FOREST ENTOMOLOGY

Trap Lure Blend of Pine Volatiles and Bark Beetle Pheromones for *Monochamus* spp. (Coleoptera: Cerambycidae) in Pine Forests of Canada and the United States

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ABSTRACT In 2007–2008, we examined the flight responses of *Monochamus titillator* (F.) complex [*M. titillator*, *Monochamus carolinensis* (Olivier), and any possible hybrids], *Monochamus scutellatus* (Say), *Monochamus clamator* (LeConte), *Monochamus obtusus* Casey, and *Monochamus mutator* LeConte (Coleoptera: Cerambycidae) to multiple-funnel traps baited with and without host volatiles and bark beetle pheromones. Experiments were conducted in mature pine (*Pinus*) stands in Alberta (Canada), and Arkansas, Arizona, California, Florida, Idaho, Michigan, Montana, New Hampshire, North Carolina, Ohio, Oregon, Tennessee, Utah, and Wisconsin (United States). At each location, traps were deployed in 10 replicate blocks of four traps per block. The trap treatments were: 1) blank control; 2) ipsenol and ipsdienol; 3) ethanol and α-pinene; and 4) a quaternary blend of ipsenol, ipsdienol, ethanol, and α-pinene. All five species or species complex of *Monochamus* preferred traps baited with the quaternary blend over all other treatments. The consistency of these results across such a large geographic area suggests that similar selection pressures may be acting on *Monochamus* spp. in pine forests, regardless of variation in stand composition and climatic conditions. Our results suggest that multiple-funnel traps baited with the quaternary blend of ipsenol, ipsdienol, ethanol, and α-pinene may be highly effective for monitoring various *Monochamus* spp. in pine forests of North America, and may have utility in trapping and detection programs in North America and overseas.

KEY WORDS α-pinene, ethanol, ipsenol, ipsdienol, kairomone

Nonindigenous forest insects continue to invade Canada, the United States, and other countries, adversely affecting ecosystems, industries, and private landowners (Aukema et al. 2010). Early detection of these species is critical in countering their possible impacts on native trees and forests (Chornesky et al. 2005). Nonnative species of bark- and wood-boring beetles are able to enter the United States and Canada through such pathways as wooden packing material and live plants (Allen and Humble 2002, Haack 2006, Liebhold et al. 2012). In the United States, national programs administered by the U.S. Department of Agriculture, such as the Animal and Plant Health Inspection Services–Cooperative Agricultural Pest Survey (CAPS) and the Forest Service–Early Detection and Rapid Response program, use multiple-funnel traps baited with various lures to detect and monitor invasions by bark- and wood-boring beetles (Rabaglia et al. 2008, Jackson et al. 2010).

Sawyer beetles, such as *Monochamus titillator* (F.) and *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae), attack recently dead, downed, dying, or fire-stressed conifers, and freshly felled trees (Furniss and Carolin 1980, USDA–FS 1985). Female pine sawyers chew slits in the bark of tree boles and branches into which they oviposit (Furniss and Carolin 1980, USDA–FS 1985). After eclosion, the larvae mine the phloem and sapwood (and occasionally the heartwood) of trees extensively, causing significant damage that degrades forestry products through the presence

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of large-diameter holes and tunnels (Cerezke 1977, Vallentgoed 1991). Larval feeding by *Monochamus* spp. can also result in significant levels of tree mortality. For example, Fettig et al. (2008) reported that cerambycids contributed directly to tree mortality in fire-injured trees in California.

The impact from sawyer beetles to forest industries in the United States is high, due largely to export restrictions of forestry products associated with the pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickel (Tylenchida: Aphenlenchoididae) (Dwinell 1997, Webster 2003). The pine wood nematode, vectored by *Monochamus* spp., is endemic to North America and a major threat to coniferous forests around the world by causing a fatal wilting disease in some species of pines (Wingfield et al. 1982, Linit 1988, Evans et al. 1996). Pine forests in Japan experienced widespread damage and losses due to because of pine wilt disease after the introduction of pine wood nematode into Japan before 1905, with infestations affecting >28% of their pine forests in 2000 alone (Mamiya 2003). Pine wood nematodes have also been introduced into Taiwan, South Korea, and China (Evans et al. 1996). By 2000, >20 million pine trees had died from pine wilt disease over an area of 75,000 ha in China, since discovery of pine wood nematodes there in 1982 (Yang 2003). In 1999, pine wood nematodes were discovered in Portugal (Vicente et al. 2012).

