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RESPONSE OF SOME SCOLYTIDS AND THEIR PREDATORS TO ETHANOL AND 4-ALLYLANISOLE IN PINE FORESTS OF CENTRAL OREGON

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Abstract—Lindgren multiple funnel traps were set up in pine forests of central Oregon to determine the response of scolytid bark beetles to ethanol and 4-allylanisole (4AA). Traps were baited with two release rates of ethanol (4.5 or 41.4 mg/hr) and three release rates of 4AA (0, 0.6, or 4.3 mg/hr) in a 2×3 factorial design. All traps also released a 1:1 mixture of α- and β-pinene at 11.4 mg/hr. Of 13,396 scolytids caught, *Dendroctonus valens* made up 60%, *Hylurgops* spp. 18.5%, *Ips* spp. 16%, *Hylastes* spp. 1.8%, *Ganthotrichus retusus* 0.9%, and bark beetle predators another 2.8%. Increasing the release rate of ethanol in the absence of 4AA increased the number of most scolytid species caught by 1.5–3.7 times, confirming its role as an attractant. *Ips latidens*, *Temnochila chlorodia*, and clerid predators were exceptions and did not show a response to higher ethanol release rates. Release of 4AA at the lowest rate inhibited attraction of most scolytids, with a significant reduction in *G. retusus*, *Hylastes macer*, and *Hylurgops porosus* when compared to traps without 4AA. A high release rate of 4AA further inhibited responses for most beetles compared to low 4AA. Seven species were significantly deterred by high 4AA, including the latter three, and *Hylastes longicollis*, *Hylastes nigrinus*, *Hylurgops reticulatus*, and *Ips latidens*. Exceptions include *Hylurgops subcostulatus*, which was significantly attracted to both low and high 4AA, and *I. pini*, which was attracted to low and high 4AA in combination with low ethanol, but unaffected by either release of 4AA with high ethanol. *Dendroctonus valens* was significantly attracted to low 4AA and

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unaffected by high 4AA. Predators appeared to be less inhibited by 4AA than most bark beetles. Although 4AA can deter the attraction of some secondary bark beetles to ethanol in combination with α- and β-pinene, this inhibition could be weakened for certain species by increasing ethanol release rates. 4-Allylanisole may have some utility for managing the behavior of secondary bark beetles sensitive to this compound.

Key Words—Methyl chavicol, bark beetles, primary attraction, host selection, host volatiles.

INTRODUCTION

The compound 4-allylanisole [4AA; 1-methoxy-4-(2-propenyl)benzene] is present in oleoresin of various pine species (Drew and Pylant, 1966; Werner, 1972; Pierce et al., 1987; Hayes et al., 1994) and is a known deterrent to primary bark beetles (Hayes et al., 1994; Hayes and Strom, 1994; Werner, 1995). It has been tested extensively in the lab and field as a potential antiaggregation semiochemical. *Dendroctonus frontalis* Zimmerman (Hayes et al., 1994), *D. rufipennis* (Kirby) (Werner, 1995), *D. ponderosae* Hopkins, *D. brevicomis* LeConte (Hayes and Strom, 1994; Hobson, 1996), and *Ips pini* (Say) (Hayes and Strom, 1994) were all significantly inhibited by 4AA in the presence of their specific aggregation pheromones.

Oleoresin in healthy trees usually contains higher concentrations of 4AA than stressed trees. For instance, quantities of 4AA in lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var. *latifolia* Engelm.) infected with Comandra blister rust (*Cronartium comandrae* Pk.) or armillaria [*Armillaria mellea* (Vahl.: Fr.) Kummer] were 43.6–63% less than in healthy trees (Nebeker et al., 1995). Similarly, concentrations of 4AA in ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) damaged by smog were 71% less than in undamaged trees (Cobb et al., 1972). Lower quantities of 4AA in smog stressed pine could be partially responsible for their greater vulnerability to bark beetle attacks than healthy trees (Stark et al., 1968).

Ethanol also occurs naturally in trees and is an important host-derived semiochemical. It is a product of fermentative respiration in plant tissues and is usually associated with hypoxic or anoxic conditions (Davies, 1980; Bennett and Freeling, 1987; Harry and Kimmerer, 1991). In contrast to 4AA, ethanol accumulates in severely stressed, dying, or recently dead trees. High ethanol concentrations have been reported in tissues of flooded (Crawford and Baines, 1977; Crawford and Finegan, 1989; Joseph and Kelsey, 1997), mechanically injured (Sjödin et al., 1989), or diseased trees (Gara et al., 1993; Kelsey and Joseph, 1998; Kelsey et al., 1998), severely water stressed branches (Kelsey and Joseph, 2001), stumps (von Sydow and Birgersson, 1997; Kelsey and Joseph, 1999a), and logs (Kelsey, 1994a,b; Kelsey and Joseph, 1997, 1999b). Ethanol, released alone or in

combination with host terpenes, is a well-known primary attractant for various species of weevils and scolytid secondary bark beetles (Moeck, 1970; Klimetzek et al., 1986; Nordlander et al., 1986; Liu and McLean, 1989; Phillips et al., 1988; Chénier and Philogène, 1989; Schroeder and Lindelöw, 1989; Sjödin et al., 1989; Byers, 1992; Kelsey, 1994a,b). If ethanol accumulates and 4AA declines in severely stressed pine trees, they are likely to be more susceptible to attack by secondary bark beetles than healthy trees.

