Ipsenol and Ipsdienol Attract *Monochamus titillator* (Coleoptera: Cerambycidae) and Associated Large Pine Woodborers in Southeastern United States

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ABSTRACT We determined the responses of the southern pine sawyer, *Monochamus titillator* (F.) (Coleoptera: Cerambycidae), to the pheromones (ipsenol, ipsdienol, and lanierone) used by pine engraver beetles (Coleoptera: Scolytidae) in the southeastern United States. (±)-Ipsenol, (±)-ipsdienol, or a combination increased catches of *M. titillator* in Florida, Louisiana, Georgia, and North Carolina. Catches of *Acanthocinus obsoletus* (Olivier) (Cerambycidae) were increased by (±)-ipsenol and (±)-ipsdienol in Florida and North Carolina, whereas only (±)-ipsenol was attractive in Georgia. (±)-Ipsenol and (±)-ipsdienol were attractive to *Pachylobius picivorus* (Germar) (Coleoptera: Curculionidae) in Florida, whereas only (±)-ipsdienol was active in Louisiana. In Florida, catches of *M. titillator*, *A. obsoletus*, and *P. picivorus* were greatest in traps baited with both (±)-ipsenol and (±)-ipsdienol. In Louisiana, catches of the woodborer *Chalcophora virginiensis* (Drury) (Buprestidae) were increased by (±)-ipsenol. Lanierone did not affect trap catches of the aforementioned species. The combination of (±)-ipsenol and (±)-ipsdienol may be a cost-effective lure for these four species because we found no evidence of interruption in attraction to baited traps, and the cost of the lure combination is relatively low.

KEY WORDS *Monochamus titillator*, *Acanthocinus obsoletus*, ipsenol, ipsdienol, trap lure

Cerambycidae and other xylophagous insects play critical roles in nutrient cycling within forested stands (Dajoz 2000). Holes and tunnels created by feeding adults and larvae permit entry of many associated invertebrates and fungi, greatly accelerating the rate of decomposition and mineralization of wood. However, activities of woodborers can have significant adverse economic impacts. Sawyer beetles, such as southern pine sawyer, *Monochamus titillator* (F.), and *M. scutellatus* (Say) (Coleoptera: Cerambycidae), attack recently dead, downed, dying, or fire-stressed conifers, and freshly felled trees (Furniss and Carolin 1980, USDA–Forest Service 1985). The larvae mine extensively throughout the phloem and sapwood (and occasionally the heartwood) of trees, causing significant levels of degrade damage to forestry products through the presence of large-diameter holes and tunnels (Cerezke 1977, Vallentgoed 1991).

The impact of sawyer beetles to the forest industry is even higher with respect to export products because of the transmission of the pine wood nematode, *Bursaphelencus xylophilus* (Steiner & Buhrer) Nickel (Tylenchida: Aphenlenchoididae) by sawyer beetles (Dwinell 1997). The pine wood nematode, endemic to North America, causes a fatal wilting disease in some species of pines (Wingfield et al. 1982, Mamiya 1983). Pine forests in Japan experienced widespread damage and losses after the introduction of pine wood nematode into Japan before 1905 (Mamiya 2003).

Detection of pine wood nematodes in export wood products, such as pine chips and softwood lumber, from Canada and the United States (Dwinell 1997, Webster 2003), has resulted in quarantine restrictions on the export of North American wood products (Bolla and Wood 2003, Suzuki 2003, Yang 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 (Dwinell 1997, 2004; Bolla and Wood 2003).

A trapping system for sawyer beetles at ports of entry and departure, and at certified wood processing areas, would be invaluable in minimizing the threats to overseas regions and North American markets. Moreover, such trapping systems could be deployed in containment and eradication programs after inadvertent introductions. Several commercial traps, such as the multiple funnel trap and the intercept trap, are currently available for trapping wood boring beetles; researchers, in recent years, have sought to improve

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existing designs (de Groot and Nott 2001, McIntosh et al. 2001, Morewood et al. 2002).