Detection of pine wood nematodes in export wood products, such as pine chips and softwood lumber from the United States, has resulted in quarantine restrictions on the export of North American wood products (Bolla and Wood 2003). European countries stopped importation of pine wood chips from the United States in 1988 and currently require extensive treatments for solid wood products before importation, to ensure the lack of both pine wood nematode and sawyer beetles (Bolla and Wood 2003, Dwinell 2004).

There are eight recognized species of *Monochamus* in North America (Monné and Bezark 2012). *Monochamus carolinensis* (Olivier), *Monochamus marmorator* Kirby, *Monochamus notatus* (Drury), and *M. titillator* are found throughout eastern North America, whereas *Monochamus clamator* (LeConte) and *Monochamus obtusus* (Casey) are found in western North America. *M. scutellatus* is transcontinental in distribution and *Monochamus mutator* LeConte is found primarily in central Canada. The hosts for all species, except *M. marmorator*, include pines (*Pinus* spp.) (Furniss and Carolin 1980, USDA–FS 1985, Lingafelter 2007). Most of the pine species of sawyer beetles are known to vector the pine wood nematode (Evans et al. 1996).

An effective and broadly applicable lure for North American *Monochamus* spp. would be an important tool in detection programs in countries outside of North America and at ports-of-departure within North America. Various species of Cerambycidae are attracted to volatiles, such as ethanol and α-pinene, released by damaged branches and trunks of pine trees (Chénier and Philogène 1989; Allison et al. 2001, 2003, 2004; Miller 2006; Costello et al. 2008; Miller et al. 2011; Hanks et al. 2012). In North America, pheromones of bark beetles (Coleoptera: Curculionidae), such as ipsenol and ipsdienol, are attractive to pine sawyers, likely indicating an ephemeral brood host for *Monochamus* spp. (Billings and Cameron 1984; Allison et al. 2001, 2004, 2013; de Groot and Nott 2004; Miller and Asaro 2005; Miller et al. 2011). Combining host volatiles with bark beetle pheromones can enhance attraction of some *Monochamus* spp. (Billings 1985, Allison et al. 2001, 2003; de Groot and Nott 2004, Costello et al. 2008).

In the southeastern United States, traps baited with a quaternary blend of two host volatiles, ethanol and α-pinene, and two bark beetle pheromones, ipsenol and ipsdienol, resulted in greater catches of *M. titillator–M. carolinensis* complex (see explanation in Methods) and *M. scutellatus* than traps baited solely with the host blend or bark beetle pheromones (Miller et al. 2011). Similarly, Allison et al. (2003) found that the same quaternary blend was attractive to *M. scutellatus* and *M. clamator* in British Columbia, Canada. Therefore, our objective was to determine the attractiveness of this quaternary blend to various species of *Monochamus* over a broad geographic range in Canada and the United States.

Methods and Materials

In 2007–2008, we conducted separate trapping experiments in stands of mature pine at each of 16 locations in Canada and the United States, using the same randomized complete block design (Table 1). At each location, we deployed 40 multiple-funnel traps (Contech Enterprises Inc., Victoria, BC, Canada, or Synergy Semiochemicals Corp., Burnaby, BC, Canada, for any given location) set in 10 replicate blocks (n = 10) of four traps per block. The number of blocks was reduced to nine in Montana (n = 9) owing to the disappearance of one trap early in the study. Sixteen-unit traps were used in California, whereas 12-unit traps were used in Michigan, New Hampshire, Ohio, Utah, and Wisconsin, and 8-unit traps were used at the remaining locations. Traps were spaced 10–25 m apart within blocks, with replicate blocks spaced ≥15 m apart. Each trap was suspended between trees by rope or on metal conduit stands such that each trap was >2 m from any tree and the bottom of each trap was 0.5–1.0 m above ground level. At each location, traps were deployed during the summer months for a period of ≈12 wk (Table 1).

