Journal of Economic Entomology, 117(4), 2024, 1526–1536
https://doi.org/10.1093/jee/toae100
Advance Access Publication Date: 15 May 2024
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Forest Entomology

Enantiomeric composition of α-pinene affects catches of bark and wood boring beetles, and associated species, in ethanol-baited multiple-funnel traps

Daniel R. Miller[1,*], Albert E. Mayfield III[2,4], Therese M. Poland[3]

[1]Southern Research Station, USDA Forest Service, 320 Green Street, Athens, GA 30602, USA, [2]Florida Forest Service, Florida Department of Agriculture and Consumer Services, 1911 SW 34th Street, Gainesville, FL 32608, USA, [3]Northern Research Station, USDA Forest Service, 2601 Coolidge Road, Ste. 203, East Lansing, MI 48823, USA, [4]Present Address: Southern Research Station, USDA Forest Service, 200 W. T. Weaver Boulevard, Asheville, NC 28804, USA *Corresponding author, mail: Daniel.Miller1@usda.gov

Subject Editor: Christopher Fettig

Received on 12 March 2024; revised on 16 April 2024; accepted on 1 May 2024

In 2009, we determined the effects of the enantiomeric composition of the kairomone, α-pinene, on trap catches of arboreal beetles (Coleoptera) in stands of eastern pine trees with resin dominated by (+)-α-pinene. We hypothesized that the responses of beetles would correlate with the predominant enantiomer of α-pinene found in host pines. Lures of (+)-, racemic (±), and (–)-α-pinene were added separately to ethanol-baited multiple-funnel traps. Species such as *Monarthrum mali* (Fitch), *Dendroctonus terebrans* (Olivier), *Ips grandicollis* (Eichhoff), and *Pachylobius picivorus* (Germar) (Coleoptera: Curculionidae) showed a preference for traps co-baited with (–)-α-pinene. α-Pinene enhanced attraction of *Hylastes salebrosus* Eichhoff, *Hylastes porculus* Erickson and *Hylastes tenuis* Eichhoff (Coleoptera: Curculionidae) to ethanol-baited traps with no effects from enantiomeric composition of α-pinene. The attraction of the ambrosia beetles, *Xyleborinus saxesenii* (Ratzeburg) and *Dryoxylon onoharaense* (Murayama) (Coleoptera: Curculionidae) to ethanol-baited traps was interrupted by the addition of α-pinene, regardless of enantiomeric composition. Species such as *Xylosandrus germanus* (Blandford), *Cnestus mutilatus* (Blandford) and *Stenoscelis brevis* (Boheman) (Coleoptera: Curculionidae) were unaffected by the presence of α-pinene. Trap catches of some species of longhorn beetles and bark beetle predators (Coleoptera: Cerambycidae, Cleridae, Elateridae, Histeridae, and Trogossitidae) were increased by the addition of α-pinene, although results varied by location. *Platysoma* spp. (Coleoptera: Histeridae) showed a marked preference for traps co-baited with (+)-α-pinene in Florida and Georgia. In summary, we found that the enantiomeric composition of α-pinene in hosts was not a good predictor of enantiomeric preferences by beetles.

Key words: Scolytinae, Cerambycidae, predator, kairomone, α-pinene

Introduction

Detection programs for bark and woodboring beetles commonly use trap lures releasing host-produced compounds such as ethanol and α-pinene (Brockerhoff et al. 2006, 2023, Fan et al. 2019, Poland and Rassati 2019, Rabaglia et al. 2019, CAPS 2024). Ethanol and α-pinene are broadly attractive to numerous species of bark and woodboring beetles (Chénier and Philogène 1989, Allison et al. 2004, Miller 2006, Miller and Rabaglia 2009, Gandhi et al. 2010, Miller et al. 2015). Ethanol production is commonly associated with dead or stressed phloem tissues (Kelsey 1994, Kelsey and Westlind 2017), whereas α-pinene is a common monoterpene constituent of pine resin (Mirov 1961, Shrimpton 1974, Smith 2000).

The addition of α-pinene can increase the attraction of bark and woodboring beetles to their respective pheromones (e.g., Miller et al. 2003, Poland et al. 2003, Erbilgin et al. 2007, Hofstetter et al. 2008, Allison et al. 2012, Duduman and Olenici 2015, Miller 2020). As such, detection programs targeting bark and woodboring beetles may incorporate α-pinene into broad-spectrum lure blends to broaden their efficacy (Hanks et al. 2012, Miller et al. 2013, Sweeney et al. 2014, Boone et al. 2019, Fan et al. 2019, Hoch et al. 2020).

Table 1. Locations, coordinates, dominant tree species, brands of antifreeze, and trapping dates for field studies conducted in 2009 to determine responses of beetles to enantiomeric blends of α-pinene in ethanol-baited funnel traps at 3 sites: Florida, Georgia, and Michigan

Site	Location	Coordinates	Tree species	Brand of RV antifreeze	Dates
FL	Austin Cary Memorial Forest, Alachua Co., FL, USA	29.738° N, 82.219° W	*Pinus palustris* Miller	Prestone Low Tox Antifreeze, Prestone Products, Danbury, CT, USA	22 April–11 June
GA	Oconee National Forest, Putnam Co., GA, USA	33.377° N, 83.519° W	*Pinus taeda* L.	Splash RV & Marine Antifreeze, Fox Packaging Inc., St. Paul, MN, USA	28 April–10 July
MI	Kellogg Experimental Forest, Kalamazoo Co., MI, USA	42.372° N, 85.321° W	*Pinus resinosa* Solander *ex* Aiton	SuperTech RV & Marine Antifreeze, Wal-Mart, Bentonville, AR, USA	28 May–18 August

Table 2. Trap catches of common pine bark and wood boring beetles, and associated species (Coleoptera), in field studies with chiral α-pinene at 3 sites in the United States: Florida, Georgia, and Michigan

Family, Species	FL	GA	MI	Total
Buprestidae				
Buprestis spp.	27	25	23	75
Chalcophora virginiensis (Drury)	82	58	–	140
Cerambycidae				
Acanthocinus nodosus (F.)	8	13	–	21
Acanthocinus obsoletus (Olivier)	7	19	10	36
Asemum striatum (L.)	–	–	232	232
Astylopsis sexguttata (Say)	–	–	5	5
Gaurotes cyanipennis (Say)	–	–	7	7
Monochamus carolinensis (Olivier)	–	–	5	5
Monochamus scutellatus (Say)	–	–	9	9
Monochamus titillator (F.)	71	133	–	204
Neoclytus spp.	–	15	–	15
Rhagium inquisitor L.	–	8	–	8
Xylotrechus colonus (F.)	–	17	–	17
Xylotrechus sagittatus (Germar)	45	280	100	425
Cleridae				
Thanasimus dubius (F.)	–	88	431	519
Curculionidae				
Cnestus mutilatus (Blandford)	–	74	–	74
Dendroctonus terebrans (Olivier)	112	80	–	192
Dendroctonus valens LeConte	–	–	250	250
Dryocoetes autographus (Ratzeburg)	–	–	43	43
Dryoxylon onoharaense (Murayama)	47	229	2	278
Gnathotrichus materiarius (Fitch)	16	–	–	16
Hylastes porculus Erichson	37	–	–	37
Hylastes salebrosus Eichhoff	87	1,132	66	1,285
Hylastes tenuis Eichhoff	–	327	3	330
Hylobius pales (Herbst)	30	395	69	494
Ips grandicollis (Eichhoff)	248	157	378	783
Monarthrum mali (Fitch)	–	–	153	153
Myoplatypus flavicornis (F.)	2	5	–	7
Orthotomicus caelatus (Eichhoff)	12	–	62	74
Pachylobius picivorus (Germar)	853	100	–	953
Pissodes spp.	–	–	358	358
Stenoscelis brevis (Boheman)	–	166	63	229
Tomicus piniperda (L.)	–	–	24	24
Xyleborinus saxesenii (Ratzeburg)	444	599	5	1,048
Xyleborus spp.	238	168	3	409
Xylosandrus compactus (Eichhoff)	6	–	–	6
Xylosandrus crassiusculus (Motschulsky)	210	133	–	343
Xylosandrus germanus (Blandford)	–	–	883	883
Elateridae				
Alaus myops (F.)	171	167	–	338
Histeridae				
Platysoma spp.	136	345	–	481
Passandridae				
Catogenus rufus F.	20	128	–	148
Trogossitidae				
Temnoscheila virescens (F.)	179	482	–	661
Tenebroides spp.	6	194	16	216
Total	3,094	5,537	3,200	11,831

Like many monoterpenes, α-pinene is a chiral compound existing as 2 optical stereoisomers (enantiomers): (*S*)-(−)-α-pinene and (*R*)-(+)-α-pinene (Hobson et al. 1993). In older publications such as Mirov (1961), the (−) and (+) optical enantiomers are often denoted as levorotatory (*l*) and dextrorotatory (*d*), respectively; the racemic (50:50) mixture of the 2 enantiomers denoted as *dl*. In North America, the enantiomeric composition of α-pinene in the resin of pine trees varies by species, geography, and season (Mirov 1961, Hobson et al. 1993, Phillips et al. 1999, Erbilgin et al. 2001, Marques et al. 2012, Collignon et al. 2016).