A critical feature for any trapping system is an effective lure. Because no pheromones have yet been identified for North American woodborers, the most promising lures for an array of *Monochamus* species and other Cerambycidae include *Ips* (Scolytidae) pheromones and host tree volatiles (Allison et al. 2004). Various species of *Monochamus* are commonly associated with bark beetles, acting as competitors and predators on bark beetle larvae (Coulson et al. 1976, 1980; Dodds et al. 2001). The response of woodborers to bark beetle pheromones may facilitate use of an ephemeral resource (Allison et al. 2004). In British Columbia, two common *Ips* pheromones, ipsenol and ipsdienol, are attractants for various *Monochamus* species (Miller and Borden 1990; Allison et al. 2001, 2003). Similarly, in eastern Canada, ipsenol is an attractant for several eastern species of *Monochamus* (Allison et al. 2001, de Groot and Nott 2004). In Europe, the *Ips* pheromones, ipsenol and the combination of ipsdienol, *cis*-verbenol, and 2-methyl-3-butenol, are attractants for *Monochamus galloprovincialis* (Olivier) (Pajares et al. 2004).

Billings and Cameron (1984) and Billings (1985) found that the combination of ipsenol, ipsdienol, and *cis*-verbenol was attractive to *M. titillator* in Texas. However, these compounds have not been tested in other regions of the southern United States. Geographic variation in the response of *M. scutellatus* was observed in British Columbia with northern populations expressing less discrimination to host volatiles and bark beetle pheromones than southern populations (Allison et al. 2001). Moreover, ipsenol and ipsdienol have not been tested individually, or in combination with lanierone, in any of the southern states.

Our objective was to determine the response of *M. titillator* to three common *Ips* pheromones (ipsenol, ipsdienol, and lanierone), separately and in combinations, across the southeastern United States. Our hope was to evaluate the efficacy of these readily available and inexpensive commercial lures for a broad spectrum of woodborer species before exploring the possible benefits of costlier devices with greater enantiospecificity or higher release rates (Strom et al. 2003). We also determined the responses of the following three associated species of pine xylophagous and phloeophagous beetles: *Acanthocinus obsoletus* (Olivier) (Cerambycidae), *Pachylobius picivorus* (Germar) (Curculionidae), and *Chalcophora virginiensis* (Drury) (Buprestidae). *A. obsoletus* and *C. virginiensis* are wood-boring beetles, commonly associated with southern pines (USDA–Forest Service 1985). Pitch-eating weevils, *P. picivorus,* feed on the bark of small pine seedlings and roots of freshly damaged southern pines (USDA–Forest Service 1985).

Materials and Methods

Semiochemical Release Devices. Phero Tech Inc. (Delta, British Columbia, Canada) supplied bubble-cap release devices for (±)-ipsenol (=racemic ipsenol, 50:50 mix of the two enantiomers), (±)-ipsdienol (=racemic ipsdienol, 50:50 mix of the two enantiomers), and lanierone (chemical purities >98%). The release rates for (±)-ipsenol, (±)-ipsdienol, and lanierone were ≈0.2, 0.2, and 0.02 mg/d, respectively, at 22–24°C. Release rates were determined by Phero Tech Inc. through collection of volatiles on Porapak-Q and quantitative analysis by gas chromatography. These devices are readily available commercial release devices used in lures for various species of engraver beetles in North America and Europe (Phero Tech Inc. 2005). The combination of (±)-ipsdienol and lanierone in a 10:1 ratio is used specifically as a lure for eastern populations of *Ips pini* (Say) and *Ips avulsus* (Eichoff) (Scolytidae) (Teale et al. 1991; Miller et al. 1997, 2003).

Experiments. Experiments were conducted in 2003–2004 to determine the response of *M. titillator* and associated large woodborers to ipsenol, ipsdienol, and lanierone in southeastern United States. The same experiment was conducted in each of the following locations: Oconee National Forest near Eatonton, GA; Coweeta Hydrological Laboratory near Otto, NC; Apalachicola National Forest near Tallahassee, FL; and Kisatchie National Forest near Winnfield, LA. The experiment in Georgia was conducted in mature stands of loblolly pine, *Pinus taeda* L., whereas the experiment in North Carolina was conducted in mature stands of eastern white pine, *Pinus strobus* L. Experiments in Florida and Louisiana were conducted in stands of longleaf, *Pinus palustris* Mill. and slash pine, *Pinus elliottii* Engelm., and loblolly and longleaf pine, respectively.

