the north side of the tree compared with the south side in the 2- and 3-year-old fires ($\chi^2 = 12.46$, d.f. = 1, $P < 0.001$ and $\chi^2 = 23.54$, d.f. = 1, $P < 0.001$, respectively, Bonferroni adjustments for comparisons, $\alpha \leq 0.017$ when comparing fires and tree-facing aspect), although no differences between aspects were observed in the 1-year-old fire ($\chi^2 = 0.15$, d.f. = 1, $P = 0.7$) (Fig. 3). By contrast, there were more borer perforations in the xylem counted on the south side of trees than the north side of trees in both the 1- and 3-year-old fires ($\chi^2 \geq 39.63$, d.f. = 1, $P < 0.001$), although not the 2-year-old fire ($\chi^2 = 5.26$, d.f. = 1, $P = 0.022$) (Fig. 4).

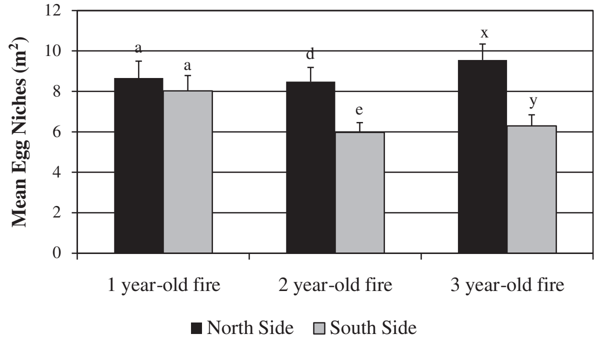

Figure 3 Mean number of egg niches counted in the north and south aspects of ponderosa pine tree in 1-, 2- and 3-year-old fires. Means labelled with the same letter are not significantly different based on effects estimated in PROC GENMOD. Years analyzed separately, Bonferroni adjusted, $\alpha = 0.017$, Black Hills National Forest, South Dakota, summer 2004.

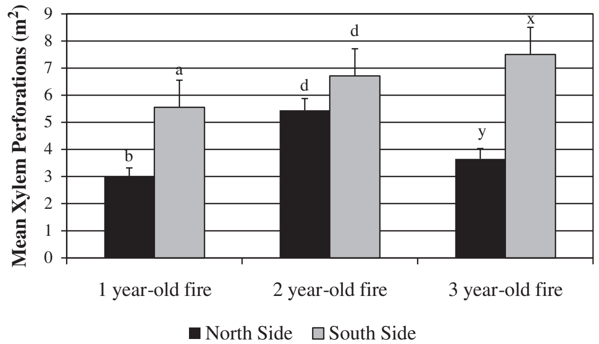

Figure 4 Mean number of borer perforations (holes) in the xylem counted in the north and south aspects of ponderosa pine trees within 1-, 2- and 3-year-old fires. Means labelled with the same letter are not significantly different based on effects estimated in PROC GENMOD. Years analyzed separately, Bonferroni adjusted, $\alpha = 0.017$, Black Hills National Forest, South Dakota, summer 2004.

Species collected

There were 144 larvae collected from bark samples, comprising 138 cerambycids and six buprestids. The cerambycids were identified to genus and species when possible. There were 36 *Acanthocinus* spp., 50 *Monochamus* spp., three *Rhagium inquisitor* (L.), four *Stictoleptura canadensis* (LeConte), four individuals in the subfamily Lamiinae, 25 in the subfamily Lepturinae and 16 not identifiable further than belonging to the Cerambycidae. The six buprestids were identified to genus as five *Chalcophora* spp. and one *Chrysobothris* sp. The majority of larvae were collected from the 1-year-old fire followed by the 2- and 3-year-old fires, 112, 27 and five larvae, respectively. Eighty-nine larvae were collected from the north aspect, compared with 55 larvae collected from the south aspect of trees.

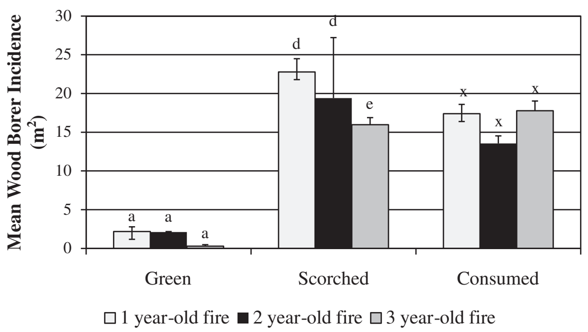

Figure 2 Mean wood borer incidence (egg niches, larvae and borer perforations in the xylem) counted in 1-, 2- and 3-year-old fires in ponderosa pine trees containing green, scorched, and consumed needles. Means labelled with the same letter are not significantly different based on effects estimated in PROC GENMOD. Needle damage classes analyzed separately, Bonferroni adjusted, $\alpha = 0.0056$, Black Hills National Forest, South Dakota, summer 2004.