Each collection cup contained 150–200 ml of antifreeze solution as a killing and preservation agent (Miller and Duerr 2008). Catches were collected every 2–3 wk with new antifreeze solution added on each occasion. The following brands of antifreeze solutions were used in the trapping studies (Table 1): 1) Prestone Low Tox Antifreeze, Prestone Products Corp., Danbury, CT; 2) Splash RV & Marine Antifreeze, Fox Packaging Inc., St. Paul, MN; 3) Zecol RV Antifreeze, Zecol Products, Hamel, MN; 4) Arctic Ban Antifreeze,

Table 1. Locations, predominant pine species, brands of antifreeze, and trapping dates for each of 16 experiments in which the flight responses of *Monochamus* spp. to multiple-funnel traps baited with host volatiles and bark beetle pheromones were determined

Experiment	Location	Coordinates	Predominant pine species	Antifreeze brand[a]	Trapping dates
1	Lac La Biche, AB	55.091N, 111.987W	*Pinus banksiana* Lamb.	Prestone Low Tox	19 June-11 Sept. 2007
2	Fort Assiniboine Sandhills Wildland Park, AB	54.443N, 114.517W	*Pinus contorta* Dougl.	Prestone Low Tox	5 Jun-30 Aug. 2008
3	Kaibab NF, Coconino Co., AZ	35.381N, 111.901W	*Pinus ponderosa* Dougl. ex Laws.	Splash	6 June-29 Aug. 2008
4	Ouachita NF, Yell Co., AR	35.040N, 93.668W	*Pinus taeda* L.	Splash	23 June-17 Sept. 2008
5	Tahoe NF, Nevada Co., CA	39.395N, 120.156W	*P. ponderosa* and *Pinus jeffreyi* Balf.	Zecol and Arctic Ban	18 May-10 Aug. 2007
6	Austin Cary Memorial Forest, Alachua Co., FL	29.742N, 82.201W	*P. taeda*	Easy Going	23 April-16 July 2008
7	Idaho Panhandle NF, Bonner Co., ID	48.000N, 116.733W	*P. ponderosa* and *P. contorta*	Splash	3 June-2 Sept. 2008
8	Kellogg Research Forest, Kalamazoo Co., MI	42.358N, 85.375W	*Pinus resinosa* Sol. ex Aiten	SuperTech	17 May-7 Sept. 2007
9	Beaverhead-Deerlodge NF, Beaverhead Co., MT	45.570N, 112.940W	*P. contorta*	Arctic Ban and Splash	12 June-5 Sept. 2007
10	Bear Brook State Park, Merrimack Co., NH	43.139N, 71.367W	*Pinus strobus* L.	Prestone Low Tox	15 June-20 Sept. 2007
11	Nantahala NF, Cherokee Co., NC	35.093N, 84.134W	*Pinus echinata* Mill.	Peak	4 June-27 Aug. 2008
12	Blue Rock State Park, Muskingum Co., OH	39.823N, 81.835W	*P. strobus*	Meijer	15 May-7 Aug. 2008
13	Deschutes NF, Jefferson Co., OR	44.400N, 121.650W	*P. ponderosae*	20/10	14 May-6 Aug. 2007
14	Cherokee NF, Johnson Co., TN	36.374N, 81.949W	*P. strobus*	Peak	13 June-4 Sept. 2007
15	Uinta-Wasatch-Cache NF, Summit Co., UT	40.854N, 110.891W	*P. contorta*	Winter Ban	26 June-18 Sept. 2008
16	La Crosse County Forest, La Crosse Co., WI	44.059N, 91.073W	*P. resinosa*	Peak	10 June-2 Sept. 2008

[a] See text for names and locations of manufacturers.