Stands at all four locations had experienced some disturbance in the past year. The traps in North Carolina were located within an active infestation of *Dendroctonus frontalis* Zimmermann (Scolytidae) with many trees coattacked by *Ips* beetles. Salvage logging had removed a small infestation of *D. frontalis* from the stands used in Georgia, 1 yr before our study. Stands in Florida and Louisiana were subjected to prescribed burns 3–6 mo before trap deployment with stands in Florida routinely burned on a 3- to 4-yr cycle. There was evidence of high tree mortality in North Carolina (from beetle attacks) but low tree mortality in Louisiana (from fire damage). There was no evidence of any current tree mortality in either Georgia or Florida. At the conclusion of our study in Louisiana, we noted abundant activity by ambrosia beetles (Scolytidae), particularly on broadleaf trees.

A randomized block design was used at all four locations. At each location, two separate replicate groups of eight eight-unit multiple-funnel traps (Phero Tech Inc.) per group were set at each of three sites in each National Forest and at each of two sites in the Coweeta Hydrological Laboratory. Traps within a replicate group were set in a 2 by 4 grid or eight-trap semicircular transect. Trap groups within a site, and traps within groups, were spaced 10–15 m apart. Sites within the Florida, Georgia, and Louisiana locations were spaced 200–500 m apart, whereas the spacing between the two sites in North Carolina was 50 m.

Each trap was suspended between trees by rope such that the bottom of each trap was 0.2–0.5 m above ground level. No trap was within 2 m of any tree. Collection cups contained 150–200 ml of pink propylene glycol solution (Peak RV and Marine Antifreeze, Old World Industries Inc., Northbrook IL) as a killing and preservation agent. Voucher specimens were deposited into the Entomology Collection, Museum of Natural History, University of Georgia (Athens, GA).

The experimental design at each location consisted of three factors (ipsenol, ipsdienol, and lanierone), each at two levels (presence and absence). In each experiment, the following eight treatments were randomly assigned to traps within each replicate group of traps: 1) blank control, 2) (±)-ipsenol, 3) (±)-ipsdienol, 4) lanierone, 5) (±)-ipsenol + (±)-ipsdienol, 6) (±)-ipsenol + lanierone, 7) (±)-ipsdienol + lanierone, and 8) (±)-ipsenol + (±)-ipsdienol + lanierone. The number of replicates was six in experiments 1, 3, and 4 and four in experiment 2. The trapping periods for experiments in Georgia, North Carolina, Florida, and Louisiana were as follows: 11 April–8 July 2003; 12 May–30 July 2003; 30 March–16 June 2004; and 28 April–22 June 2004, respectively.

Statistical Analyses. Data were analyzed using the SYSTAT statistical package version 11.00.01 (SYSTAT Software Inc., Richmond CA). Trap catch data (total number of beetles per trap for each species) were transformed by $\ln(Y + 1)$ to remove heteroscedasticity (Pepper et al. 1997). Trap catch data for species occurring in more than one location (Florida, Louisiana, Georgia, and North Carolina) were subjected to two-way analyses of variance (ANOVAs) to test for an interaction between location (2–4 levels) and treatment (six or eight levels), by using the following model components: 1) replicate (nested within location); 2) location; 3) treatment; and 4) location × treatment. All eight treatment levels were used for *P. picivorus* and *C. virginiensis.* Only six levels of treatments were used in analyses of data for *M. titillator* and *A. obsoletus* because no beetles were captured in blank control traps and traps baited only with lanierone, resulting in no variance and a clear violation of the assumption of homoscedasticity (Cobb 1998).

For each location, trap catch data for all four species were subjected separately to two-way ANOVAs by using the following model components to test for site × treatment interaction: 1) site, 2) replicate (nested within site), 3) treatment, and 4) site × treatment. One or two contrasts were conducted for each data set when treatment effect was significant at $P < 0.05$.