Estimated probability of infestation

Estimated probability of infestation was modelled by time subsequent to a fire and needle damage classes. Models estimating the probability of wood borer infestation were developed for fire ages by needle damage classes, except for trees with green needles in the 3-year-old fire-killed trees because only one tree was infested. Models included the most important tree measurement

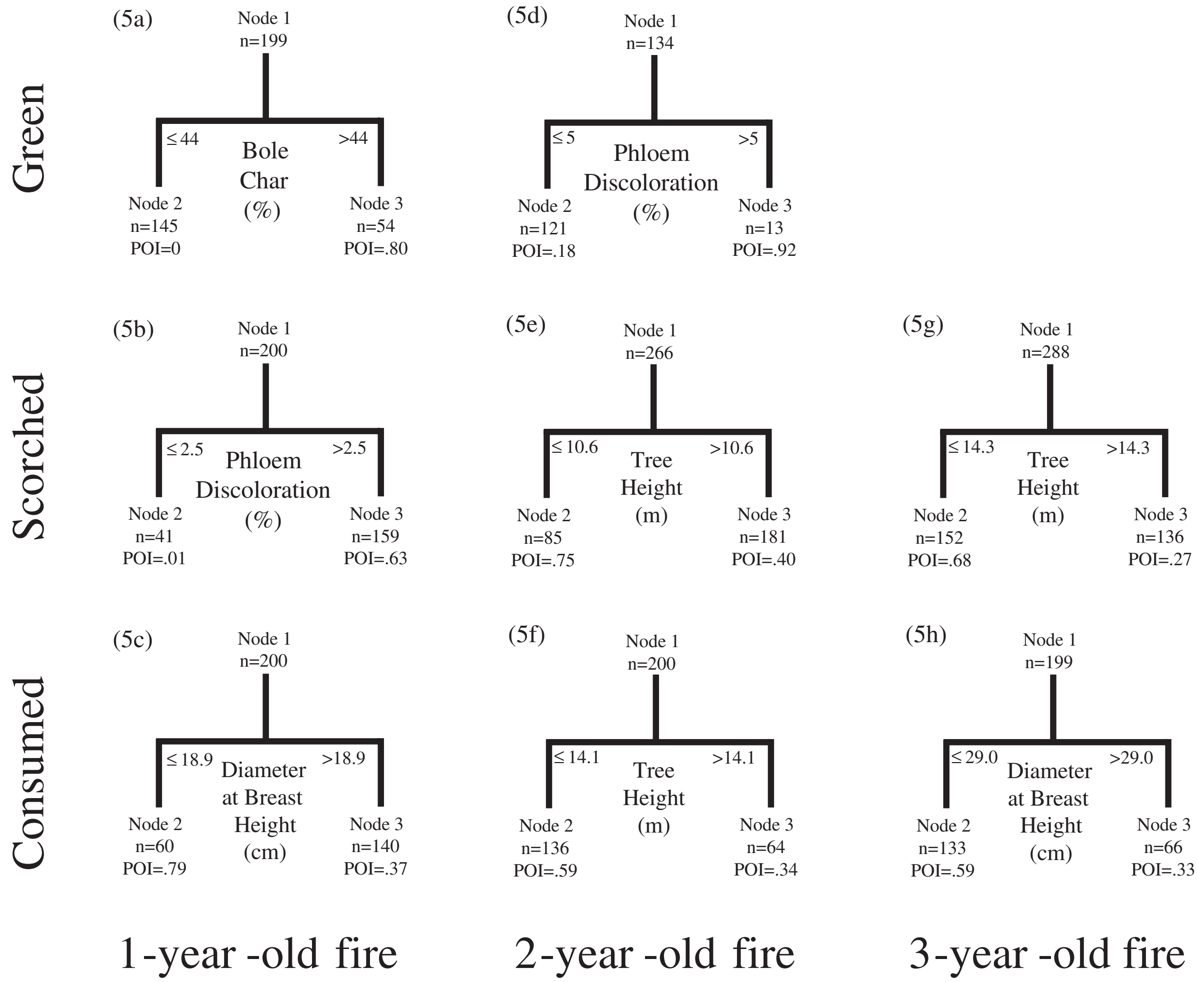

Figure 5 Classification trees for estimating probability of infestation by wood borers in ponderosa pine trees, Black Hills, South Dakota, 2004, in: (a) 1-year-old fire, trees with green needles, Misclassification error rate (MER): 0.23; (b) 1-year-old fire, trees with scorched needles, MER: 0.36; (c) 1-year-old fire, trees with consumed needles, MER: 0.31; (d) 2-year-old fire, green needles, MER: 0.30; (e) 2-year-old fire, scorched needles, MER: 0.41; (f) 2-year-old fire, consumed needles, MER: 0.41; (g) 3-year-old fire, scorched needles, MER: 0.34; and (h) 3-year-old fire, consumed needles, MER: 0.42. Bole Char, height of highest bole char on tree, expressed as a percentage of tree height; POI, probability of infestation.