CAMCO Mfg. Inc., Greensboro, NC; 5) Easy Going, CAMCO Mfg. Inc.; 6) SuperTech RV & Marine Antifreeze, Wal-Mart, Bentonville, AR; 7) Peak RV & Marine Antifreeze, Old World Industries, Northbrook, IL; 8) Meijer Marine & RV Antifreeze, Meijer Distribution Inc., Grand Rapids, MI; 9) 20/10 RV Antifreeze, 20/10 Products Inc., Salem, OR; and 10) Winter Ban −50 Antifreeze, CAMCO Mfg. Inc. All brands, except Arctic Ban, contained solutions of propylene glycol and water with either a pink or green dye. Arctic Ban contained water and ethanol (20%). Inadvertently, Arctic Ban was used briefly at the beginning of the trapping period in Montana and at the end of the trapping period in California. The concentrations of propylene glycol in the other brands ranged from 6 to 37%, each with no ethanol content (verified by examination of product labels and associated Material Safety Data Sheets).

Contech Enterprises Inc. supplied ultra-high-release (UHR) plastic pouch lures containing either ethanol (150 ml) or α-pinene (200 ml). The enantiomeric purity of α-pinene was >95%-(−). The release rate of ethanol from ethanol UHR pouches was 0.6 g/d at 25–28°C, whereas α-pinene was released at 2–6 g/d from α-pinene UHR pouches at 25–28°C (determined by weight loss). Bubble-cap lures containing either racemic ipsenol or racemic ipsdienol [chemical purities >95%, enantiomeric composition 50:50 (+)/(−)] were obtained from ConTech Enterprises Inc. in 2007 and Synergy Semiochemicals Corp. in 2008. Ipsenol and ipsdienol were released from bubblecaps at 0.1–0.3 mg/d at 22–25°C (Contech Enterprises Inc., Synergy Semiochemical Corp.).

One of the following four treatments was allocated to each of the four traps within each block: 1) blank control, 2) ethanol + α-pinene, 3) ipsenol + ipsdienol, and 4) ethanol + α-pinene + ipsenol + ipsdienol. Species identifications, taxonomic names, and authors were determined using Lingafelter (2007) and ITIS (2013). We found separation of *M. carolinensis* from *M. titillator* to be difficult and inconsistent, using characters noted by Linsley and Chemsak (1984) and Lingafelter (2007), particularly those concerning the apical spines of the elytra. The two species are broadly sympatric in pine stands throughout eastern North America (Linsley and Chemsak 1984). Hopping (1921) noted that “In long series every variation in size, maculation and reduction of the spine into a blunt form may be found” and had placed *M. carolinensis* as a synonym of *M. titillator*. Therefore, we designated *M. titillator*, *M. carolinensis*, and any possible hybrids as *M. titillator* complex. Voucher specimens of all species were deposited in the Entomology Collection, Museum of Natural History, University of Georgia (Athens, GA).

Trap catch data were transformed by ln (Y + 1) to ensure homoscedasticity (Pepper et al. 1997) for locations where sufficient numbers of individuals ($N \geq 50$) were captured for each species. Data for blank controls were omitted from analyses when means and variances for a location were both zero because of a lack of homoscedasticity in using such data in statistical analyses (Reeve and Strom 2004). Before proceeding to analysis of variance (ANOVA), normality and homoscedasticity were verified using the Kolmogorov–Smirnov and equal variance tests, respectively, with the SigmaStat (version 3.01) statistical package (SYSTAT Software Inc., Point Richmond, CA). To determine treatment effects across locations, data were subjected to ANOVA with the SYSTAT statistical package (SYSTAT Software Inc.) by using the following model components: 1) replicate (nested within location), 2) location, 3) treatment, and 4) location × treatment. To determine treatment effects within locations, trap catch data for each location were subjected to ANOVA with the SigmaStat package by using the following model components: 1) replicate and 2) treatment. The Holm–Sidak multiple comparison procedure (Glantz 2005) was used to compare means within a location for each species exhibiting a significant treatment effect ($\alpha = 0.05$).