Data for *P. picivorus* and *C. virginiensis* also were subjected to three-way ANOVA for each location using the following model components: 1) site, 2) replicate (nested within site), 3) (±)-ipsenol, 4) (±)-ipsdienol, 5) lanierone, 6) (±)-ipsenol × (±)-ipsdienol, 7) (±)-ipsenol × lanierone, 8) (±)-ipsdienol × lanierone, and 9) (±)-ipsenol × (±)-ipsdienol × lanierone. Data for *M. titillator* and *A. obsoletus* could not be analyzed with the same model as two treatments (blank control and lanierone) had zero variances. These data were subjected to multiple one-sided *t*-tests (using a Bonferroni correction and $P = 0.10$), testing that individual treatment means were significantly greater than zero (Reeve and Strom 2004). In addition, data for *P. picivorus* and *C. virginiensis* were subjected to one-sided Dunnett's tests, comparing all treatments against the blank control at $P = 0.05$.

Results

The total number of *M. titillator* caught in traps at the four locations was 1,837 with all beetles captured in traps baited with (±)-ipsenol, (±)-ipsdienol, or a combination (Fig. 1). Blank control traps and traps baited with only lanierone caught no *M. titillator* at any location. Data for these two treatments were not included in subsequent analyses because of a lack of variance associated with these two treatments. Catches of *M. titillator* were significantly greater than zero for the remaining six treatments in Florida and Georgia and for five treatments in Louisiana (Table 1).

Trap catches of *M. titillator* were significantly affected by treatments across all four locations with no significant interaction between location and treatments (Table 2). The proportional effect of the six (±)-ipsenol and (±)-ipsdienol treatments was the same at all locations, although there were significant effects of location on trap catches (Table 2). Analyzed separately, there was no significant interaction between treatments and sites (within location) for Florida, Georgia, Louisiana, and North Carolina ($F = 0.730$; df = 10, 15; $P = 0.688$; $F = 0.648$; df = 10, 15; $P = 0.753$; $F = 0.690$; df = 10, 15; $P = 0.720$; and $F = 0.357$; df = 5, 10; $P = 0.866$, respectively).

At all four locations, we found that catches in traps baited with one of the four (±)-ipsenol treatments were greater than those in traps baited with the two treatments not containing (±)-ipsenol [(±)-ipsdienol and ipsdienol + lanierone]: Florida (contrast $F = 17.175$; df = 1, 15; $P = 0.001$); Georgia (contrast $F = 16.982$; df = 1, 15; $P = 0.001$); Louisiana (contrast $F = 9.869$; df = 1, 15; $P = 0.007$); and North Carolina (contrast $F = 4.851$; df = 1, 10; $P = 0.52$). Additionally in Florida, we found that catches of *M. titillator* in traps baited with both (±)-ipsenol and (±)-ipsdienol (with or without lanierone) were greater than those in traps baited with either (±)-ipsenol or (±)-ipsdienol (with or without lanierone) (contrast $F = 20.735$; df = 1, 15; $P < 0.001$).

We captured a total of 426 *A. obsoletus* in Florida, Georgia, and North Carolina, all in traps baited with either (±)-ipsenol, (±)-ipsdienol, or both (Fig. 2). Trap catch data from Louisiana were not analyzed because only 17 beetles were captured. No beetles were captured in blank control traps or in traps baited solely with lanierone at any location. Because of a lack of variance associated with these two treatments, we were unable to include blank and lanierone traps in our subsequent analyses. Catches of *A. obsoletus* in traps with the six treatments were all significantly