Most trapping studies targeting bark and woodboring beetles in eastern North America have used α-pinene lures dominated by the (−)-enantiomer, likely due to the commercial availability and low cost of (−)-α-pinene with high chemical purity (D.R.M., personal observation). For example, Miller and Rabaglia (2009), Miller et al. (2015), and Gandhi et al. (2010) used high-release rate α-pinene lures with an enantiomeric composition of 95% (−) for trapping numerous species of bark and woodboring beetles in eastern North America; neither racemic nor (+)-α-pinene was tested. Lures releasing α-pinene with an enantiomeric composition of approximately 75% (−) were used for trapping studies on *Tomicus piniperda* (L.) (Coleoptera: Curculionidae) (Poland et al. 2003) and *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae) (Ryall et al. 2013) in northeastern North America. In some earlier studies targeting bark and woodboring beetles, only racemic α-pinene was used (Chénier and Philogène 1989, de Groot et al. 1998, Czokajlo and Teale 1999).

The attraction of some species of bark beetles can be affected by the enantiomeric composition of α-pinene. In Ontario, Canada, the attraction of the cone beetle, *Conophthorus resinosae* Hopkins (Coleoptera: Curculionidae), to its pheromone, pityol, was directly related to the concentration of (−)-α-pinene in trap lures, decreasing with increasing concentration of (+)-α-pinene (de Groot et al. 2002). In China, catches of 7 species of bark and ambrosia beetles (Coleoptera: Curculionidae) were greater in traps baited with (−)-α-pinene than in traps baited with (+)-α-pinene (Liu and Dai 2006). In Wisconsin, traps baited with (−)-α-pinene and ethanol caught more *Pachylobius picivorus* (Germar) and *Hylobius* spp. (Coleoptera: Curculionidae) than those baited with (+)-α-pinene and ethanol (Erbilgin et al. 2001). Attraction of *Ips grandicollis* (Eichhoff) (Coleoptera: Curculionidae) to traps baited with its pheromone, ipsenol, in Wisconsin was increased more by the addition of (−)-α-pinene than the addition of (+)-α-pinene (Erbilgin and Raffa 2000). In North Carolina, catches of *Conophthorus coniperda* (Schwartz) (Coleoptera: Curculionidae) in traps baited with (−)-α-pinene and the pheromone pityol were reduced by the addition of (+)-α-pinene (Miller et al. 2003).

For some beetle species, the (+) enantiomer of α-pinene can have a positive role in attraction. In the southeastern United States, Staeben et al. (2015) found that attraction of *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae) to traps baited with its pheromone, frontalin, was enhanced more by (+)-α-pinene than (−)-α-pinene. In California, the attraction of *Dendroctonus valens* (Coleoptera: Curculionidae) to traps baited with (+)-α-pinene was interrupted by the addition of (−)-α-pinene (Hobson et al. 1993). In China, the optimal blend for the nonnative species *De. valens* consists of (+)-3-carene, (−)-β-pinene, and (+)-α-pinene in a ratio of 3:1:1 (Sun et al. 2004).

The enantiomeric compositions of α-pinene found in the resin of common pines in the southeastern United States, such as loblolly pine, *Pinus taeda* (L.), and longleaf pine, *Pinus palustris* Miller, are dominated by the (+) enantiomer (Mirov 1961, Phillips et al. 1999, Marques et al. 2012). Similarly, in the northeastern United States, the enantiomeric composition of α-pinene in the resin of red pine, *Pinus resinosa* Solander *ex* Aiton, has an excess of the (+) enantiomer (Erbilgin et al. 2001). Therefore, our goal was to clarify the effects of the enantiomeric composition of α-pinene used in trap lures on catches of bark and woodboring beetles in pine stands in the eastern United States. We hypothesized that the responses of beetles would correlate with the predominant enantiomer of α-pinene found in host pines. Additionally, we wanted to verify the efficacy of (−)-α-pinene lures in pine stands where α-pinene in tree resin is dominated by the (+) enantiomer. Data from our trapping studies could help to (i) clarify relationships between beetles and host trees and (ii) identify optimal lure composition in detection programs.

Materials and Methods

Experimental Design

In 2009, we conducted identical field studies in pine stands at 3 sites in the eastern United States to determine how the enantiomeric composition of α-pinene affects catches of bark and wood-boring beetles in ethanol-baited traps. Field locations, tree species composition, and experimental dates are provided in Table 1. Multiple-funnel traps, pouch lures releasing ethanol at 0.5 g/day at 23 °C, and 15-ml bottle lures releasing α-pinene at 150 mg/day at 23 °C were provided by

Table 3. ANOVA results for lure treatment effects on catches of ambrosia, bark, and snout beetles (Curculionidae) caught in sufficient numbers. *df* = 3, 27 for FL and GA; 3, 24 for MI

Species	Site	*F*	*P*
Ambrosia Beetles			
Cnestus mutilatus	GA	1.78	0.176
Dryoxylon onoharaense	FL	6.38	0.002
	GA	9.03	<0.001
Monarthrum mali	MI	11.64	<0.001
Xyleborinus saxesenii	FL	10.32	<0.001
	GA	4.44	0.012
Xyleborus spp.	FL	19.62	<0.001
	GA	2.38	0.092
Xylosandrus crassiusculus	FL	1.90	0.154
	GA	2.58	0.074
Xylosandrus germanus	MI	0.467	0.708
Bark Beetles			
Dendroctonus terebrans	FL	19.35	<0.001
	GA	16.66	<0.001
Dendroctonus valens	MI	13.35	<0.001
Dryocoetes autographus	MI	5.97	0.003
Hylastes porculus	FL	3.76	0.022
Hylastes salebrosus	FL	18.67	<0.001
	GA	159.76	<0.001
	MI	2.56	0.078
Hylastes tenuis	GA	22.20	<0.001
Ips grandicollis	FL	81.31	<0.001
	GA	29.28	<0.001
	MI	18.18	<0.001
Orthotomicus caelatus	MI	6.48	0.002
Snout beetles			
Hylobius pales	FL	3.74	0.023
	GA	28.00	<0.001
	MI	18.18	<0.001
Pachylobius picivorus	FL	147.95	<0.001
	GA	16.85	<0.001
Pissodes spp.	MI	11.13	<0.001
Stenoscelis brevis	GA	0.47	0.704
	MI	1.70	0.194

Contech Enterprises (Victoria BC). Release rates were determined by the manufacturer. We tested 3 different enantiomeric compositions with the α-pinene bottle lures: (+)-α-pinene [95% (+): 5% (−)]; racemic α-pinene [50% (+): 50% (−)]; and (−)-α-pinene [5% (+): 95% (−)]. All chemical purities were >95%.

At each site, we deployed 40 traps in 10 replicate blocks of 4 traps per block. We used 8-unit traps in Florida and Georgia and 12-unit traps in Michigan. Traps were spaced 10–15 m apart and suspended above ground at a height of 0.3–0.5 m to the bottom of the collection cup. Collection cups contained 100–150 ml of a solution of propylene glycol (Table 1) to kill and preserve captured insects between biweekly collections (Miller and Duerr 2008). Each of the following lure treatments was randomly allocated to a different trap within each block: ethanol control (CT); ethanol + (+)-α-pinene (P); ethanol + racemic α-pinene (PM); and ethanol + (−)-α-pinene (M). Voucher specimens were deposited in the University of Georgia Collection of Arthropods (Athens, GA, USA).

Statistical Analyses

Data for species caught in sufficient numbers for analysis ($N \geq 30$) were analyzed with the SYSTAT ver. 13.1 and SigmaStat (SigmaPlot ver. 12.5) statistical packages (SYSTAT Software Inc., Point Richmond, CA, USA). Trap catch data were transformed as needed by ln (Y + 1) to ensure homoscedasticity and normality (Pepper et al. 1997), verified with the Equal Variance and Shapiro–Wilk tests, respectively, prior to analyses. One replicate block from Michigan was deleted from the analyses due to missing data for one treatment. Data for each species at each site were analyzed separately by mixed-model ANOVA using treatment as the model factor. The Holm-Sidak multiple-comparison procedure ($\alpha = 0.05$) was conducted to compare treatment means when treatment effects were significant at $P \leq 0.05$.

Results

Ambrosia, Bark, and Snout Beetles

We caught >8,200 ambrosia, bark, and snout beetles across the 3 sites, with 19 species or genera caught in sufficient numbers for analyses (Table 2). Species composition and abundance differed markedly between the 3 sites. For example, *Dendroctonus terebrans* (Olivier) (Coleoptera: Curculionidae) was caught in Florida and Georgia, whereas *De. valens* was caught in Michigan. Some species, such as *I. grandicollis* and *Hylobius pales* Herbst (Coleoptera: Curculionidae), were caught at all 3 sites.