While secondary bark beetles and weevils are normally less aggressive than primary bark beetles, they still cause a variety of problems in forest management that warrants mitigation. For example, the value of commercial logs and lumber can be reduced by pinhole-sized galleries and stain fungi introduced to the sapwood by ambrosia beetles (McLean, 1985). Numerous other species colonize woody debris or stumps and can damage or kill regeneration seedlings or saplings (Nordlander, 1987; Ciesla, 1988; Wilson et al., 1996; Salom, 1997). In some instances larger trees under stress can be killed (Furniss and Carolin, 1977). When secondary bark beetles or weevils are attracted to trees infected with certain root disease organisms, they can vector the pathogen to adjacent healthy trees or nearby healthy stands (Harrington et al., 1985; Witcosky et al., 1986a,b; Bedard et al., 1990; Nevill and Alexander, 1992a,b; Klepzig et al., 1991, 1995).

Although 4AA inhibits the response of various primary bark beetles to their pheromones, its effect on responses of secondary bark beetles to primary host attractants, such as ethanol, has not been thoroughly tested. In one study, *Dendroctonus valens* was unaffected by 4AA when *S*-(−)-β-pinene was used as the attractant (Hobson, 1996). The objective of our experiment was to determine whether 4AA deters attraction of scolytids to ethanol released simultaneously with a mixture of α- and β-pinene and whether the deterrency of 4AA is affected by ethanol release rates. A mixture of α- and β-pinene was used at a constant release rate because they occur in ponderosa pine tissues (Drew and Pylant, 1966) when ethanol is synthesized. Furthermore, the combined release of ethanol with α - and β-pinene will attract a broader range of scolytids and in larger numbers than ethanol alone (Chénier and Philogène, 1989; Schroeder and Lindelöw, 1989; Phillips et al., 1988; Lindelöw et al., 1993).

METHODS AND MATERIALS

Chemicals and Release Rates. Release rates of 4AA (98%, Aldrich), ethanol (100% USP grade, Georgia Pacific), and a 1:1 (v/v) mixture of (±)-α-pinene (98%, Aldrich) and (1*S*)-(−)-β-pinene (99%, Aldrich) in the laboratory and field were determined gravimetrically. All compounds were released from glass scintillation vials (20 ml) inside a perforated plastic container with lid (50 ml). There were 12 holes (0.8 cm diam.) on its side and two on the bottom, allowing free exchange

of chemicals with surrounding air. This setup prevented rain from diluting the compounds and altering their release rates.

Laboratory release rates were determined in an incubator at 30°C, and on a bench at 21°C. To simulate field conditions on the bench an electric fan was used to generate a wind speed of 1.1 m/sec. Two release rates were tested for 4AA and ethanol and one release rate for the pinene mixture, each averaged from five replicates. A high release rate for 4AA was achieved by placing three string wicks into the liquid and draping them over the open vial rim. A low release rate for 4AA was achieved with an open vial without strings. Ethanol was released from vials with lids having a 0.7- or 0.2-cm-diam. hole for high and low rates. The α- and β-pinene mixture was released from a separate open vial. Field release rates were determined by weighing vials before and after use in traps. These vials were capped for transport to and from the field.

Our field design consisted of a 2×3 factorial combination with two release rates of ethanol (low or high) and three release rates of 4AA (0, low or high) for a total of six treatments. Each treatment had the same α- and β-pinene release rate.

Field Tests. Lindgren 16-unit multiple funnel traps (Phero Tech, Delta, British Columbia, Canada) were replicated at 10 sites in Central Oregon, east of La Pine at 1494 to 1525 m elevation. Five sites separated by distances of 1.0–7.2 km were located in an area near 43°43′N; 120°52′W. These sites were thinned in 1996 to obtain a species composition of about 80% ponderosa and 20% lodgepole pine with diameters of approximately 20–30 cm at breast height (dbh). About 40 km southwest, in the vicinity of 43°35′N; 121°21′W, were another five sites separated by distances of 0.4–2.2 km. These sites were thinned in 1995 to obtain a species compositon of 70–100% ponderosa and 0–30% lodgepole pine, with 10–18 cm dbh. Disturbance from thinning helped ensure adequate beetle populations were available to successfully conduct the experiment. Sites had various levels of burned or unburned slash remaining.

Temperature data were collected from one site in each of the two areas with sensors attached to a datapod (Omnidata, Logan, Utah). One sensor was placed inside a weather shelter to measure ambient temperatures, while another sensor was placed inside the plastic bait container to determine temperature changes near the chemicals. These containers were not sheltered and could have received direct sun periodically during the day depending on crown positions of adjacent trees, etc.