variable and the level of that variable that classifies and estimates the probability of infestation. For example, bole char was identified as the most important variable in the 1-year-old fire with trees with green needles. At over 44% bole char, the estimated probability of infestation was 0.8 and ≤44% bole char the estimated probability of infestation was 0.0 (Fig. 5a). The misclassification error rate (i.e. the rate at which the classification tree misclassifies the data) for the models was in the range 0.23–0.42 (Fig. 5).

One-year-old fire. Green and scorched trees were split into two terminal nodes by the percentage bole char on the high char side and percentage of phloem discolouration (Fig. 5a,b). In both models, wood borer presence was more likely in tree sections with higher bole char and higher phloem discolouration. Trees with consumed needles were split into two terminal nodes by DBH, with the smaller trees exhibiting a higher likelihood of infestation (Fig. 5c).

Two-year-old fire. Green trees were split into two terminal nodes by phloem discolouration with increased phloem discolouration resulting in higher estimated probabilities of infestation (Fig. 5d). Scorched trees and trees with consumed needles were split by tree height, with shorter trees having a greater likelihood of infestation (Fig. 5e,f).

Three-year-old fire. Tree height and DBH were the splitting variables for models with scorched and consumed needles. As with the 2-year-old fire, shorter trees and smaller DBH resulted in higher estimated probabilities of infestation (Fig. 5g,h).

Discussion

The examination of wood borer presence 1–3 years after fire indicated higher densities in trees with scorched and consumed needles. The majority of trees with green needles did not sustain sufficient damage to be adequate hosts for insects that prefer deteriorated hosts. Examination of wood borer presence by needle categories indicated no difference among years after fires for trees with green needles. Instead, wood borers preferred trees with scorched or consumed needles. Significantly higher numbers of wood borers in scorch trees in years 1 and 2 may suggest that scorched trees are preferable to trees with consumed needles, as suggested by Ross (1960) for *Monochamus oregonensis* (LeConte) (= *Monochamus clamator* (LeConte)). *Monochamus clamator* was the most abundant species in our study areas (Costello *et al*., 2008).

Most wood borer species discriminate with respect to the condition of the trees that they use for food and reproduction. *Anoplophora chinensis* (Forester) (Coleoptera: Cerambycidae) attack healthy fruit and ornamental trees, *Monochamus* spp. attack weakened or stressed hosts, and *R. inquisitor* breeds in dead hosts (Hanks, 1999). Some species such as *Melanophila californica* Van Dyke, attack stressed pines but can also attack healthy trees (Furniss & Carolin, 1977). All six genera or species of cerambycid or buprestid larvae that we identified from bark samples, *Acanthocinus* spp., *Chalcophora* spp., *Chrysobothris* sp., *Monochamus* sp., *R. inquisitor* and *S. canadensis*, are known to only attack dead and dying trees. Adults of these species are all found in the Black Hills (Costello *et al*., 2008). *Acanthocinus* spp. and *R. inquisitor* complete their life cycle in the inner bark, whereas *Monochamus* spp. bore into the sap- and heartwood (Furniss & Carolin, 1977).

Because the species of wood borers collected in the present study prefer to attack dead or dying trees, it is not surprising that the incidence of wood borers was higher in trees with scorched or consumed needles compared with trees with green needles. Nevertheless, a large number of the 41 trees with green needles and damaged phloem exhibited signs of wood borer attack. This suggests that the presence of green needles does not negate the possibility of wood borer infestation in fire damaged trees.

Successful wood borer infestation occurred in all age fires, with more than half of the trees infested and the most larvae being recovered from the 1-year-old fire. Colonization of 1-year-old fire-killed trees demonstrates that wood borers infested suitable hosts very soon after a fire. The current management practices in the Black Hills are to remove salvageable timber as soon as feasible to reduce monetary losses as a result of the xylem perforations and decomposition that wood borers introduce (B. Cook, personal communication). The findings of the present study reinforce the idea that there is a short window of opportunity for salvage logging after a fire before wood borers successfully colonize fire damaged trees.

Studies on *M. clamator*, *Monochamus carolinensis* (Olivier) and *Monochamus titillator* (F.) have demonstrated that females prefer to oviposit on shade or north sides of trees (Ross, 1966; Alya & Hain, 1985). This is consistent with the findings of the present study because data from the 2- and 3-year-old fires indicate that more egg niches were counted on the north side of the tree. Yet, there was no difference in the number of egg niches on the north or south side of the tree in the 1-year-old fire. Trees in the 1-year-old fire may contain more moisture than 2- and 3-year-old fire-exposed trees, making both sides of the tree suitable for oviposition. As trees desiccate, the south side exposed to more solar radiation could dry sooner, becoming less suitable for oviposition. This could result in preferential oviposition on the north side of trees as fire-killed trees age.