Four of 7 species or genera of ambrosia beetles were affected by trap treatments at one or more sites (Table 3). In Florida, catches of *Xyleborinus saxesenii* (Ratzeburg) (Coleoptera: Curculionidae) were lowest in all traps baited with α-pinene, regardless of enantiomeric composition (Fig. 1A). In Georgia, catches of *Xyleborinus saxesenii* were lower in traps baited with ethanol and (−)-α-pinene than in those baited solely with ethanol (Fig. 1B). Catches of *Dryoxylon onoharaense* (Murayama) (Coleoptera: Curculionidae) in Florida and Georgia were lowest in all traps baited with α-pinene, regardless of enantiomeric composition (Fig. 1C and D). Trap catches of *Xyleborus* spp. (Coleoptera: Curculionidae) in Florida were increased by the addition of α-pinene, regardless of enantiomeric composition (Fig. 1E). In Florida, trap catches of *Xyleborus* spp. (Coleoptera: Curculionidae) were increased by the addition of α-pinene, regardless of enantiomeric composition (Fig. 1E), whereas in Georgia, trap catches were unaffected by lure treatments (Table 3); mean (±SE) trap catches = 4.2 ± 0.4. In Michigan, catches of

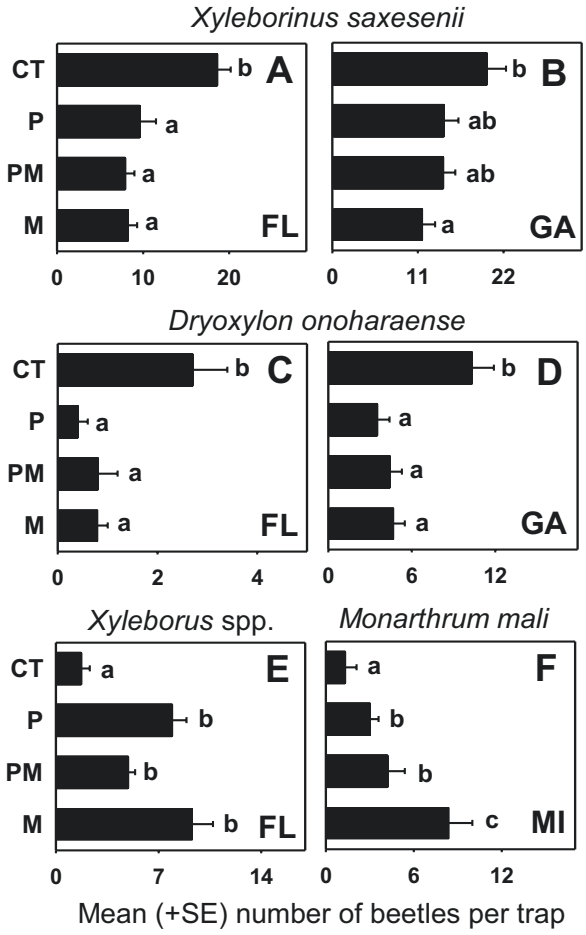

Fig. 1. Mean (+SE) catches of the ambrosia beetles *Xyleborinus saxesenii*, A and B), *Dryoxylon onoharaense*, C and D), *Xyleborus* spp., E), and *Monarthrum mali*, F) (Curculionidae) in traps baited with ethanol alone (CT), ethanol + (+)-α-pinene (P), ethanol + racemic α-pinene (PM), and ethanol + (−)-α-pinene (M) in Florida (FL), Georgia (GA), and Michigan (MI). For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak multiple-comparison test).

Monarthrum mali (Fitch) (Coleoptera: Curculionidae) were greatest in traps baited with (−)-α-pinene and lowest in traps not baited with α-pinene (Fig. 1F). Catches of *Cnestus mutilatus* (Blandford) (Coleoptera: Curculionidae) in Georgia and *Xylosandrus germanus* (Blandford) (Coleoptera: Curculionidae) in Michigan were unaffected by treatments (Table 3); mean (±SE) trap catches = 1.9 ± 0.3 and 24.5 ± 2.1, respectively. Similarly, treatments had no effect on catches of *Xylosandrus crassiusculus* (Motschulsky) (Coleoptera: Curculionidae) in Florida and Georgia (Table 3); mean (±SE) trap catches = 5.3 ± 0.6 and 3.3 ± 0.4, respectively.

Lure treatments had significant effects on catches of 8 species of bark beetles (Table 3). In Florida and Georgia, catches of *De. terebrans* were greatest in traps baited with (−)-α-pinene and lowest in traps not baited with α-pinene (Fig. 2A and B). In Michigan, catches of *De. valens* and *Dryocoetes autographus* (Ratzeburg) (Coleoptera: Curculionidae) were greater in traps baited with (−)-α-pinene or (+)-α-pinene than in those not baited α-pinene (Fig. 2C and D). For both species, catches in traps baited with (−)-α-pinene were greater than those in traps baited with racemic α-pinene. Catches of *I. grandicollis* were lowest in traps not baited with α-pinene across all 3 locations (Fig. 2E–G). The highest catches in Florida and Georgia were in traps baited with (−)-α-pinene (Fig. 2E and F), whereas the

highest catches in Michigan were in traps baited with (−)-α-pinene or racemic α-pinene. In Michigan, more *Orthotomicus caelatus* (Eichhoff) (Coleoptera: Curculionidae) were caught in traps baited with (+)-α-pinene or racemic α-pinene than in traps not baited with α-pinene (Fig. 2H). Catches of *Hylastes salebrosus* Eichhoff (Coleoptera: Curculionidae) in Florida and Georgia were greatest in traps baited with α-pinene, regardless of enantiomeric composition (Fig. 2I and J). The same was true for *Hylastes porculus* Erichson (Coleoptera: Curculionidae) in Florida (Fig. 1K) and *Hylastes tenuis* Eichhoff (Coleoptera: Curculionidae) in Georgia (Fig. 2L). There was no treatment effect on catches of *Hylastes salebrosus* in Michigan (Table 3); mean (±SE) trap catch = 1.8 ± 0.4.

Three of 4 species of snout beetles were affected by trap treatments (Table 3). Catches of *Pa. picivorus* in Florida and Georgia were lowest in traps not baited with α-pinene (Fig. 3A and B). In Florida, the greatest numbers of *Pa. picivorus* were caught in traps baited with (−)-α-pinene (Fig. 3A), whereas the greatest numbers in Georgia were caught in traps baited with racemic α-pinene or (−)-α-pinene (Fig. 3B). In Florida, catches of *Hylobius pales* were greater in traps baited with (−)-α-pinene than in those not baited with α-pinene (Fig. 3C). In Georgia, traps baited with (−)-α-pinene or (+)-α-pinene caught the greatest numbers of *Hylobius pales* whereas traps not baited with α-pinene caught the least (Fig. 3D). In Michigan, traps not baited with α-pinene caught the least numbers of *Hylobius pales* and those baited with (−)-α-pinene caught the most (Fig. 3E). All traps baited with α-pinene, regardless of enantiomeric composition, caught more *Pissodes* spp. (Coleoptera: Curculionidae) than traps not baited with α-pinene (Fig. 3F). Trap treatments had no effect on catches of *Stenoscelis brevis* Boheman (Coleoptera: Curculionidae) in Georgia and Michigan (Table 3); mean (±SE) trap catches = 4.2 ± 0.4 and 1.7 ± 0.3, respectively.

Wood Borers

We caught almost 1,200 woodboring beetles (Coleoptera: Buprestidae, and Cerambycidae) across the 3 sites, with 4 species or genera caught in sufficient numbers for analyses (Table 2). Treatment effects were found for all 4 species (Table 4). In Georgia, catches of *Chalcophora virginiensis* (Drury) (Coleoptera: Buprestidae) were greater in traps baited with (+)-α-pinene or (−)-α-pinene than in those in traps not baited with α-pinene (Fig. 4A). There was no effect on catches of *Ch. virginiensis* in Florida (Table 4); mean (±SE) trap catch = 2.1 ± 0.2. In Michigan, the greatest catches of *Asemum striatum* (L.) (Coleoptera: Cerambycidae) were in traps baited with (+)-α-pinene or racemic α-pinene and lowest in traps not baited with α-pinene (Fig. 4B). Catches