At each site, six funnel traps were placed a minimum of 50 m apart along a transect. Traps were hung 0.5–1.0 m above ground from rope tied between two closely spaced trees and tethered with twine to keep them from swaying with wind. Traps were baited randomly by securing a plastic container to the middle funnel. Baits were replaced with fresh chemicals every two weeks and rerandomized among traps (by moving baits only) within a site to minimize the influence of

trap location on beetle catch numbers. Collection cups contained a piece of plastic releasing 2,2-dichlorovinyl-dimethylphosphate (Peststrip, Loveland Industries, Greeley, Colorado) to kill trapped insects. Traps were initially baited on May 8, 1997, and rebaited with fresh chemicals on May 19 and 30, and June 12. Insects were collected on the latter three dates and finally on June 26. Beetles were sorted into major scolytid species or their predators and counted.

Statistical Analysis. Data were analyzed using SAS software (SAS Institute, 1989, 1996). Release rates were summarized with their mean, minimum, and maximum values. Beetle numbers for each treatment and site were summed over the four collection dates and the analyses conducted on these values. Data were analyzed as a randomized complete block design with 4AA and ethanol as two factors. Beetle numbers were square-root transformed to meet homogeneity of variance and normality assumptions. Means were back-transformed for presentation. Significant differences between means were separated using Fisher's protected LSD at $\alpha = 0.10$.

To help compare behavior among species, ratios of beetles attracted to ethanol (high–low ethanol when 4AA was absent), or 4AA with ethanol (low–zero 4AA, and high–zero 4AA) were calculated. 4AA ratios were calculated with beetle averages across low and high ethanol treatments within each level of 4AA. Values above 1 indicate beetle attraction, while values below 1 show the degree of deterrence to each chemical.

RESULTS

Release Rates. There was substantial variation between laboratory and field release rates (Table 1). All chemicals, except the high ethanol treatment, had lower field release rates than in the laboratory at 21°C with air movement. Ambient field

TABLE 1. RELEASE RATES OF HOST VOLATILES IN INCUBATOR, LABORATORY, AND FIELD

Volatile	Release rates (mean, mg/hr)[a]		
	Incubator (30°C)	Laboratory (21°C)	Field (min 3.3, max 19.7°C)
α- + β-Pinene mixture	6.1 (5.7–6.3)	25.2 (14.6–34.1)	11.4 (6.4–16.3)
High ethanol	34.2 (33.7–35.0)	30.8 (28.1–37.2)	41.4 (30.1–57.2)
Low ethanol	11.7 (11.1–12.8)	6.7 (5.7–8.0)	4.5 (3.7–5.0)
High 4-allylanisole	5.2 (3.3–6.6)	10.4 (7.3–14.9)	4.3 (3.1–5.9)
Low 4-allylanisole	0.5 (0.3–0.7)	0.8 (0.1–0.8)	0.6 (0.5–0.9)

[a]The incubator (30°C) had no air movement, but in the laboratory (21°C) a fan generated a wind speed of 1.1 m/sec. Wind speed in the field was not measured. Numbers in parentheses are the range of release rates.

TABLE 2. SCOLYTIDS AND PREDATORS COLLECTED FROM 60 FUNNEL TRAPS (4 COLLECTION DATES) BAITED WITH α- AND β-PINENE PLUS DIFFERENT RELEASE RATES OF ETHANOL AND 4-ALLYLANISOLE, MAY 8–JUNE 26, 1997, IN PINE FORESTS OF CENTRAL OREGON

Beetle species	Number trapped	% of total
Bark beetles (Scolytidae)		
Dendroctonus valens	7,962	59.4
Ips latidens	1,989	14.8
Hylurgops porosus	1,349	10.1
Hylurgops subcostulatus	972	7.3
Ips pini	214	1.6
Hylurgops reticulatus	150	1.1
Hylastes macer	130	0.9
Gnathotrichus retusus	122	0.9
Hylastes nigrinus	74	0.5
Hylastes longicollis	53	0.4
Predator beetles		
Cleridae	240	1.8
Temnochila chlorodia (Trogositidae)	141	1.0
Total number of beetles	13,396	100.0

temperatures in weather shelters ranged from 3.3 to 19.7°C (average min–max). Inside plastic bait containers, average minimum and maximum temperatures were 2.1°C cooler at night, or 2.6°C warmer during the day than ambient temperatures, probably because these containers were not sheltered.

Field Test. In ponderosa pine forests of central Oregon, 10 species of secondary scolytid beetles and some of their predators were attracted to ethanol released in combination with a mixture of α- and β-pinene. *Dendroctonus valens* LeConte was the most abundant scolytid species trapped, comprising 59.4% of the total beetles caught (Table 2). Other abundant speices included *Ips latidens* LeConte at 14.8%, *Hylurgops porosus* (LeConte) 10.1%, and *Hylurgops subcostulatus* (Mannerheim) 7.3%. No primary bark beetles such as *Dendroctonus brevicomis* or *D. ponderosae* were caught in any traps. Aerial survey maps for 1996 and 1997 indicated endemic levels of activity for *D. brevicomis* and *D. ponderosae* in the forest surrounding our sites. Bark beetle predators such as clerids and *Temnochila chlorodia* (Mannerheim) were a small fraction of total beetles caught.