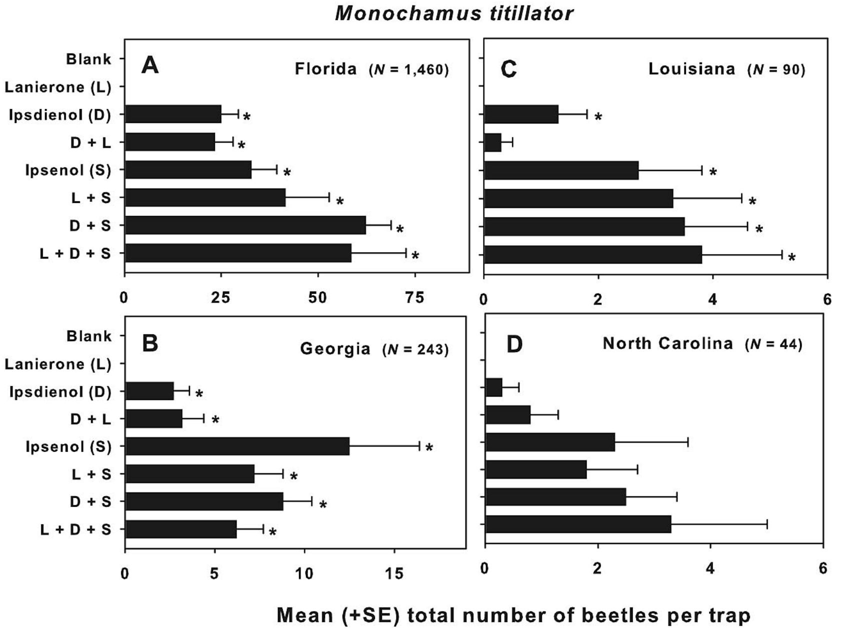

Fig. 1. Effects of ipsenol, ipsdienol, and lanierone on trap catches of *M. titillator* in Florida (A) and Louisiana (C) in 2004 and in Georgia (B) and North Carolina (D) in 2003. Means followed by an asterisk (*) are significantly different from zero (see Table 2).

greater than zero in Florida (Table 3; Fig. 2A), whereas only catches in traps baited solely with ipsenol were significantly greater than zero in Georgia (Table 3; Fig. 2B). In North Carolina, catches associated with four of the six treatments were significantly greater than zero (Table 3; Fig. 2C).

We found a significant effect among the six (±)-ipsenol and/or (±)-ipsdienol treatments on catches of *A. obsoletus* across the three locations (Florida, Georgia, and North Carolina). The relative effects of the six treatments were not the same between the three locations because the interaction term between treatments and location was significant (Table 2). Analyzed separately, there was a significant effect among the six treatments in Florida ($F = 5.515$; df = 5, 15; $P = 0.004$) but not in Georgia ($F = 0.965$; df = 5, 15; $P = 0.470$) or North Carolina ($F = 1.787$; df = 5, 10; $P = 0.203$). There was no significant interaction between site and treat-

Table 1. Significance levels (Bonferroni adjusted) for multiple *t*-tests on trap catches of *M. titillator* in multiple-funnel traps baited with ips pheromones in southeastern United States

Treatment	Florida			Georgia			Louisiana			North Carolina		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Ipsenol (S)	5	17.807	<0.001	5	8.561	0.001	5	3.501	0.052	3	2.300	0.315
Ipsdienol (D)	5	17.547	<0.001	5	6.321	0.004	5	2.936	0.097	3	1.000	1.000
Lanierone (L) + D	5	14.450	<0.001	5	5.162	0.011	5	1.581	0.524	3	1.650	0.593
L + S	5	18.120	<0.001	5	9.120	0.001	5	5.174	0.011	3	2.502	0.263
S + D	5	37.427	<0.001	5	11.202	<0.001	5	3.946	0.033	3	2.969	0.177
S + D + L	5	19.084	<0.001	5	8.722	0.001	5	4.310	0.023	3	2.577	0.246

H_O: $\mu = 0$; H_A: $\mu > 0$).

Table 2. Effects of location (Florida, Georgia, Louisiana, and North Carolina) and treatments (six or eight) on trap catches of *M. titillator*, *A. obsoletus*, and *P. picivorus* in multiple-funnel traps baited with ips pheromones in southeastern United States

Source	*M. titillator*			*A. obsoletus*			*P. picivorus*		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Replicate (location)	18	1.268	0.228	13	1.114	0.364	10	3.164	0.002
Location (L)	3	53.500	<0.001	2	70.498	<0.001	1	40.324	<0.001
Treatment (T)	5	3.406	<0.001	5	2.797	0.024	7	8.069	0.003
L × T	15	0.728	0.751	10	2.360	0.018	7	3.535	0.003
Error	90			65			70		

[a] *M. titillater*, four locations, six treatments; *A. obsoletus*, three locations, six treatments; and *P. picivorus*, two locations, eight treatments.