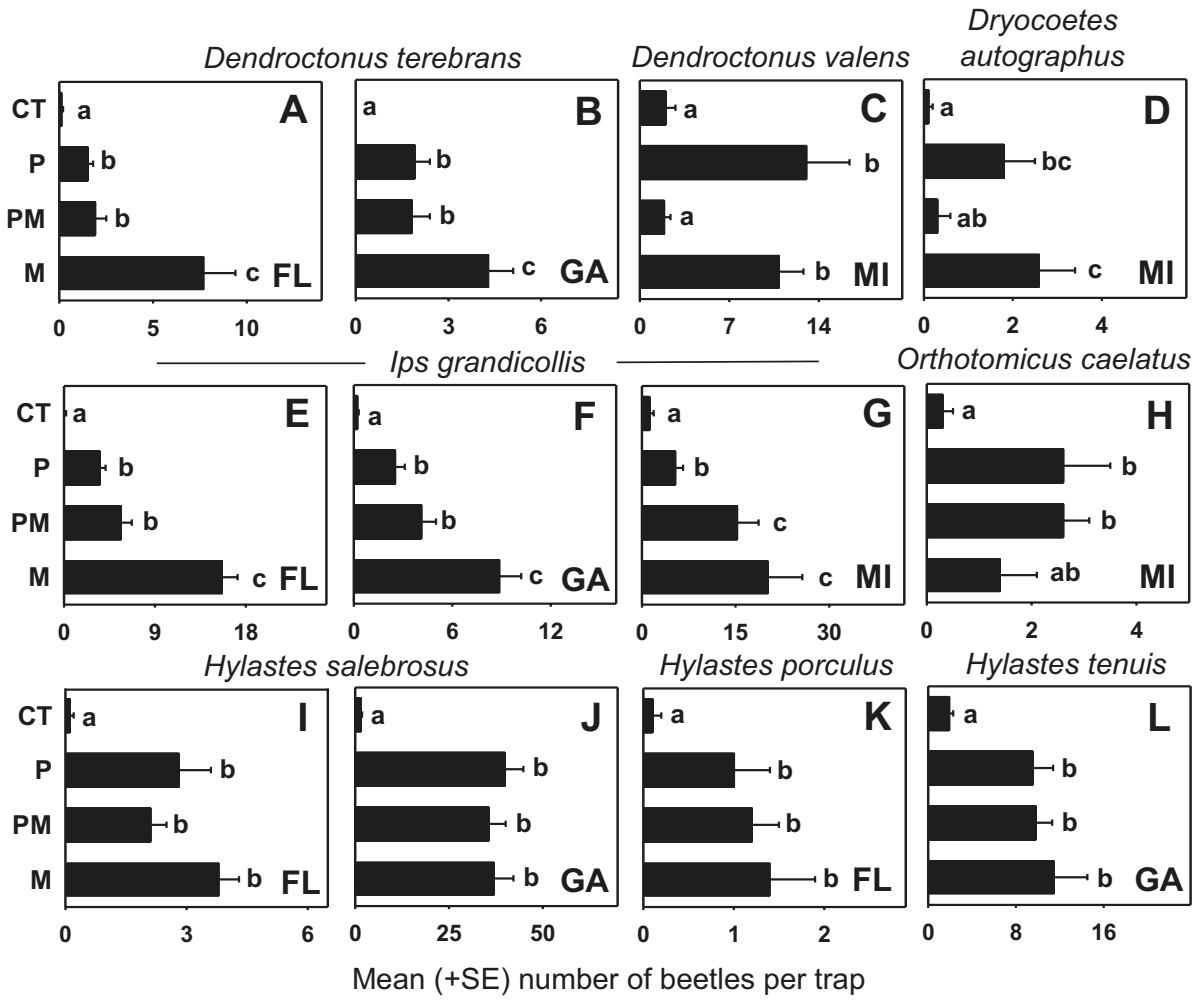

Fig. 2. Mean (+SE) catches of the bark beetles *Dendroctonus terebrans*, A and B), *Dendroctonus valens*, C), *Dryocoetes autographus*, D), *Ips grandicollis*, E–G), *Orthotomicus caelatus*, H), *Hylastes salebrosus*, I and J), *Hylastes porculus*, K), and *Hylastes tenuis*, L) (Curculionidae)in traps baited with ethanol alone (CT), ethanol + (+)-α-pinene (P), ethanol + racemic α-pinene (PM), and ethanol + (-)-α-pinene (M) in Florida (FL), Georgia (GA) and Michigan (MI). For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm-Sidak multiple-comparison test).

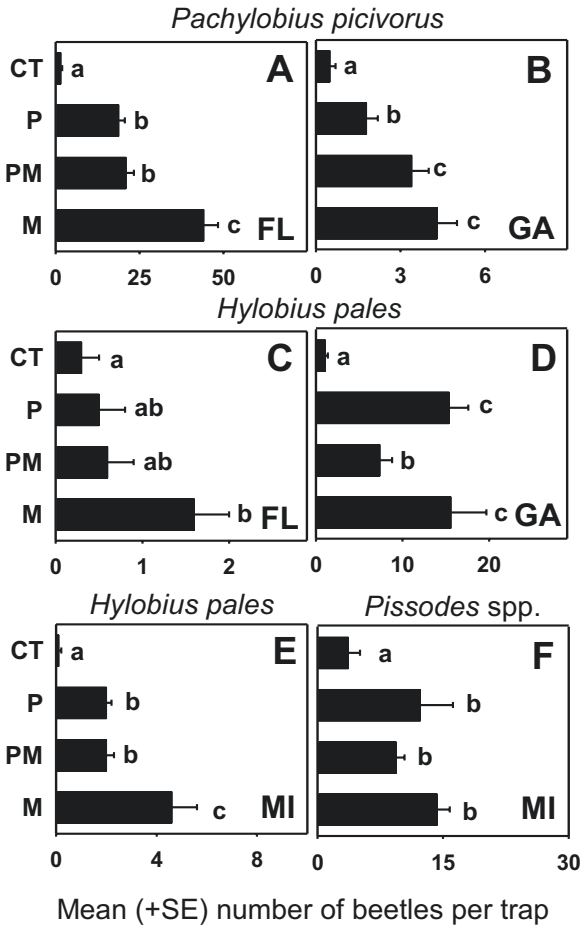

Fig. 3. Mean (+SE) catches of the snout weevils *Pachylobius picivorus*, A and B), *Hylobius pales*, C–E), and *Pissodes* spp., F) (Curculionidae) in traps baited with ethanol alone (CT), ethanol + (+)-α-pinene (P), ethanol + racemic α-pinene (PM), and ethanol + (−)-α-pinene (M) in Florida (FL), Georgia (GA), and Michigan (MI). For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak multiple-comparison test).

of *Xylotrechus sagittatus* (Germar) (Coleoptera: Cerambycidae) in Florida were greater in traps baited with (−)-α-pinene than any other treatment (Fig. 4C). In Georgia and Michigan, catches of *Xylotrechus sagittatus* were greater in traps baited with α-pinene than in those not baited with α-pinene (Fig. 4D and E). In Georgia, catches in traps baited with (−)-α-pinene were greater than those in traps baited with racemic α-pinene (Fig. 4D) whereas in Michigan catches in traps baited with (−)-α-pinene or racemic α-pinene were lower than those baited with (+)-α-pinene (Fig. 4E). Trap catches of *Monochamus titillator* (F.) (Coleoptera: Curculionidae) in traps not baited with α-pinene were lower than those baited with (+)-α-pinene in Florida (4F) and lower than all traps baited with α-pinene in Georgia, regardless of enantiomeric composition (4G).

Beetle Predators

Numerous species across several families of predators prey on bark and woodboring beetles, particularly on larval prey in host trees (USDA 1985). We caught >2,300 predators of bark and woodboring beetles across 5 families (Cleridae, Elateridae, Histeridae, Passandridae, and Trogossitidae) with 6 species or genera caught in sufficient numbers for analyses (Table 2) and 5 with significant treatment effects (Table 4). In Georgia and Michigan, catches of *Thanasimus dubius* (F.) (Coleoptera: Cleridae) in traps baited with (+)-α-pinene or racemic α-pinene were greater than those in traps not baited with α-pinene (Fig. 5A and B). In Michigan, catches of *Th. dubius* in traps baited with (−)-α-pinene were greater than those not baited with α-pinene but less than those in traps baited with (+)-α-pinene or racemic α-pinene (Fig. 5B). In Florida and Georgia, more *Alaus myops* (F.) (Coleoptera: Elateridae) were caught in traps baited with α-pinene than in those not baited with α-pinene regardless of enantiomeric composition (Fig. 5C and D). In Florida and Georgia, catches of *Platysoma* spp. (Coleoptera: Histeridae) were greatest in traps baited with (+)-α-pinene (Fig. 5E and F). There was no difference in catches among the remaining 3 treatments in Florida (Fig. 5E), whereas in Georgia, catches of *Platysoma* spp. in traps baited with racemic α-pinene were greater than those in traps not baited with α-pinene (Fig. 5F).

In Florida, catches of *Temnoscheila virescens* (F.) (Coleoptera: Trogossitidae) were greatest in traps baited with α-pinene, regardless of enantiomeric composition (Fig. 5G). In Georgia, traps baited with (+)-α-pinene or racemic α-pinene caught more *Te. virescens* than those not baited with α-pinene; traps baited with (−)-α-pinene caught less than those baited with (+)-α-pinene (Fig. 5H). Catches of *Tenebroides* spp. were increased by the addition of α-pinene regardless of enantiomeric composition; trap catches were greater in traps baited with (−)-α-pinene than in traps baited with (+)-α-pinene or racemic α-pinene (Fig. 5I). Trap treatments had no effect on catches *Catogenus rufus* F. (Coleoptera: Passandridae) (Table 4); mean (±SE) trap catch = 3.2 ± 0.5.

Table 4. ANOVA results for lure treatment effects on catches of wood borers and predators caught in sufficient numbers. $df = 3, 27$ for FL and GA; 3, 24 for MI

Family, Species	Site	*F*	*P*
Woodborers			
Buprestidae			
Chalcophora virginiensis	FL	2.21	0.110
	GA	5.73	0.004
Cerambycidae			
Asemum striatum	MI	27.22	<0.001
Monochamus titillator	FL	9.02	<0.001
	GA	22.47	<0.001
Xylotrechus sagittatus	FL	11.42	<0.001
	GA	47.42	<0.001
	MI	12.95	<0.001
Predators			
Cleridae			
Thanasimus dubius	GA	9.00	<0.001
	MI	26.82	<0.001
Elateridae			
Alaus myops	FL	22.15	<0.001
	GA	6.21	0.002
Histeridae			
Platysoma spp.	FL	49.75	<0.001
	GA	103.30	<0.001
Passandridae			
Catogenus rufus	GA	0.72	0.551
Trogossitidae			
Temnoscheila virescens	FL	25.20	<0.001
	GA	9.90	<0.001
Tenebroides spp.	GA	28.41	<0.001

Discussion

Bark and woodboring beetles have a complex relationship with conifers. Coniferous trees use various physical, chemical, and biological defenses against invasions by insects, bacteria, and fungi