Results

We collected sufficient numbers of individuals ($N \geq 50$) to conduct statistical analyses on all but two species of *Monochamus* in Canada and the United States. *M. notatus* was captured in small numbers (<15 at any location), whereas *M. marmorator* was not captured at any location. *M. titillator* complex was captured in sufficient numbers for analyses at seven locations ranging from Florida to Arkansas and Wisconsin (Fig. 1), with a significant treatment effect on trap catches across the locations (Table 2). The blank treatments were omitted from the analysis because mean catch and variance were zero in Florida, Michigan, and Tennessee (Fig. 1B, C, F). At all seven locations, catches of *M. titillator* complex were highest in traps baited with the quaternary blend (Fig. 1). Although there was a significant interaction between location and the three treatments (Table 2), traps baited with the binary blend of ipsenol and ipsdienol outperformed those baited with the binary blend of ethanol and α-pinene at all seven locations (Fig. 1). We caught seven *M. titillator* complex in New Hampshire, too few for analysis. *M. titillator* complex was not captured at the other locations.

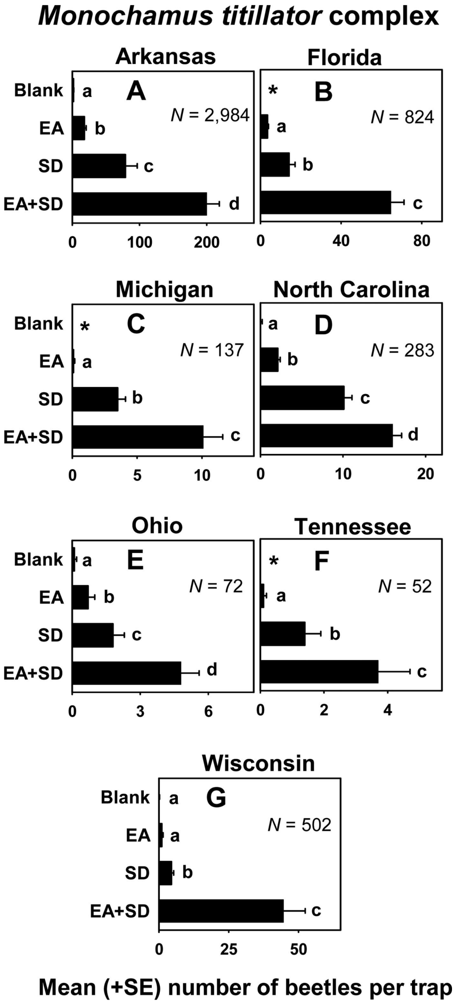

Fig. 1. Mean (+SE) number of *Monochamus titillator* complex captured in multiple-funnel traps baited with ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) in Arkansas (A), Florida (B), Michigan (C), North Carolina (D), Ohio (E), Tennessee (F), and Wisconsin (G). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatment with an asterisk had zero catches. N = Total trap catch of *M. titillator* complex per location.

There was a significant treatment effect on catches of *M. scutellatus* in New Hampshire, Ohio, Utah, and Wisconsin (Table 2). At all four locations, catches of *M. scutellatus* were highest in traps baited with the quaternary blend (Fig. 2). We found a significant interaction between location and treatments on trap catches (Table 2). Catches of *M. scutellatus* were greater in traps baited with ipsenol and ipsdienol than in traps baited with ethanol and α-pinene in New Hampshire, Ohio, and Wisconsin, whereas there was no significant difference between these two treatments in Utah. We caught low numbers of *M. scutellatus* in Alberta in 2007 and 2008, and in Michigan, Montana, and Oregon (N = 6, 8, 31, 15, and 4, respectively), too few for analysis. *M. scutellatus* was not captured at the other locations.

We captured sufficient numbers of *M. clamator* for analyses in five locations, with a significant treatment effect and a significant interaction between location and treatment (Table 2). Traps baited with the quaternary blend outperformed the other treatments in Arizona, California, and Idaho (Fig. 3A-C). In Montana, catches of *M. clamator* in traps with the quaternary blend were greater than those in blank control traps, but not those baited with either binary blend (Fig. 3D). In Oregon, traps with the quaternary blend outperformed blank control traps and traps baited with ethanol and α-pinene, but not those baited with

Table 2. Analysis of variance table for effects of treatment (T), location (L), treatment and location interaction (L × T), and replicate nested within location (R{L}) on catches of *M. titillator* complex, *M. scutellatus*, *M. clamator*, *M. obtusus*, and *M. mutator* in North America. . . . .