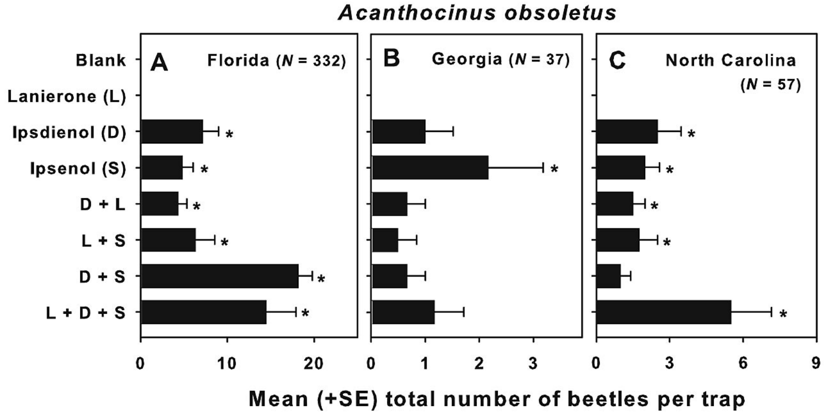

Fig. 2. Effects of ipsenol, ipsdienol, and lanierone on trap catches of *A. obsoletus* in Florida (A) in 2004 and Georgia (B) and North Carolina (C) in 2003. Means followed by an asterisk (*) are significantly different from zero (see Table 2).

ment in Florida on catches of *A. obsoletus* ($F = 0.483$; df = 10, 15; $P = 0.876$). In Florida, catches of *A. obsoletus* in traps baited with both (±)-ipsenol and (±)-ipsdienol (with or without lanierone) were significantly greater than those in traps with the remaining four treatments (contrast $F = 25.354$; df = 1, 15; $P < 0.001$).

We captured a total of 317 *P. picivorus* in Florida and Louisiana (Fig. 3A and B); none were caught in Georgia or North Carolina. The relative effects of the treatments were not the same between the three locations because the interaction term between treatments and location was significant (Table 2). Analyzed separately, there were no significant interactions between site and treatment on catches of weevils in either Florida or Louisiana ($F = 1.037$; df = 14, 21; $P = 0.457$ and $F = 1.217$; df = 14, 21; $P = 0.333$, respectively).

Catches of *P. picivorus* in Florida were significantly increased by (±)-ipsenol and (±)-ipsdienol in Florida (Table 4). For five of the six ipsenol or ipsdienol treatments, catches of weevils were greater than those in blank control traps (Fig. 3A). The mean catches of *P. picivorus* in any trap baited with both (±)-ipsenol and (±)-ipsdienol (alone or with lanierone) were significantly greater than those baited with either (±)-ipsenol or (±)-ipsdienol (alone or with lanierone) (contrast $F = 12.868$; df = 1, 21; $P = 0.002$).

Table 3. Significance levels (Bonferroni adjusted) for multiple *t*-tests on trap catches of *A. obsoletus* in multiple-funnel traps baited with ips pheromones in southeastern United States

Treatment	Florida			Georgia			North Carolina		
	df	*t*	*P*	df	*t*	*P*	df	*t*	*P*
Ipsenol (S)	5	6.976	0.003	5	3.369	0.060	3	5.196	0.042
Ipsdienol (D)	5	7.658	0.002	5	2.091	0.273	3	4.202	0.074
Lanierone (L) + D	5	9.870	0.001	5	2.126	0.261	3	5.000	0.046
L + S	5	5.847	0.006	5	1.524	0.564	3	5.195	0.042
S + D	5	34.943	<0.001	5	2.126	0.261	3	2.724	0.217
S + D + L	5	11.800	<0.001	5	2.208	0.235	3	2.961	0.178

H_O: $\mu = 0$; H_A: $\mu > 0$).