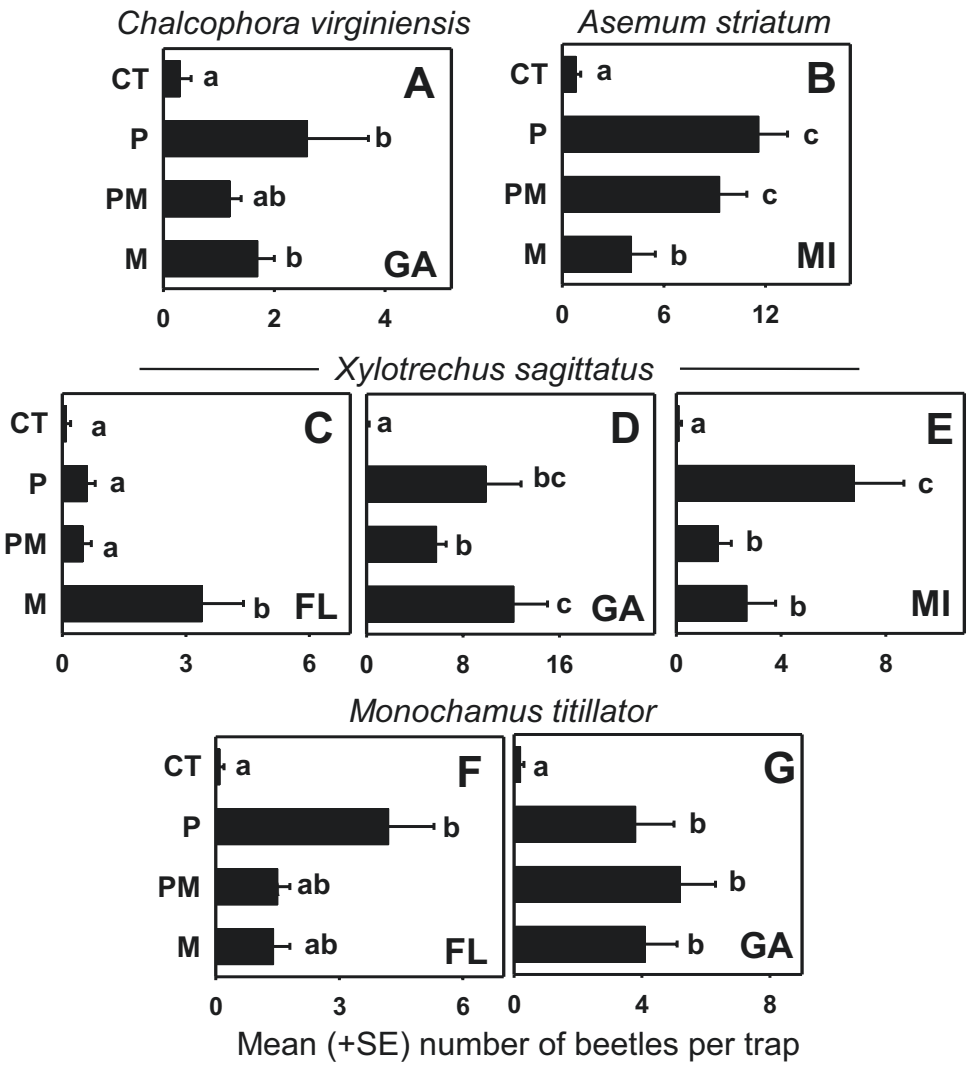

Fig. 4. Mean (+SE) catches of the woodboring beetles *Chalcophora virginiensis* (Buprestidae), A), *Asemum striatum*, B), *Xylotrechus sagittatus*, C–E), and *Monochamus titillator*, F and G) (Cerambycidae) in traps baited with ethanol alone (CT), ethanol + (+)-α-pinene (P), ethanol + racemic α-pinene (PM), and ethanol + (−)-α-pinene (M) in Florida (FL), Georgia (GA), and Michigan (MI). For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak multiple-comparison test).

(Krokene 2015, Raffa et al. 2015). With respect to bark and woodboring beetles, resin pressure and composition are of particular importance. Healthy trees can localize resin flow, forcing out and drowning beetles attempting to bore into the phloem (Smith 1972). In addition, resins in pine trees are composed of monoterpenes, some of which can be toxic to bark and woodboring beetles, necessitating judicious selection of hosts by bark beetles (Krokene 2015, Raffa et al. 2015). Although attracted by low levels of α-pinene, high-release rates of α-pinene can reduce attraction of bark beetles such as *Co. coniperda* (Miller et al. 2003), *Ips pini* (Say) (Coleoptera: Curculionidae) (Erbilgin et al. 2003), and *Ips avulsus* (Eichhoff) (Coleoptera: Curculionidae) (Sullivan 2023) to traps baited with their respective pheromones. Monoterpenes such as α-pinene are also used to produce pheromones such as *cis*- and *trans*-verbenol (e.g., Vanderwel and Oehlschlager 1987, Blomquist et al. 2010, Keeling et al. 2021).

Pine tree resins contain a diversity of monoterpenes such as α-pinene, β-pinene, 3-carene, limonene, myrcene, and β-phellandrene with significant variation in monoterpene composition by species (e.g., Mirov 1961, Coyne and Keith 1972, Rockwood 1973, Gansel and Squillace 1976, Hodges et al. 1979, Squillace and Wells 1981, Clark et al. 2010). When released from bark wounds, woody debris or stumps of felled trees, monoterpenes in the resin can act as kairomones, indicating suitable host material for bark and wood boring beetles (e.g., Wood 1982, Coulson et al. 1986, Sjödin et al. 1989, Fletchmann et al. 1999, Fettig et al. 2006, Kelsey and Westlind 2017).

Variations in monoterpene composition among different species of pines may allow bark and woodboring beetles to be selective in choosing hosts if necessary. For example, β-phellandrene is the dominant monoterpene in the resin of lodgepole pine, *Pinus contorta* Douglas *ex* Loudon in western North America (Zavarin et al. 1969, Smith 2000, Pureswaran and Borden 2005, Ankney et al. 2022). Traps baited with lures releasing β-phellandrene are highly attractive in a dose-dependent fashion to *I. pini*, *Orthotomicus latidens* (LeConte) (Coleoptera: Curculionidae), and *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), *Monochamus clamator* (LeConte) (Coleoptera: Cerambycidae), and several species of bark beetle predators (Miller and Borden 1990a, 1990b, 2000) that attack or prey on beetles in lodgepole pine.

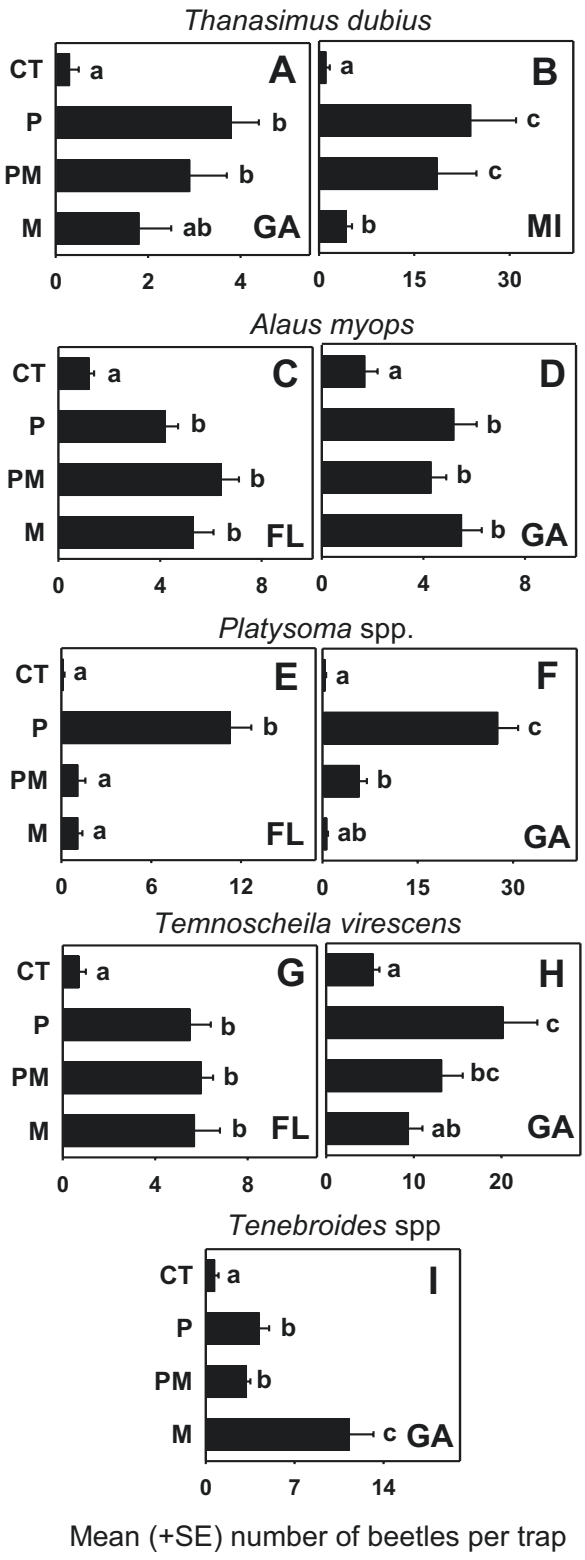

Fig. 5. Mean (+SE) catches of the predators *Thanasimus dubius* (Cleridae), A and B), *Alaus myops* (Elateridae), C and D), *Platysoma* spp. (Histeridae), E and F), *Temnoscheila virescens*, G and H), and *Tenebroides* spp. (Trogossitidae), I) in traps baited with ethanol alone (CT), ethanol + (+)-α-pinene (P), ethanol + racemic α-pinene (PM), and ethanol + (–)-α-pinene (M) in Florida (FL), Georgia (GA), and Michigan (MI). For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak multiple-comparison test).