Dendroctonus valens responded about four times more frequently to traps with high ethanol compared to low ethanol regardless of 4AA levels (Figure 1). Low 4AA treatment caught significantly more *D. valens* than either the high ($P < 0.002$) or zero 4AA ($P = 0.029$). There was no difference in beetle numbers between high and zero 4AA ($P = 0.270$).

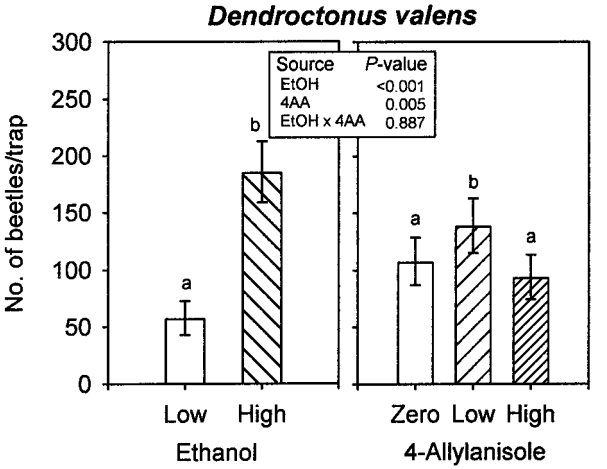

FIG. 1. Response of *D. valens* to traps baited with α- and β-pinene, ethanol, and 4-allylanisole. Vertical bars are means $\pm$ SE, $N = 10$.

Ips latidens was unaffected by ethanol treatments ($P = 0.288$), but was deterred at high 4AA compared to zero ($P = 0.004$) and low 4AA ($P = 0.037$, Figure 2). Beetle catches were not different between low and zero 4AA ($P = 0.385$). In contrast, *I. pini* showed a significant interaction between ethanol and 4AA (Figure 2). When 4AA was absent, *I. pini* numbers were greater at high ethanol than low ethanol ($P = 0.035$). The opposite was observed with low 4AA present ($P = 0.061$), and there was no difference in trap catches between ethanol release rates at high 4AA ($P = 0.974$). Low ethanol with either low or high 4AA attracted more *I. pini* than low ethanol alone ($P = 0.017$ and 0.054, respectively). Attraction of *I. pini* to high ethanol was unaffected by the presence of 4AA. There was a decrease in numbers in combination with low 4AA, but this was not significantly lower than trap catches for high ethanol with zero or high 4AA ($P = 0.113$, and 0.154, respectively).

All three *Hylurgops* species responded more strongly to high ethanol than low ethanol, regardless of amounts of 4AA (P values in Figure 3), but they each responded differently to 4AA. High and low 4AA inhibited *Hylurgops porosus* compared to zero 4AA ($P < 0.001$ and $P = 0.092$, respectively), whereas both release rates attracted *H. subcostulatus* ($P = 0.008$ and 0.052, respectively). *Hylurgops reticulatus* Wood was inhibited by high 4AA ($P < 0.014$), but not low 4AA ($P = 0.858$). Trap catches with high 4AA were smaller than those with low 4AA for *H. porosus* ($P < 0.030$) and *H. reticulatus* ($P = 0.009$), but not *H. subcostulatus* ($P = 0.432$).

Hylastes longicollis Swaine showed a significant 4AA and ethanol interaction (Figure 4). High ethanol caught more beetles than low ethanol at both zero

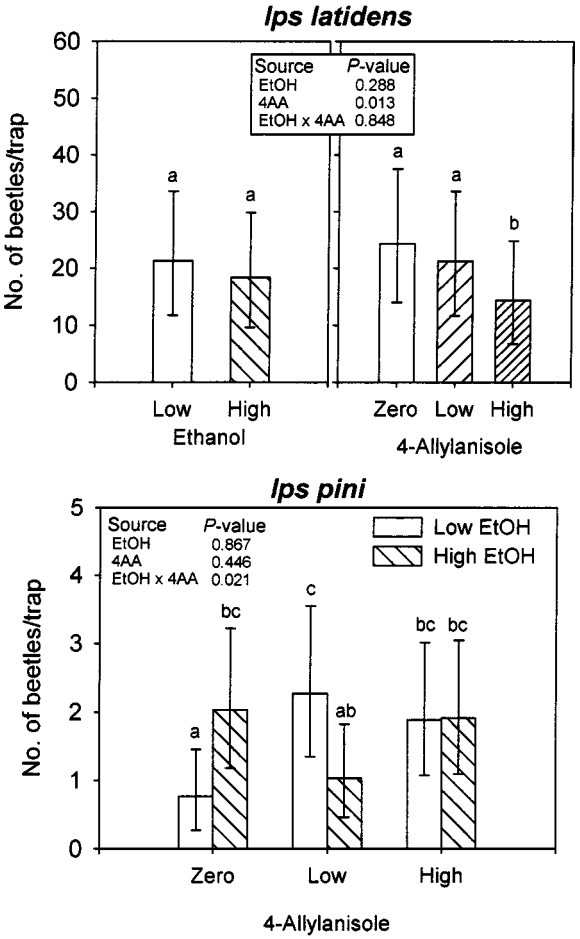

FIG. 2. Response of *Ips* spp. to traps baited with α- and β-pinene, ethanol, and 4-allylanisole. Vertical bars are means $\pm$ SE, $N = 10$.