More borer perforations in the xylem were counted on the south side of trees in both the 1- and 3-year-old fires, suggesting an aspect preference by wood borer larvae. Ross (1966) exposed bolts to shade and sun and demonstrated that *Monochamus scutellatus* (Say) larvae tunnelled more successfully in the wood in sun exposed bolts. Although Ross (1966) did not examine tree aspect, it is suggested that tunnels are made in warmer portions of trees, possibly the south side of the tree in the present study. The difference in aspect preference for oviposition by adults versus borer perforations by larvae suggests that egg development is more successful on the tree's northern, cooler side, although larval wood borers prefer to develop on the tree's south, warmer side.

The present study determined characteristics associated with the presence of wood borer infestation of *P. ponderosa* trees after fires. Although there were no differences between years after fires in the density of wood borers in trees with green needles, the probability of wood borer infestation in green trees was estimated based on variables related to tree injury, bole char or phloem discolouration in the 1- and 2-year-old fires, respectively. Both these measures are related to the amount of cambial damage, indicating that measures of tree injury can be used in estimating the likelihood of wood borer presence in trees with green needles (Fowler & Sieg, 2004).

There were also no differences in the density of wood borers in trees with scorched needles between 1- and 2-year-old fires, yet the probability of wood borer infestation was estimated using different variables: phloem discolouration and tree height. Significantly less wood borers were observed in trees with scorched needles in the 3-year-old fire compared with the 1- and 2-year-old fires. Nevertheless, tree height was also the best variable estimating the probability of infestation. For trees with consumed needles, there were no differences in wood borer densities among the three fire ages, and measures of tree size, DBH or tree height, were the best estimators of the likelihood of infestation.

In all instances, smaller trees (modelled by DBH or tree height) exhibited a higher probability of observing wood borers, indicating that smaller trees could be suitable for wood borer infestation sooner after fire damage than larger trees. Fire injury is often more severe in smaller trees because cambium injury increases with decreasing bark thickness and bark thickness increases with tree diameter (Martin, 1963; Vines, 1968; Ryan & Reinhardt, 1988). Other studies have reported a relationship between decreasing tree diameter and increasing probability of tree death (Wyant *et al*., 1986; McHugh & Kolb, 2003), which would suggest increased probability of wood borer infestation. However, the results obtained in the 1-year-old fire differ from those of Saint-Germain *et al*. (2004a), who found *M. scutellatus* entry borer perforations in the xylem increased as tree diameter increased. Because the splitting variable diameter in our 3-year-old fire model was larger with needles consumed (29.0 cm) compared with the 1-year-old fire with needles consumed (18.9 cm), it is possible that, over time, larger trees are becoming infested as smaller trees are being depleted. Alternatively, because larger trees take longer to succumb after a fire than smaller trees, they become more likely to be attacked as the time subsequent to a fire increases.

We initially assumed that either a tree injury or size variable would predict wood borer infestation. The observation that the amount of needle damage and the year subsequent to a burn could affect the predictor variables was unexpected. Tree injury variables were the primary splitting variables in models with trees containing green needles and tree size variables such as tree height and DBH were the primary splitting variables in all trees containing consumed needles within each fire. These results indicate that when trees are still alive or beginning to succumb, a measure of tree injury is important in predicting wood borer presence. However, where tree needles are 100% consumed at the time of the fire, resulting in complete crown and cambial damage, tree size becomes more important in determining the likelihood of infestation. Trees with scorched needles showed variation over time subsequent to a fire with respect to whether tree injury or tree size was the most important predictor in infestation. Tree injury was the primary splitting variable in the 1-year-old fire, compared with tree size variables in the 2- and 3-year-old fires. This could be an effect of tree mortality over time, resulting in a shift away from tree injury being an indicator of wood borer presence.

In conclusion, in the present study, wood borers preferred trees with scorched or consumed needles to trees with green needles. Densities of wood borers in trees were similar among each needle damage class among all fire ages sampled. There was also a trend towards preference of scorched trees in 1- and 2-year-old fires. However, variables associated with the estimated probability of infestation differed depending on the needle damage class and years subsequent to a fire. Oviposition and the presence of borer perforations in the xylem occurred on different tree aspects. The level of tree injury and preference over time for different size trees may influence the movement of wood borer populations and organisms that prey upon them within a site or landscape. Taking into consideration the variability associated with different wildfires and time subsequent to a fire, this information could be useful when management objectives include the rapid extraction of fire-damaged trees at the same time as maintaining an important food source for various woodpecker species.

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