Factor	*M. titillator* complex			*M. scutellatus*			*M. clamator*			*M. obtusus*			*M. mutator*		
	df	*F*	*P*	df	*F*	*P*	df	*F*	P	df	*F*	*P*	df	*F*	*P*
T	2	408.27	<0.01	3	86.46	<0.01	3	128.17	<0.01	2	88.42	<0.01	2	46.45	<0.01
L	6	210.83	<0.01	3	69.04	<0.01	4	29.56	<0.01	1	67.31	<0.01	1	8.01	<0.01
T × L	12	9.01	<0.01	9	12.24	<0.01	12	11.54	<0.01	2	6.97	<0.01	3	1.76	0.19
R{L}	63	1.67	<0.01	36	2.41	<0.01	44	1.89	<0.01	18	1.22	0.30	18	0.92	0.57
Error	126			108			132			36			36		

ipsenol and ipsdienol (Fig. 3E). Differences in the relative attractiveness of the two binary blends were evident among locations (Fig. 3). In Arizona, catches of *M. clamator* in traps baited with ethanol and α-pinene were greater than those baited with ipsenol and ipsdienol, whereas the opposite was true in California. There was no difference in catches of *M. clamator* between those baited with the two binary blends in the remaining locations. *M. clamator* was not captured at the other locations.

There was a significant treatment effect on catches of *M. obtusus* in Idaho and Oregon (Table 2). The blank treatments were omitted from the analysis because mean catch and variance were zero in Idaho (Fig. 4A). At both locations, traps baited with the quaternary blend caught more beetles than any of the other treatments (Fig. 4). There was a significant interaction between location and treatment on catches of *M. obtusus* (Table 2). Catches of beetles in traps baited with ipsenol and ipsdienol were greater than those in traps baited with ethanol and α-pinene in Oregon, but not in Idaho. We caught 12 *M. obtusus* in California, too few for analysis. *M. obtusus* was not captured at the other locations.

M. mutator was captured only in Alberta, but at two locations ≈175 km apart. There was a significant treatment effect on catches of *M. mutator*, but no significant interaction between location and treatment was observed (Table 2). The blank treatments were omitted from the analyses because mean catch and variance were zero at both locations (Fig. 5). Traps baited with the quaternary blend outperformed those with either of the binary blends.

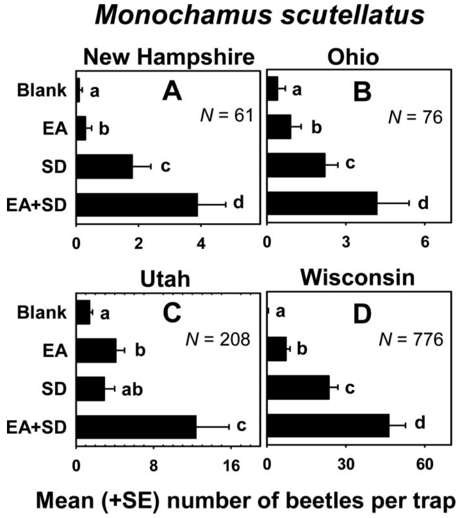

Fig. 2. Mean (+SE) number of *Monochamus scutellatus* captured in multiple-funnel traps baited with ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) in New Hampshire (A), Ohio (B), Utah (C), and Wisconsin (D). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). N = Total trap catch of *M. scutellatus* per location.