However, responses to other monoterpenes in lodgepole pine can vary between these same 3 species of bark beetles in lodgepole pine. Increasing release rates of myrcene decreased catches of *I. pini* and *O. latidens* in pheromone-baited traps, whereas catches *De. ponderosae* increased with the increasing release rate of myrcene (Miller and Borden 2000). In contrast, catches of *I. pini* and *De. ponderosae* increased with increasing release rates of 3-carene, whereas catches of *O. latidens* decreased (Miller and Borden 2000). Increasing release rates of β-pinene increased catches of *I. pini* but had no effects on catches of *O. latidens* and *De. ponderosae* (Miller and Borden 2000).

Such results support the hypothesis that bark beetles can be selective in choosing individual host trees as well as timing or host conditions for attack based on monoterpene blend composition in order to maximize success in establishing broods and partition resources for reproductive isolation or to avoid competition. Enantiomeric preferences may also play a role associated with host preferences. In California, the attraction of *De. valens* to traps baited with (+)-α-pinene was interrupted by the addition of (–)-α-pinene in a stand of ponderosa pine, *Pinus ponderosa* Douglas *ex* Lawson, and sugar pine, *Pinus lambertiana* Douglas (Hobson et al. 1993). Hobson et al. (1993) found that the enantiomeric composition of α-pinene was 94% (–) in ponderosa pine but only 31% (–) in sugar pine, suggesting a preference by *D. valens* for sugar pine.

In our study, we found several patterns of responses common to bark beetles, woodborers, and predators. For example, the enantiomeric composition did not affect the responses of the bark beetles *O. caelatus*, *Hylastes salebrosus*, *Hylastes porculus*, and *Hylastes tenuis* to α-pinene. Their attraction to ethanol-baited traps was enhanced by α-pinene, regardless of enantiomeric composition (Fig. 2H–L). The same was true for the ambrosia beetles *Xyleborus* spp. in Florida (Fig. 1E), the weevils *Pissodes* spp. in Michigan (Fig. 3F), the woodborers *Ch. virginiensis* and *Monochamus titillator* in Georgia (Fig. 4A, F, and G), and the predators *Th. dubius* in Georgia (Fig. 5A), *Al. myops* in Florida and Georgia (Fig. 5C and D), and *Te. virescens* in Florida (Fig. 5G). These species at these locations do not seem to use the enantiomeric composition of α-pinene to locate specific hosts.

However, several species demonstrated a preference for traps baited with (+)-α-pinene, consistent with the enantiomeric composition of α-pinene in pines in the immediate proximity of our traps, including longleaf, loblolly and red pine that all have predominantly (+)-α-pinene (Mirov 1961, Phillips et al. 1999, Erbilgin et al. 2001, Marques et al. 2012). Traps baited with (+)-α-pinene were preferred over traps baited with (–)-α-pinene for the woodborer *As. striatum* (Fig. 4B), and the predators *Th. dubius* in Michigan (Fig. 5B), *Platysoma* spp. in Florida and Georgia (Fig. 5E and F), and *Te. virescens* in Georgia (Fig. 5H).

In contrast, the bark beetles *De. valens* and *Dr. autographus* exhibited equal attraction to traps baited with (+)- or (–)-α-pinene in Michigan and were generally less attracted to traps baited with racemic α-pinene (Fig. 2C and D). The same was true for *Hylobius pales* and *Xylotrechus sagittatus* in Georgia (Figs. 3D and 4D). These results suggest the avoidance of trees with resin containing racemic α-pinene, possibly eastern white pine, *Pinus strobus* L. (Mirov 1961). Eastern white pine is common in Michigan, as well as northeastern Georgia (Wendel and Smith 1990).

Results for other species did not support the hypothesis that beetles are attracted to traps baited with enantiomeric compositions of α-pinene that reflect the resin composition of trees in the area. The bark beetles *De. terebrans* and *I. grandicollis* exhibited a clear

preference for (−)-α-pinene over (+)-α-pinene (Fig. 2A, B, and E–G). The same was true for the ambrosia beetle *Monarthrum mali* in Michigan (Fig. 1F), the weevils *Pa. picivorus* (Fig. 3A and B) in Florida and Georgia, and *Hylobius pales* in Florida and Michigan (Fig. 3C and E), the woodborer *Xylotrechus sagittatus* in Florida (Fig. 4C), and the predators *Tenebroides* spp. in Georgia (Fig. 5I). Yet the traps were all located within stands of pines including loblolly, longleaf, and red pine with resin known to have an excess of the (+) enantiomer of α-pinene (Mirov 1961, Phillips et al. 1999, Erbilgin et al. 2001, Marques et al. 2012).

Some beetle species had variable responses to the enantiomeric composition of α-pinene at different locations in our study. Catches of *Pa. picivorus* were greater in traps baited with (−)-α-pinene than in those baited with racemic α-pinene in Florida but not in Georgia (Fig. 3A and B). *Hylobius pales* preferred traps baited with (−)-α-pinene in Michigan, whereas in Georgia, traps baited with either (+)- or (−)-α-pinene were preferred (Fig. 3D and E). Responses by *Xylotrechus sagittatus* differed across all 3 locations, preferring (−)-α-pinene in Florida, (+)-α-pinene in Michigan, and both (−)- and (+)-α-pinene in Georgia (Fig. 4C–E). In Florida, catches of *Te. virescens* were not affected by the enantiomeric composition of α-pinene (Fig. 5G), whereas in Georgia, catches of *Te. virescens* in traps baited with (+)-α-pinene were greater than those baited with (−)-α-pinene (Fig. 5H). Such variation in responses at different locations may reflect differences in the overall composition of monoterpene blends in different pine species, differences in competitor and natural enemy communities, and possible variations in enantiomeric composition over time and under different host conditions.

A greater understanding of the role of enantiomeric composition of pine resins, including α-pinene is needed to better understand variation in beetle responses. There are numerous determinations of monoterpene composition due in part to the turpentine industry (Silvestre and Gandini 2008), but very few studies have assessed enantiomeric composition. Further assessments of the enantiomeric composition of α-pinene are needed, particularly at times when beetles are attacking or inhabiting pine trees. Behavioral responses to α-pinene may vary when pheromones are also present.

Olfactory responses of *De. frontalis* can vary depending on which of the 2 enantiomers of α-pinene is present or more abundant (Staeben et al. 2015, Sullivan 2016). In the field, catches of *De. frontalis* were greater in traps baited with the pheromone frontalin when co-baited with the (+) enantiomer of α-pinene [98% (+)] than with the (−) enantiomer of α-pinene [97% (−)] (Staeben et al. 2015). The resin of most common pines in the southeastern United States is dominated by the (+) enantiomer of α-pinene (Mirov 1961, Phillips et al. 1999). Attraction of *De. frontalis* to traps baited with frontalin is enhanced by both (±)-α-pinene and (−)-β-pinene (Munro et al. 2020). One supplier of lures (Synergy Semiochemicals Inc., Delta, BC, Canada) for the southern pine beetle detection program adjusted the lure to a 7:3 blend of 75% (+)-α-pinene and (−)-β-pinene to better match the monoterpene composition found in southern pines and help minimize the variation in population predictions based on models of trapping results (Sullivan et al. 2021). Further studies on the enantiomeric composition of host volatiles and beetle responses may be critical in optimizing detection protocols such as those used for the Southern Pine Beetle Detection and Prediction program.

In conclusion, we found that the enantiomeric composition of α-pinene in the resin of host trees is not a good predictor of preferences by bark and woodboring beetles and associated predators. Behavioral responses by beetles to different enantiomers of α-pinene varied substantially by species/genera and geographic region. Our data could be useful in the optimization of lures for our native species targeted as nonnatives in other countries.

Acknowledgments

We thank Alison Barc, Stephen Burr, Tina Ciaramitaro, Chris Crowe, and Jeff Eickwort for field assistance. We are sincerely grateful to E. R. Hoebeke (University of Georgia Collection of Arthropods) for verification of insect identifications. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official United States Department of Agriculture (USDA) or United States Government determination or policy. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the USDA of any product or service.

Funding

This research was supported by the USDA, Forest Service. The USDA is an equal opportunity provider, employer, and lender.

Author Contributions

Daniel Miller (Conceptualization [lead], Formal analysis [lead], Investigation [equal], Methodology [lead], Resources [equal], Writing—original draft [lead], Writing—review & editing [equal]), Albert Mayfield (Conceptualization [supporting], Formal analysis [supporting], Investigation [equal], Methodology [supporting], Resources [equal], Writing—original draft [supporting], Writing—review & editing [equal]), and Therese Poland (Conceptualization [supporting], Formal analysis [supporting], Investigation [equal], Methodology [supporting], Resources [equal], Writing—original draft [supporting], Writing—review & editing [equal])

References

Allison JD, Borden JH, Seybold SJ. A review of the chemical ecology of the Cerambycidae (Coleoptera). Chemoecology. 2004:14(3–4):123–150.