Table 4. Significance levels for ANOVAs on trap catches of *P. picivorus* and *C. virginiensis* in multiple-funnel traps baited with ips pheromones in Florida and Louisiana

Source	df	*P. picivorus*				*C. virginiana*	
		Florida		Louisiana		Louisiana	
		F	*P*	*F*	*P*	*F*	*P*
Site	2	8.091	0.001	0.789	0.462	4.039	0.026
Ipsdienol (D)	1	48.242	<0.001	16.589	<0.001	2.792	0.104
Ipsenol (S)	1	18.593	<0.001	1.186	0.284	6.753	0.014
Lanierone (L)	1	0.430	0.516	0.145	0.706	0.064	0.802
S × D	1	1.607	0.213	0.140	0.710	2.050	0.161
L × S	1	0.430	0.516	0.215	0.646	0.215	0.646
L × D	1	0.516	0.477	0.074	0.788	1.160	0.289
S × D × L	1	0.178	0.675	1.561	0.220	0.079	0.781
Replicate (site)	3	2.592	0.068	1.428	0.251	0.879	0.461
Error	35						

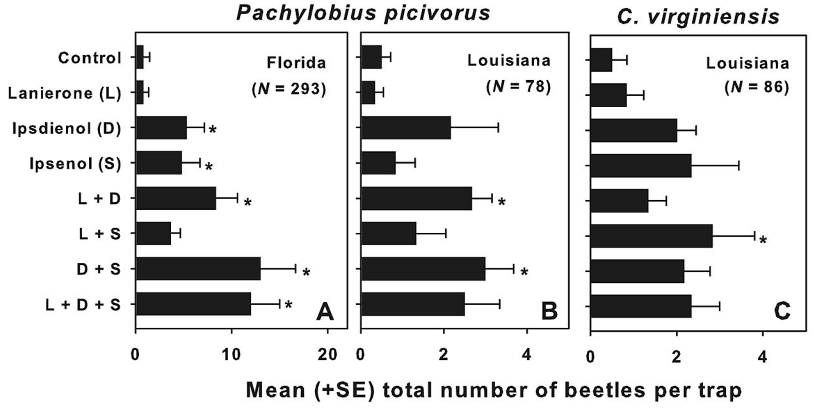

Fig. 3. Effects of ipsenol, ipsdienol, and lanierone in 2004 on trap catches of *P. picivorus* in Florida (A) and Louisiana (B) and *C. virginiensis* in Louisiana (C). Means followed by an asterisk (*) are significantly different from those for blank control traps (Dunnett's test, $P < 0.05$).

As in Florida, mean catches of *P. picivorus* in Louisiana were significantly increased by (±)-ipsdienol (Table 4). The mean catches of *P. picivorus* in any trap baited with (±)-ipsdienol (alone or with other components) were significantly greater than those in control traps (contrast $F = 8.671$; df = 1, 21; $P = 0.008$) with two significantly different from controls in direct comparison (Fig. 3B). In contrast to Florida, (±)-ipsenol had no significant effect on catches of *P. picivorus* in Louisiana (Table 4). Lanierone had no effect on catches of *P. picivorus* at either location.

A total of 86 *C. virginiensis* were captured in Louisiana (Fig. 3C) with no significant interaction between site and treatment ($F = 1.070$; df = 14, 21; $P = 0.433$). Catches of *C. virginiensis* were significantly increased by (±)-ipsenol (Table 4). Mean catch of *C. virginiensis* in any trap baited with (±)-ipsenol (alone or with other compounds) was significantly greater than that in control traps (contrast $F = 9.172$; df = 1, 21; $P = 0.006$) with one treatment significantly different from control in direct comparison (Fig. 3C).

Discussion

Our results with (±)-ipsenol and (±)-ipsdienol on the attraction of *M. titillator* to multiple-funnel traps are consistent with those for *Monochamus* species in Canada and Europe (Miller and Borden 1990; Allison et al. 2001, 2003; de Groot and Nott 2004; Pajares et al. 2004). Traps baited with commercial, readily available lures releasing either (±)-ipsenol, (±)-ipsdienol, or both were clearly attractive in Florida, Georgia, and Louisiana (Table 1; Fig. 1). The lack of significance in trap catches in North Carolina was likely a consequence of low population levels and overall low catches of beetles because we found no significant interaction between treatment and location across all four locations (Table 2). Moreover, all *M. titillator* were captured in traps baited with (±)-ipsenol, (±)-ipsdienol, or both; none were caught in blank control traps (Fig. 1).