($P < 0.001$) and low 4AA ($P = 0.025$), but not at high 4AA ($P = 1.000$). Low ethanol attracted the same number of *H. longicollis* regardless of 4AA treatments ($P \geq 0.727$). However, when the ethanol release rate was high, the high 4AA treatment reduced beetle numbers compared to zero ($P = 0.001$) and low 4AA ($P = 0.011$). *Hylastes macer* LeConte and *H. nigrinus* (Mannerheim) responded more strongly to high ethanol than low ethanol release rates (*P* values in Figure 4). Increasing the 4AA release rate from zero to low, and low to high, reduced *H. macer* almost linearly (all $P \leq 0.062$), whereas high, but not low 4AA reduced trap catches for *H. nigrinus* ($P = 0.074$ and 0.187, respectively).

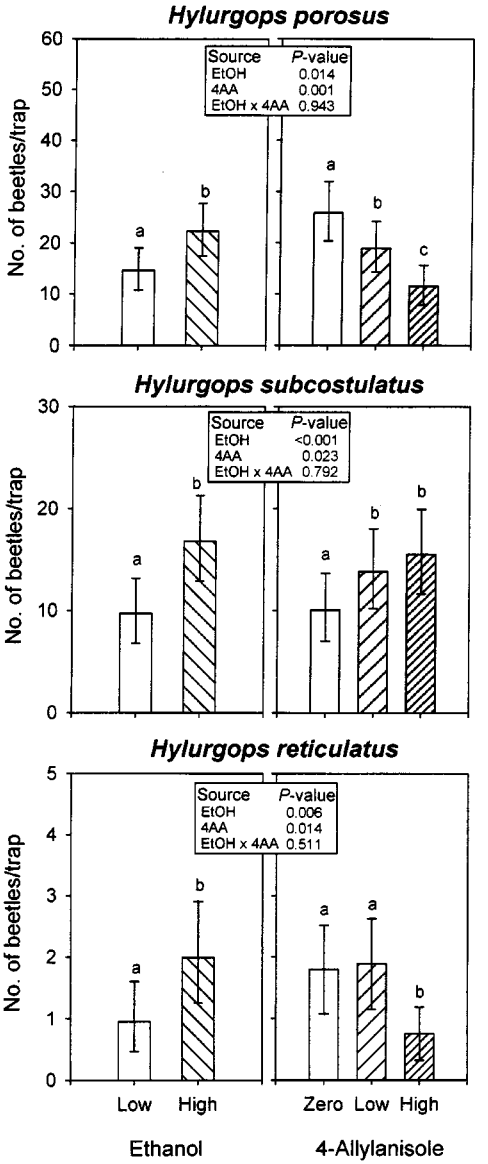

FIG. 3. Response of *Hylurgops* spp. to traps baited with α- and β-pinene, ethanol, and 4-allylanisole. Vertical bars are means $\pm$ SE, $N = 10$.