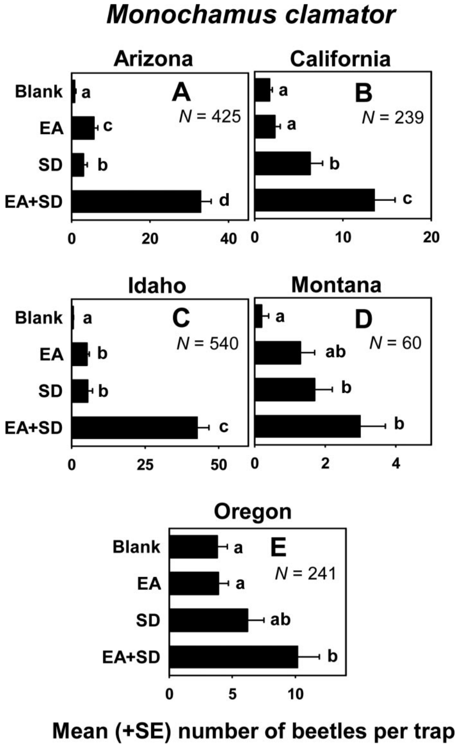

Fig. 3. Mean (+SE) number of *Monochamus clamator* captured in multiple-funnel traps baited with ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) in Arizona (A), California (B), Idaho (C), Montana (D), and Oregon (E). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). N = Total trap catch of *M. clamator* per location.

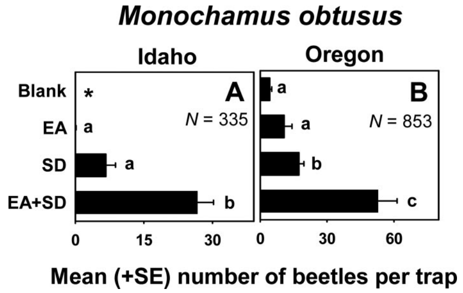

Fig. 4. Mean (+ SE) number of *Monochamus obtusus* captured in multiple-funnel traps baited with ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) in Idaho (A) and Oregon (B). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatment with an asterisk had zero catches. N = Total trap catch of *M. obtusus* per location.

Discussion

Catches of all five species or species complex of *Monochamus* were highest in traps baited with the quaternary blend over all other treatments (Figs. 1–5). The consistency of this result across such a large geographic area suggests that similar selection pressures may be acting on *Monochamus* spp. in pine forests, regardless of variation in forest composition and climatic conditions. Ethanol and α-pinene occur naturally in pine forests and are likely associated with host conditions favorable for feeding, mating, and oviposition by *Monochamus* spp. M*onochamus* spp. colonize stressed, dead, and dying trees (Furniss and Carolin 1980). Ethanol is produced by conifers that are temporarily stressed and by tissues in dead and dying trees (Kelsey 1994, 1996; Kelsey and Joseph 1998, 2003). The monoterpene α-pinene is a major constituent of the oleoresin of most pines (Mirov 1961, Smith 2000). In addition, adult sawyer beetles are relatively long-lived and feed on pine foliage and twigs throughout their breeding period. Selection should favor individuals that can locate quality forage, possibly indicated by the release of α-pinene from needles. The foliage of pines such as loblolly pine, *Pinus. taeda* L., is rich in terpenes such as α-pinene (Schultz 1997). Selection should also favor attraction of beetles to α-pinene if it ensures that beetles are attracted to the same locations for mating. Therefore, selection for response to α-pinene and ethanol may be related to three biological functions that may, at times, occur at different locations: adult feeding, mating, and oviposition.

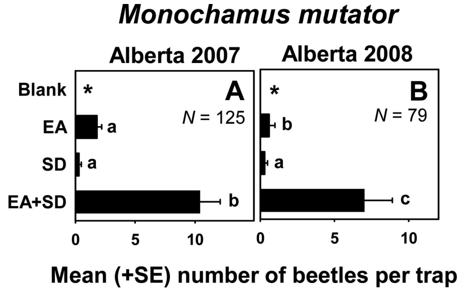

Fig. 5. Mean (+ SE) number of *Monochamus mutator* captured in multiple-funnel traps baited with ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) in Alberta in 2007 (A) and 2008 (B). Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatment with an asterisk had zero catches. N = Total trap catch of *M. mutator* per location.

Ipsenol and ipsdienol occur naturally in pine forests. Throughout North America, engraver beetles, *Ips* De Geer spp., are typically the earliest invaders of certain types of host material, such as lightning-struck trees or recently downed live trees or limbs (Furniss and Carolin 1980, USDA–FS 1985), invading the phloem tissue and producing such pheromones as ipsenol and ipsdienol (Borden 1982; Smith et al. 1993; Allison et al. 2004, 2013). The additive effect of ipsenol and ipsdienol in attracting the *M. titillator* complex to ethanol and α-pinene likely reflects conditions with a higher likelihood of host suitability for oviposition and larval development (Miller et al. 2011). The same host material should be ideal for brood development by the *M. titillator* complex before further host deterioration.