The responses of *M. titillator* to ipsenol and ipsdienol in the southern region of the United States are consistent with the semiochemical ecology of the southern pine engravers. *I. pini* is common in northern Georgia and western North Carolina and uses ipsdienol and lanierone as pheromones (Birgersson et al. 1995, Miller et al. 2003). *I. calligraphus* is common in the Piedmont and Coastal Plain regions of the United States and uses ipsdienol and *cis*-verbenol as pheromones (Smith et al. 1993). The remaining two species, *I. avulsus* and *I. grandicollis*, are abundant throughout the southern states (USDA–Forest Service 1985). Ipsenol and *cis*-verbenol are used by *I. grandicollis* (Smith et al. 1993), whereas *I. avulsus* uses ipsdienol and lanierone (Smith et al. 1993, Birgersson et al. 1995, Miller et al. 2003, Strom et al. 2003).

The combination of (±)-ipsenol and (±)-ipsdienol may be an effective lure for numerous species of *Monochamus*, native to Canada and the United States. At all locations, traps baited with both (±)-ipsenol and (±)-ipsdienol caught as much, if not more, *M. titillator* than traps baited with either compound alone (Fig. 1). There is an added benefit in using this combination because we found that traps baited with the two-component lure also were attractive to *A. obsoletus*, *P. picivorus*, and *C. virginiensis* (Figs. 2 and 3). The potential role of the fourth ips pheromone, *cis*-verbenol, in attracting woodborers still needs to be determined.

The benefit of adding host compounds to the trapping system remains to be determined. We found that lanierone had no effect on catches of any of the beetles in this study. It is possible that the release rate was below the critical threshold because the rate of release of lanierone was 1/10 that of ipsenol and ipsdienol. However, the lure combination of ipsdienol and lanierone at rates used in this study is attractive to *I. pini* and *I. avulsus* (Birgersson et al. 1995, Miller et al. 2003). If the responses of species such as *M. titillator* are keyed to the pheromone production of *Ips* species then we should expect that the lanierone lure used in our study should have had an effect. However, if lanierone is always associated with ipsenol and/or ipsdienol then there may not be an advantage to responding to lanierone as well. In terms of using a broad-spectrum lure, the addition of lanierone to the system might increase the likelihood of catching several species of North American pine engraver beetles and their associates (Birgersson et al. 1995; Miller et al. 1991, 1997, 2003; Strom et al. 2003) without affecting the likelihood of catching *Monochamus* species (Fig. 1).

Attraction of *Monochamus* species to ethanol and α-pinene has been demonstrated in numerous studies (Allison et al. 2004). Billings (1985) found that the addition of turpentine to the combination of ipsenol, ipsdienol, and *cis*-verbenol significantly increased attraction of *M. titillator* in Texas. de Groot and Nott (2004) found that α-pinene significantly increased catches of three species of *Monochamus* to ipsdienol-baited traps. Therefore, there is a need to determine the benefits of adding host compounds, such as ethanol and α-pinene, to the trapping system for *Monochamus* species. Additional factors to be considered in the development of an optimal lure for sawyer beetles may include release rates and enantiomeric composition of ipsenol and ipsdienol because these factors have been found to be critical with respect to pine engravers (Byers 1989).

The efficacy and cost-effectiveness of any trapping system for bark and wood-boring beetles will have to be determined in operational settings. At a cost of ≈U.S$ 6.00 (Bruce Thomson, personal communication), the lure combination of (±)-ipsenol and (±)-ipsdienol would likely be cost-effective at ports of departure and certified mills and production centers in North America as well as at overseas ports of entry and processing areas. Currently, managers use lures releasing α-pinene and ethanol at a cost of ≈U.S.$ 18.00 per combination (Bruce Thomson, personal communication).

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