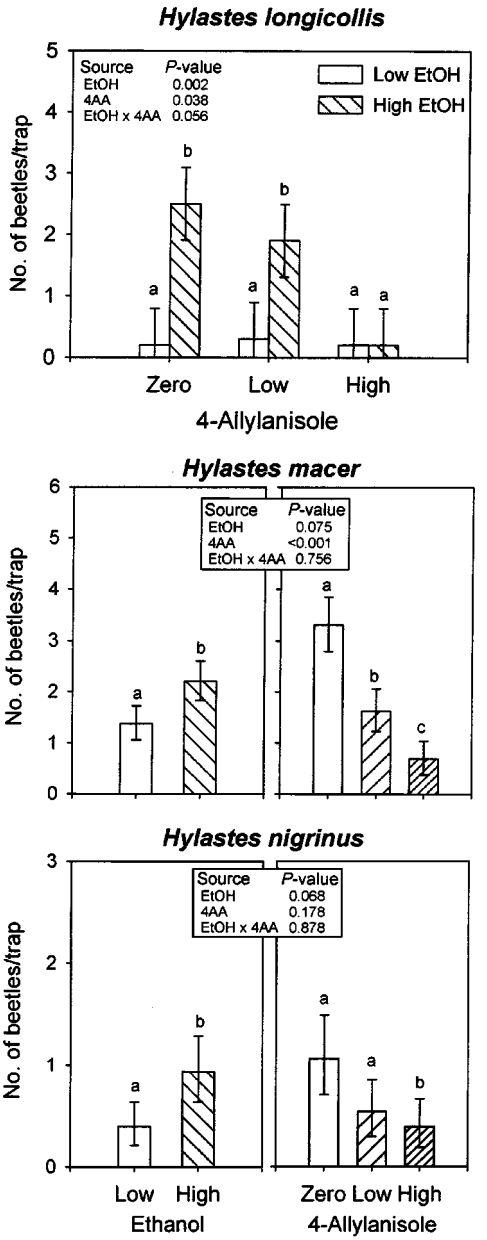

FIG. 4. Response of *Hylastes* spp. to traps baited with α- and β-pinene, ethanol, and 4-allylanisole. Vertical bars are means $\pm$ SE, $N = 10$.

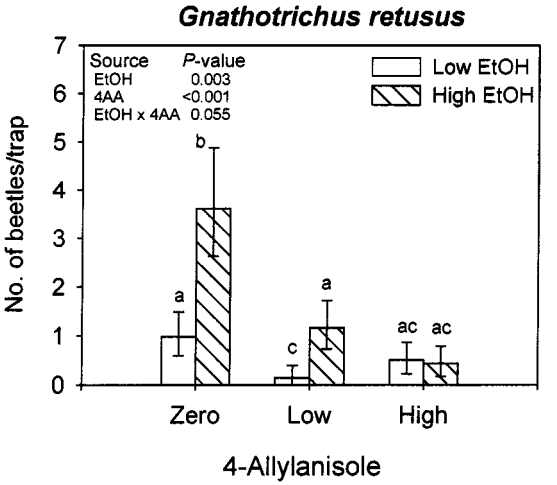

FIG. 5. Response of *G. retusus* to traps baited with α- and β-pinene, ethanol, and 4-allylanisole. Vertical bars are means $\pm$ SE, $N = 10$.

Gnathotrichus retusus (LeConte) numbers showed a significant interaction between 4AA and ethanol (Figure 5) similar to *Hylastes longicollis*. When 4AA was absent or low, the high ethanol release rate caught more beetles than low ethanol ($P = 0.003$ and $P = 0.014$), but when 4AA was high there was no difference in beetle numbers between ethanol treatments ($P = 0.858$). When ethanol was low, trap catches were inhibited by low 4AA, but not high 4AA, compared with zero 4AA ($P = 0.031$ and 0.287, respectively). When ethanol was high, trap catches of *G. retusus* were reduced by both low and high 4AA compared with zero 4AA ($P = 0.008$ and <0.001, respectively).

Clerids and *Temnochila chlorodia* were the only predators caught. Most clerids were either *Enoclerus* spp. or *Thanasimus* spp. However, neither clerids nor *Temnochila chlorodia* responded significantly to ethanol or 4AA treatments (*P* values are in Figure 6).

Relative responses of all species to ethanol and 4AA are shown in Figure 7. Most beetles responded 1.5–3.7 times more frequently to traps with high ethanol release rates (41.4 mg/hr) than those with low release rates (4.5 mg/hr) when 4AA was absent, except *Hylastes longicollis*, which was 12.5 times higher. Responses of *Ips latidens*, *T. chlorodia*, and clerids were not affected by ethanol release rates. Low release of 4AA reduced trap catches of four species by 25% or more, with significant inhibition for three of them compared to zero 4AA (*Gnathotrichus retusus*, *Hylastes macer*, and *Hylurgops porosus*). In contrast, *Hylurgops subcostulatus*, *I. pini*, and *D. valens* were attracted to low 4AA. Increasing the release rate of 4AA enhanced repellency, with significant inhibition for seven species. At high

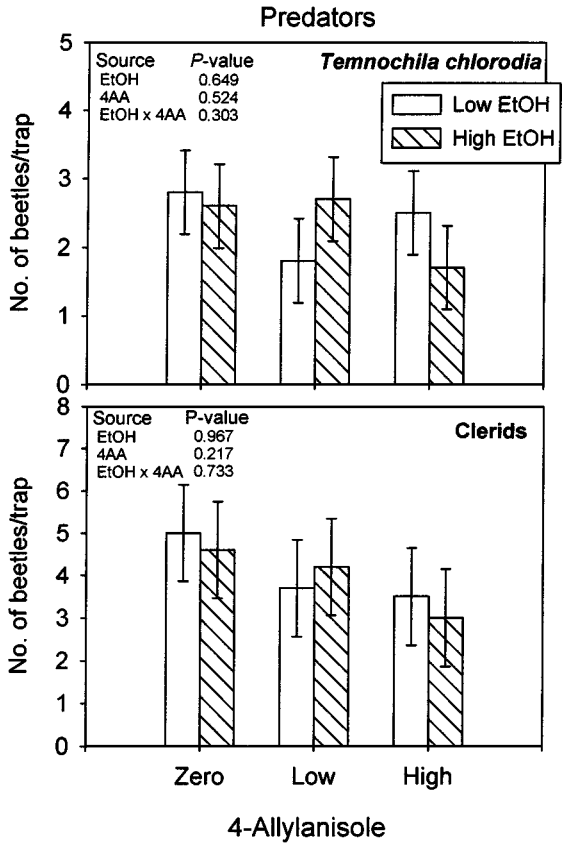

FIG. 6. Response of *T. chlorodia* and clerid predators to traps baited with α- and β-pinene, ethanol, and 4-allylanisole. Vertical bars are means $\pm$ SE, $N = 10$.