Allison JD, McKenney JL, Millar JG, McElfresh JS, Mitchell RF, Hanks LM. Response of the woodborers *Monochamus carolinensis* and *Monochamus titillator* (Coleoptera: Cerambycidae) to known cerambycid pheromones in the presence and absence of the host plant volatile α-pinene. Environ Entomol. 2012:41(6):1587–1596. https://doi.org/10.1603/en12185

Ankney E, Swor K, Satyal P, Setzer WN. Essential oil compositions of *Pinus* species (*P. contorta* subsp. *contorta*, *P. ponderosa* var. *ponderosa*, and *P. flexilis*); enantiomeric distribution of terpenoids in *Pinus* species. Molecules. 2022:27(17):5658. https://doi.org/10.3390/molecules27175658

Blomquist GJ, Figeroa-Teran R, Aw M, Song M, Gorzalski A, Abbott NL, Chang E, Tittiger C. Pheromone production in bark beetles. Insect Biochem Mol Biol. 2010:40:699–712.

Boone CK, Sweeney J, Silk P, Hughes C, Webster RP, Stephen F, Maclauchlan L, Bentz B, Drumont A, Zhao B, et al. *Monochamus* species from different continents can be effectively detected with the same trapping protocol. J Pest Sci. 2019:92(1):3–11. https://doi.org/10.1007/s10340-018-0954-4

Brockerhoff EG, Corley JC, Jactel H, Miller DR, Rabaglia RJ, Sweeney J. Chapter 19 – Monitoring and surveillance of forest insects. In: Allison JD, Paine TD, Slippers B, Wingfield MJ, editors. Forest entomology and pathology. Volume 1: entomology. Cham, Switzerland: Springer Nature Switzerland AG; 2023. p. 669–704.

Brockerhoff EG, Jones DC, Kimberley MO, Suckling DM, Donaldson T. Nationwide survey for invasive wood-boring and bark beetles (Coleoptera) using traps baited with pheromones and kairomones. Forest Ecol Manag. 2006:228(1-3):234–240. https://doi.org/10.1016/j.foreco.2006.02.046

(CAPS) Cooperative Agricultural Pest Survey. Exotic wood borer/ bark beetle survey reference – 2024; 2024 [accessed 2024 Jan 3]. https://caps.ceris.purdue.edu/survey-manuals?list=ewb-bb&year=2024.

Chénier JVR, Philogène BJR. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. J Chem Ecol. 1989:15(6):1729–1745.

Clark EL, Carroll AL, Huber DPW. Differences in the constitutive terpene profile of lodgepole pine across a geographical range in British Columbia,

and correlation with historical attack by the mountain pine beetle. Can Entomol. 2010:142:557–573.
Collignon RM, Swift IP, Zou Y, McElfresh JS, Hanks LM, Millar JG. The influence of host plant volatiles on the attraction of longhorn beetles to pheromones. J Chem Ecol. 2016:42(3):215–229. https://doi.org/10.1007/s10886-016-0679-x
Coulson RN, Flamm RO, Pulley PE, Payne TL, Rykiel EJ, Wagner TL. Response of the southern pine bark beetle guild (Coleoptera: Scolytidae) to host disturbance. Environ Entomol. 1986:15(4):850–858. https://doi.org/10.1093/ee/15.4.850
Coyne JF, Keith GC. Geographic survey of monoterpenes in loblolly and shortleaf pines. Washington (DC): United States Department of Agriculture–Forest Service Res. Pap. SO-79; 1972.
Czokajlo D, Teale SA. Synergistic effect of ethanol to α-pinene in primary attraction of the larger pine shoot beetle, *Tomicus piniperda*. J Chem Ecol. 1999:25(5):1121–1130.
de Groot P, DeBarr GL, Birgersson G. Field bioassays of synthetic pheromones and host monoterpenes for *Conophthorus coniperda* (Coleoptera: Scolytidae). Environ Entomol. 1998:27(2):382–387.
de Groot P, Nott R, MacDonald L. Influence of enantiomers of α-pinene on the response of the red pine cone beetle, *Conophthorus resinosae* to its pheromone pityol. Entomol Exp Appl. 2002:105(2):169–174. https://doi.org/10.1046/j.1570-7458.2002.01045.x
Duduman M-L, Olenici N. Non-target bark beetles in *Ips duplicatus* (Sahlberg) pheromone traps baited with host volatiles. Not Bot Horti Agrobo. 2015:43(2):576–581.
Erbilgin N, Krokene P, Kvamme T, Christiansen E. A host monoterpene influences *Ips typographus* (Coleoptera: Curculionidae, Scolytinae) responses to its aggregation pheromone. Agric For Entomol. 2007:9(2):135–140. https://doi.org/10.1111/j.1461-9563.2007.00329.x
Erbilgin N, Powell JS, Raffa KF. Effect of varying monoterpene concentrations on the response of *Ips pini* (Coleoptera: Scolytidae) to its aggregation pheromone: implications for pest management and ecology of bark beetles. Agric For Entomol. 2003:5(4):269–274. https://doi.org/10.1046/j.1461-9563.2003.00186.x
Erbilgin N, Raffa KF. Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromones. J Chem Ecol. 2000:26(11):2527–2548.
Erbilgin N, Szele A, Klepzig KD, Raffa KF. Trap type, chirality of α-pinene, and geographic region affect sampling efficiency of root and lower stem insects in pine. J Econ Entomol. 2001:94(5):1113–1121. https://doi.org/10.1603/0022-0493-94.5.1113
Fan J-T, Denux O, Courtin C, Bernard A, Javal M, Millar JG, Hanks LM, Roques A. Multi-component blends for trapping native and exotic longhorn beetles at potential points-of-entry and in forests. J Pest Sci. 2019:92:281–297.
Fettig CJ, McMillin JD, Anhold JA, Hamud SM, Borys RR, Dabney CP, Seybold SJ. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. Forest Ecol Manag. 2006:230(1-3):55–68. https://doi.org/10.1016/j.foreco.2006.04.018
Fletchmann CAH, Dalusky MJ, Berisford CW. Bark and ambrosia beetle (Coleoptera: Scolytidae) responses to volatiles from aging loblolly pine billets. Environ Entomol. 1999:28(4):638–648.
Gandhi KJK, Cognato AI, Lightle DM, Mosley BJ, Nielsen DG, Herms DA. Species composition, seasonal activity, and semiochemical response of native and exotic bark and ambrosia beetles (Coleoptera: Curculionidae) in northeastern Ohio. J Econ Entomol. 2010:103(4):1187–1195. https://doi.org/10.1603/ec10026
Gansel CR, Squillace AE. Geographic variation of monoterpene in cortical oleoresin of slash pine. Silvae Genet. 1976:25(5–6):150–154.
Hanks LM, Millar JG, Mongold-Diers JA, Wong JCH, Meier LR, Reagel PF, Mitchell RF. Using blends of cerambycid pheromones and host volatiles to simultaneously attract a diversity of cerambycid species. Can J For Res. 2012:42:1050–1059.
Hobson KR, Wood DL, Cool LG, White PR, Ohtsuka T, Kubo I, Zavarin E. Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. J Chem Ecol. 1993:19(9):1837–1846. https://doi.org/10.1007/BF00983790
Hoch G, Connell J, Roques A. Testing multi-lure traps for surveillance of native and alien longhorn beetles (Coleoptera, Cerambycidae) at ports of entry and in forests in Austria. Manag Biol Invasions. 2020:11(4):677–688. https://doi.org/10.3391/mbi.2020.11.4.04
Hodges JD, Elam WW, Watson WF, Nebeker TE. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. Can Entomol. 1979:111(8):889–896. https://doi.org/10.4039/ent111889-8
Hofstetter RW, Chen Z, Gaylord ML, McMillin JD, Wagner MR. Synergistic effects of α-pinene and *exo*-brevicomin on pine bark beetles and associated insects in Arizona. J Appl Entomol. 2008:132(5):387–397. https://doi.org/10.1111/j.1439-0418.2007.01263.x
Keeling CI, Tittiger C, MacLean M, Blomquist GJ. Chapter 4 – Pheromone production in bark beetles. In: Blomquist GJ, Vogt RG, editors. Insect pheromone biochemistry and molecular biology. 2nd ed. New York (NY): Elsevier, Academic Press; 2021. p. 123–162.
Kelsey KG, Westlind DJ. Ethanol and primary attraction of red turpentine beetle in fire stressed ponderosa pine. For Ecol Manag. 2017:396:44–54.
Kelsey RG. Ethanol synthesis in Douglas-fir logs felled in November, January, and March and its relationship to ambrosia beetle attack. Can J For Res. 1994:24(10):2096–2104. https://doi.org/10.1139/x94-269
Krokene P. Conifer defense and resistance to bark beetles. In: Vega FE, Hofstetter RW, editors. Bark beetles. Biology and ecology of native and invasive species. New York (NY): Elsevier, Academic Press; 2015. p. 177–207.
Liu Y, Dai H. Application of bark beetle semiochemicals for quarantine of bark beetles in China. J Insect Sci. 2006:6(41):1–6. https://doi.org/10.1673/031.006.4101
Marques FA, Frensch G, Zaleski SRM, Nagata N, Sales Maia BHLN, Lazzari SMN, Lenz CA, Corrêa AG. Differentiation of five pine species cultivated in Brazil based on chemometric analysis of their volatiles identified by gas chromatography-mass spectrometry. J Braz Chem Soc. 2012:23(9):1756–1761.
Miller DR. Ethanol and (–)-α-pinene: Attractant kairomones for some large wood-boring beetles in southeastern USA. J Chem Ecol. 2006:32(4):779–794. https://doi.org/10.1007/s10886-006-9037-8
Miller DR. Effects of ethanol and α-pinene in a generic trap lure blend for pine bark and wood-boring beetles in southeastern United States. J Entomol Sci. 2020:55(3):310–320. https://doi.org/10.18474/0749-8004-55.3.310
Miller DR, Borden JH. β-Phellandrene: Kairomone for pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). J Chem Ecol. 1990b:16(8):2519–2531. https://doi.org/10.1007/BF01017475
Miller DR, Borden JH. The use of monoterpenes as kairomones by *Ips latidens* (LeConte) (Coleoptera: Scolytidae). Can Entomol. 1990a:122(2):301–307. https://doi.org/10.4039/ent122301-3
Miller DR, Borden JH. Dose-dependent and species-specific responses of pine bark beetles (Coleoptera: Scolytidae) to monoterpenes in association with pheromones. Can Entomol. 2000:132(2):183–195. https://doi.org/10.4039/ent132183-2
Miller DR, Crowe CM, Asaro C, DeBarr GL. Dose and enantiospecific responses of white pine cone beetles, *Conophthorus coniperda*, to α-pinene in an eastern white pine seed orchard. J Chem Ecol. 2003:29(2):437–451. https://doi.org/10.1023/a:1022642314029
Miller DR, Crowe CM, Dodds KJ, Galligan LD, Groot P. de, Hoebeke ER, Mayfield AE III, Poland TM, Raffa KF, Sweeney JD. Ipsenol, ipsdienol, ethanol, and α-pinene: trap lure blend for Cerambycidae and Buprestidae (Coleoptera) in pine forests of eastern North America. J Econ Entomol. 2015:108(4):1837–1851.
Miller DR, Dodds KJ, Eglitis A, Fettig CJ, Hofstetter RW, Langor DW, Mayfield AE III, Munson AS, Poland TM, Raffa KF. Trap lure blend of pine volatiles and bark beetle pheromones for *Monochamus* spp. (Coleoptera: Cerambycidae) in pine forests of Canada and the United States. J Econ Entomol. 2013:106(4):1684–1692.
Miller DR, Duerr DA. Comparison or arboreal beetle catches in wet and dry collection cups with Lindgren multiple funnel traps. J Econ Entomol. 2008:101(1):107–113. https://doi.org/10.1603/0022-0493(2008)101[107:coabci]2.0.co;2