Selection pressures may be similar in the chemical ecology of other species of *Monochamus* as well (Allison et al. 2004). Allison et al. (2001) reported a kairomonal response by four *Monochamus* spp. in Canada (*M. clamator*, *M. scutellatus*, *M. notatus*, and *M. obtusus*) to a blend of ipsenol, ipsdienol, 3-methyl-2-cyclohexenone, and frontalin. Further work confirmed ipsenol and ipsdienol increased the attraction of *M. clamator* and *M. scutellatus* to ethanol and α-pinene (Allison et al. 2003). In western North America, ipsdienol is produced by male western pine beetle, *Dendroctonus brevicomis* LeConte (Coleoptera: Curculionidae) (Byers 1982), during the latter stages of host colonization, and by sympatric *Ips* spp. (Byers 1989). In this context, ipsdienol may signal an increase in host suitability for the secondary pest *Monochamus* spp., as tree defensive mechanisms are sufficiently compromised by *D. brevicomis* attacks, but before substantial host deterioration has occurred.

The responses of *Monochamus* spp. to ipsenol and ipsdienol may also relate to an ecological role as facultative intraguild predators of bark beetles and associated species (Dodds et al. 2001, Schoeller et al. 2012). Foraging by larval *M. titillator* can have a significant impact on brood production of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coulson et al. 1980), and the sixspined ips, *Ips calligraphus* (Germar) (Coleoptera: Curculionidae) (Miller 1986). In the laboratory, Dodds et al. (2001) reported high mortality of larval bark beetles from attacks or ingestion by larval *M. carolinensis.* Through DNA analyses, Schoeller et al. (2012) found that 9.6% of larval *M. titillator* collected in the wild tested positive for consumption of *I. calligraphus* and the eastern fivespined ips, *Ips grandicollis* (Eichhoff). Although the small southern pine engraver, *Ips avulsus* (Eichhoff), was present in significant numbers in phloem tissue of pine trees, Schoeller et al. (2012) were unable to assay its DNA presence in larval *M. titillator* owing to an inability to amplify primers for *I. avulsus* in larval tissues. The direct fitness benefit to larval *Monochamus* from ingestion of bark beetle larvae remains to be determined.

The addition of the *Monochamus* spp. pheromone monochamol may further enhance the efficacy of the quaternary blend for *Monochamus* spp. (Macias-Samano et al. 2012). There are 12 species of *Monochamus* native to Asia and Europe, none in the southern hemisphere (Evans et al. 1996, Sama 2002). After introductions of pine wood nematode into Asia and Portugal, *Monochamus alternatus* Hope and *Monochamus galloprovincialis* Olivier were found to vector the pine wood nematode in their respective regions (Mamiya 2003, Yang 2003, Vicente et al. 2012). Attraction to host odors is enhanced by pheromones such as ipsenol for *M. galloprovincialis* (Pajares et al. 2004, Ibeas et al. 2006) but not for *M. alternatus* (Fan et al. 2010). However, both species are attracted to monochamol (Pajares et al. 2010, Teale et al. 2011) as are a number of North American species (Allison et al. 2012, Fierke et al. 2012).

The use of a standardized single lure blend in a single trap rather than the use of separate traps with different lures in detection and survey programs could reduce expenses associated with national programs (Hanks et al. 2012). We suggest that traps baited with the quaternary blend of ipsenol, ipsdienol, ethanol, and α-pinene could be a useful detection tool at ports-of-arrival in countries outside of North America and at ports-of-departure and manufacturing sites within North America. This quaternary blend is an effective lure for five North American species or species complex of *Monochamus* within North America (Figs. 1–5) as well as other species of pine-inhabiting Cerambycidae in the southeastern United States, such as *Acanthocinus nodosus* (F.), *Acanthocinus obsoletus* (Olivier), *Rhagium inquisitor* (L.), *Astylopsis arcuata* (LeConte), and *Astylopsis sexguttata* (Say) (Allison et al. 2003, Miller et al. 2011).

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