4AA, *Hylastes longicollis*, *Hylastes macer*, and *G. retusus* were most inhibited, while *Hylurgops subcostulatus* and *I. pini* (with low ethanol only) were attracted. Increasing the release rate of 4AA from 0.6 to 4.3 mg/hr had its greatest impact on *Hylastes longicollis* and *Hylurgops reticulatus* and least affect on *G. retusus*, *Hylastes nigrinus*, *Hylurgops subcostulatus*, and *I. pini*.

DISCUSSION

Ethanol, released in combination with α- and β-pinene, is an important primary attractant for many secondary bark beetles in ponderosa pine forests of central Oregon. Attraction of *Dendroctonus valens* to a similar combination was previously demonstrated in Wisconsin forests where traps baited with a 1:1

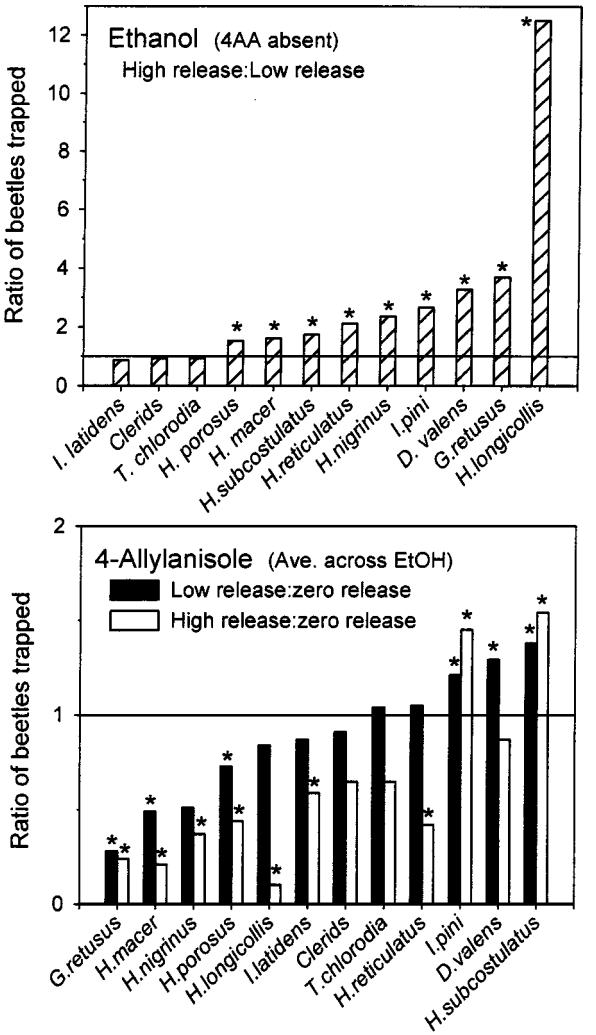

FIG. 7. Ratios of beetles trapped by different release rates of ethanol or 4AA. For species with a significant interaction between 4AA and ethanol, we used the main effect means for 0, low, and high 4AA. Values greater than 1 (horizontal line) indicate attraction and values less than 1 indicate deterrence. Asterisks indicate species where the number of beetles captured by treatments used in the numerator and denominator of a ratio were significantly different by ANOVA. *Ips pini* was attracted to 4AA only in combination with low ethanol release rates (see Figure 2 for details).

ethanol–terpentine (α- and β-pinene plus other terpenes) mixture captured 60 times more beetles than traps with terpentine alone (Klepzig et al., 1991). All *Hylastes* and *Hylurgops* at our sites preferred traps with the highest ethanol release rate, much like related species in Europe. For example, ethanol alone attracts *Hylurgops palliatus* (Gyll.) and the beetle numbers rise as the release rate increases (Klimetzek et al., 1986; Schroeder, 1988; Schroeder and Lindelöw, 1989; Byers, 1992). α-Pinene alone does not attract this species, but the combination of α-pinene and ethanol results in a synergistic response, with greater trap catches than the total from both compounds individually (Schroeder, 1988; Schroeder and Lindelöw, 1989; Byers, 1992). Although *Hylastes longicollis* in this experiment showed the largest proportional increase in trap catches between the two release rates of ethanol, this could have resulted, in part, from the low number of individuals trapped. Their typical response to ethanol is probably more similar to the other species. Numbers of *G. retusus* captured were low also, but their affinity for a high ethanol release rate reflects their preference for logs with high ethanol concentrations over logs with low concentrations (Kelsey, 1994a,b; Kelsey and Joseph, 1999b). α-Pinene most likely does not enhance, and may inhibit, the attraction of *Gnathotrichus* spp. to ethanol (Kelsey and Joseph, 1997).