Miller DR, Rabaglia RJ. Ethanol and (–)-α-pinene: Attractant kairomones for bark and ambrosia beetles in the southeastern US. J Chem Ecol. 2009:35(4):435–448. https://doi.org/10.1007/s10886-009-9613-9

Mirov NT. Composition of gum turpentines of pines. Washington (DC): United States Department of Agriculture–Forest Service, Tech. Bull. 1239; 1961.

Munro HL, Gandhi KJK, Barnes BF, Montes CR, Nowak JT, Shepherd WP, Villari C, Sullivan BT. Electrophysiological and behavioral responses of *Dendroctonus frontalis* and *D. terebrans* (Coleoptera: Curculiinidae) to resin odors of host pines (*Pinus* spp.). Chemoecology. 2020:31(1):75–75. https://doi.org/10.1007/s00049-020-00328-y

Pepper WD, Zarnoch SJ, DeBarr GL, de Groot P, Tangren CD. Choosing a transformation in analyses of insect counts from contagious distributions with low means. Asheville (NC): United States Department of Agriculture–Forest Service, Res. Pap. SRS–5; 1997.

Phillips MA, Savage TJ, Croteau R. Monoterpene synthases of loblolly pine (*Pinus taeda*) produce pinene isomers and enantiomers. Arch Biochem Biophys. 1999:372(1):197–204. https://doi.org/10.1006/abbi.1999.1467

Poland TM, de Groot P, Burke S, Wakarchuk D, Haack RA, Nott R, Scarr T. Development of an improved attractive lure for the pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae). Agric For Entomol. 2003:5:293–300.

Poland TM, Rassati D. Improved biosecurity surveillance of non-native forest insects: a review of current methods. J Pest Sci. 2019:92(1):37–49. https://doi.org/10.1007/s10340-018-1004-y

Pureswaran DS, Borden JH. Primary attraction and kairomonal host discrimination in three species of *Dendroctonus* (Coleoptera: Scolytidae). Agric For Entomol. 2005:7(3):219–230. https://doi.org/10.1111/j.1461-9555.2005.00264.x

Rabaglia RJ, Cognato AI, Hoebeke ER, Johnson CW, Labonte JR, Carter ME, Vlach JJ. Early detection and rapid response. A 10-year summary of the USDA Forest Service program of surveillance for non-native bark and ambrosia beetles. Am Entomol. 2019:65(1):29–42. https://doi.org/10.1093/ae/tmz015

Raffa KF, Grégoire J-C, Lindgren BS. Chapter 1 – Natural history and ecology of bark beetles. In: Vega FE, Hofstetter RW, editors. Bark beetles. Biology and ecology of native and invasive species. New York (NY): Elsevier, Academic Press; 2015. p. 1–40.

Rockwood DL. Variation in the monoterpene composition of two oleoresin systems of loblolly pine. For Sci. 1973:19(2):147–153.

Ryall KL, Silk P, Thurston GS, Scarr TA, Groot P. de. Elucidating pheromone and host volatile components to the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Curculionidae), in eastern Canada. Can Entomol. 2013:145:406–415.

Shrimpton DM. Composition of volatile oil from the bark of lodgepole pine. Can For Serv Bi-Monthly Res Notes. 1974:30:12.

Silvestre AJD, Gandini A. Terpenes: major sources, properties and applications. In: Belmaker MN, Gandini A, editors. Monomers, polymers and composites from renewable resources. New York (NY): Elsevier Ltd; 2008. p. 17–38.

Sjödin K, Schroeder LM, Eidmann HH, Norin T, Wold S. Attack rates of scolytids and composition of wood constituents in healthy and mechanically weakened pine trees. Scand J For Res. 1989:4:379–391.

Smith RH. Xylem resin in the resistance of the Pinaceae to bark beetles. Albany (CA): United States Department of Agriculture–Forest Service, Gen. Tech. Rep. PSW–GTR–1; 1972.

Smith RH. Xylem monoterpenes of pines: distribution, variation, genetics, function. Albany (CA): United States Department of Agriculture–Forest Service, Gen. Tech. Rep. PSW–GTR–177; 2000.

Squillace AE, Wells OO. Geographic variation of monoterpenes in cortical oleoresin of loblolly pine. Silvae Genet. 1981:30(4–5):127–135.

Staeben JC, Sullivan BT, Nowak JT, Gandhi KJK. Enantiospecific responses of southern pine beetle (*Dendroctonus frontalis*) and its clerid predator, *Thanasimus dubius*, to α-pinene. Chemoecology. 2015:25(2):73–83. https://doi.org/10.1007/s00049-014-0175-0

Sullivan BT. Chapter Four – Semiochemicals in the natural history of southern pine beetle *Dendroctonus frontalis* Zimmermann and their role in pest management. In: Tittiger C, Blomquist GJ, editors. Advances in insect physiology. Vol. 50. Oxford (UK): Academic Press, Elsevier Ltd; 2016. p. 129–193.

Sullivan BT. Host odour *alpha*-pinene increases or reduces response of *Ips avulsus* (Coleoptera: Curculionidae) to its aggregation pheromone, depending on separation of release points. Can Entomol. 2023:155:e4.

Sullivan BT, Shepherd WP, Nowak JT, Clarke SR, Merten PR, Billings RF, Upton WW, Riggins JJ, Brownie C. Alternative formulations of trap lures for operational detection, population monitoring, and outbreak forecasting of southern pine beetles in the United States. J Econ Entomol. 2021:114(3):1189–1200. https://doi.org/10.1093/jee/toab062

Sun J, Miao Z, Zhang Z, Zhang Z, Gillette NE. Red turpentine beetle, *Dendroctonus valens* LeConte (Coleoptera: Scolytidae), response to host semiochemicals in China. Environ Entomol. 2004:33(2):206–212. https://doi.org/10.1603/0046-225x-33.2.206

Sweeney JD, Silk PJ, Grebennikov V. Efficacy of semiochemical-baited traps for detection of longhorn beetles (Coleoptera: Cerambycidae) in the Russian Far East. Eur J Entomol. 2014:111(3):397–406. https://doi.org/10.14411/eje.2014.049

(USDA) U.S. Department of Agriculture–Forest Service. Insects of eastern forests. Washington (DC): United States Department of Agriculture–Forest Service Misc. Publ. No. 1426; 1985.

Vanderwel D, Oehlschlager AC. Biosynthesis of pheromones and endocrine regulation of pheromone production in Coleoptera. In: Blomquist GJ, Prestwich GD, editors. Pheromone biochemistry. Oxford (UK): Academic Press Inc., Elsevier Ltd; 1987. p. 175–215.

Wendel GW, Smith HC. *Pinus strobus* L: Eastern white pine. In: Burns RM, Honkala BH (Tech. Coords.), editors. Silvics of North America. vol. 1. Conifers. Washington (DC): United States Department of Agriculture, Agric. Handbook. No. 654; 1990. p. 476–488.

Wood DL. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annu Rev Entomol. 1982:27(1):411–446. https://doi.org/10.1146/annurev.en.27.010182.002211

Zavarin E, Critchfield WB, Snajberk K. Turpentine composition of *Pinus contorta* X *Pinus banksiana* hybrids and hybrid derivatives. Can J Bot. 1969:47(9):1443–1453. https://doi.org/10.1139/b69-206