Ips latidens was not attracted to ethanol, which is similar to *I. grandicollis* (Eichhoff) (Chénier and Philogène, 1989) and *I. typographus* (L.) (Klimetzek et al., 1986). For the latter species, combining ethanol with its pheromone reduced the beetle numbers compared to traps baited with pheromone alone, although the differences were not significant. In contrast, *I. pini* in the current experiment was attracted to ethanol. Why it responded differently than the *Ips* species listed above is unclear. Increasing the ethanol release rate also failed to enhance trap catches of clerids and *Temnochila chlorodia* in central Oregon. Other clerid predators, such as *Thanasimus formicarius* (L.) in Sweden (Schroeder, 1988) or *T. dubius* (Fabricius) in Canada (Chénier and Philogène, 1989), are attracted to α-pinene but not ethanol or their combination.

Effectiveness of 4AA in central Oregon as a repellent for secondary bark beetles attracted to host kairomones is dependent on the beetle species, and release rates of 4AA and ethanol. In general, 4AA was effective at inhibiting some beetles, such as *G. retusus* and the three species of *Hylastes.* In contrast, one or both release rates of 4AA attracted other species, including *Hylurgops subcostulatus*, *I. pini*, and *D. valens.* Hobson (1996) reports 4AA failed to inhibit attraction of *D. valens* to β-pinene. His release rate of 4AA was nearly 19 times (80 mg/hr) greater than our highest level. The response of *D. valens* to traps baited with ethanol and 4AA is consistent with their preference for colonizing the base of diseased ponderosa pine boles (Moeck et al., 1981), which can have lower amounts of 4AA (Nebeker et al., 1995) and higher ethanol concentrations than healthy trees (Kelsey et al., 1998).

Attraction of bark beetles to 4AA has been reported previously for *I. grandicollis* (Eichh.), particularly the males (Werner, 1972). In the current study, *I. pini*

was also attracted to 4AA, but only when ethanol release rates were low, whereas *I. latidens* showed no signs of attraction to 4AA. In studies where traps were baited with pheromone attractants, 4AA has inhibited the response of *I. pini.* Hobson (1996) reduced trap catches of *I. pini* by 29% with a release rate of 80 mg/hr 4AA, but it was not significant. In contrast, Hayes and Strom (1994) reported a 43% reduction in numbers of *I. pini* caught by traps in Wisconsin releasing 4AA at 6.6 mg/hr, or 1.5 times greater than our highest treatment. Attraction to 4AA also was previously reported for the bark beetle predator *T. chlorodia* when tested in Oregon, but not when tested in California (Hayes and Strom, 1994). Our trap catches of *T. chlorodia* and clerid predators were reduced by a high release rate of 4AA, but not significantly. Thus, it appears some bark beetle predators are not adversely impacted by 4AA.

It is becoming apparent that ethanol accumulates in woody tissues more often than anyone previously suspected. It can be synthesized by many tree species (Kimmerer and MacDonald, 1987; Kimmerer and Stringer, 1988; Kelsey, 1996) and by all of their tissues (Kimmerer and Stringer, 1988; Kelsey et al., 1998) under appropriate conditions. Synthesis of ethanol in small quantities is probably an important physiological process for normal tree growth (Harry and Kimmerer, 1991; Joseph and Kelsey, unpublished data). However, ethanol can accumulate to abnormally high concentrations when trees are subjected to various types of severe stress or when tissues are dying, as in logs and stumps (Kimmerer and Kozlowski, 1982; Sjödin et al., 1989; Kelsey, 1994a,b; von Sydow and Birgersson, 1997; Kelsey and Joseph, 1999a,b, 2001). Quantities of ethanol synthesized in wood residues are highly variable and strongly influenced by environmental parameters such as precipitation, and temperature (Kelsey and Joseph, 1999a,b). This variability can provide opportunities to manipulate ethanol production and mitigate the behavior of some secondary bark beetles. One alternative is to minimize slash and woody debris, but stumps are usually left intact, and current forest practices are moving toward leaving more coarse woody debris in the forest to allow important ecological processes to function normally and sustainably (Schowalter and Filip, 1993). Thus, other alternatives may be needed to help manage secondary bark beetles.

4AA is an allomone with potential utility for management because it inhibits responses for a wide range of scolytid beetles to primary and secondary attractants (Hayes and Strom, 1994; Werner, 1995). It might have the added advantage of not adversely interfering with the attraction of bark beetle predators, as observed here and by others (Hayes and Strom, 1994). 4AA also has shown some promise in suppressing or reducing growth of small infestations of *D. frontalis* (Hayes and Clarke, 1998). Consequently, it seems worthwhile to further examine the use of 4AA for protecting high-value logs, individual trees, and possibly small stands or plantations from unwanted attack and colonization by secondary bark beetles that are sensitive to this compound.

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