

Attraction of Southern Pine Engravers and Associated Bark Beetles (Coleoptera: Scolytidae) to Ipsenol, Ipsdienol, and Lanierone in Southeastern United States

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ABSTRACT We determined the response of the small southern pine engraver, *Ips avulsus* (Eichhoff); eastern fivespined ips, *Ips grandicollis* (Eichhoff); sixspined ips, *Ips calligraphus* (Germar); and pine engraver, *Ips pini* (Say) to the pheromones (\pm)-ipsenol, (\pm)-ipsdienol, and lanierone in the southeastern United States. Catches of *I. avulsus* and *I. grandicollis* to baited multiple-funnel traps were increased by (\pm)-ipsenol and (\pm)-ipsdienol in Florida, Georgia, Louisiana, and North Carolina. In all four localities, the highest numbers of *I. avulsus* were caught in traps baited with the combination of (\pm)-ipsenol, (\pm)-ipsdienol, and lanierone. In Florida, the highest numbers of *I. grandicollis* were captured in traps baited with the combination of (\pm)-ipsenol and (\pm)-ipsdienol (with or without lanierone). In the remaining three localities, the largest catches of *I. grandicollis* occurred in traps baited with (\pm)-ipsenol alone or the combination of (\pm)-ipsenol and (\pm)-ipsdienol (with or without lanierone). (\pm)-Ipsdienol was the only consistent attractant for *I. calligraphus* and *I. pini*. Attraction of *I. pini* in North Carolina to (\pm)-ipsdienol-baited traps was synergized by lanierone but interrupted with (\pm)-ipsenol. The interruptive effect of (\pm)-ipsenol on attraction of *I. pini* to (\pm)-ipsdienol was negated by lanierone. (\pm)-Ipsdienol was attractive to black turpentine beetle, *Dendroctonus terebrans* (Olivier), in Florida but not North Carolina, whereas (\pm)-ipsdienol was attractive to *I. calligraphus* in Louisiana, Georgia, and Florida. Both (\pm)-ipsenol and (\pm)-ipsdienol affected catches of *Gnathotrichus materiarus* (Fitch) in North Carolina. Trap catches of *Hylurgops rugipennis pinifex* (Fitch), *Hylastes salebrosus* Eichhoff, and *Hylastes tenuis* Eichhoff were unaffected by the pheromone treatments. The combination of (\pm)-ipsenol, (\pm)-ipsdienol, and lanierone may be a cost-effective general lure for *I. avulsus*, *I. grandicollis*, and *I. pini*.

KEY WORDS *Ips*, exotic lure, quarantine, pheromone

ENGRAVER BEETLES (*Ips* DeGeer) (Coleoptera: Scolytidae) reproduce in the phloem tissue of dead, dying, downed, or stressed conifers to such population levels that they can attack live standing trees (Furniss and Carolin 1980, USDA–FS 1985). In the southern United States, mortality of pines (*Pinus* spp.) because of attacks by engraver beetles can result in significant timber losses (Thatcher 1960). Exotic engraver beetles, such as *Ips typographus* (L.), *Ips sexdentatus* (Boerner), and *Ips acuminatus* (Gyllenhal) from Europe pose additional threats to North American forests (Ciesla 2001a, b; Eglitis 2001).

The ability to monitor for introductions of exotic engraver beetles as well as populations of native beetles, requires a trapping program with cost-effective lures (Strom et al. 2003). Currently, the combination of ipsdienol, *cis*-verbenol, and methylbutenol is used

extensively with funnel traps at ports-of-entry in Canada and the United States in attempts to intercept the European pine engravers and associated beetle species arriving from Europe and Asia (unpublished data). An effective lure for southern pine engravers would be a valuable tool at foreign ports-of-entry.

In comparison with studies on the southern pine beetle, *Dendroctonus frontalis* Zimmerman, very little work has been conducted on the semiochemical ecology of southern pine engravers (Smith et al. 1993). Ipsenol is attractive to *Ips grandicollis* (Eichhoff) with attraction to (S)-(–)-ipsenol interrupted by (R)-(+)–ipsenol (Vité and Renwick 1971, Vité et al. 1976a). The combination of ipsdienol and *cis*-verbenol is attractive to *Ips calligraphus* (Germar) (Renwick and Vité 1972, Vité et al. 1976b), although attraction to (R)-(–)-ipsdienol is interrupted by (S)-(+)–ipsdienol (Vité et al. 1978). *Ips avulsus* (Eichhoff) is attracted to ipsenol and ipsdienol (Hedden et al. 1976) with attraction to (R)-(–)-ipsdienol interrupted by (S)-(+)–ipsdienol (Vité et al. 1978). Lanierone syn-

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ergizes attraction of *I. avulsus* to ipsdienol (Birgersson et al. 1995, Miller et al. 2003).

The conclusions from these studies suggest that different lures may be required for the different pine engraver species, each with different enantiomeric purities of ipsenol and ipsdienol (Skillen et al. 1997). Unfortunately, the cost of ipsenol and ipsdienol lures containing primarily one enantiomer is considerably more expensive than those containing racemic (50:50) solutions. However, Strom et al. (2003) recently found that enantiospecificity of the pheromone ipsdienol was not a concern for trapping *I. avulsus* when used in conjunction with the pheromone lanierone. In contrast to Vité et al. (1978), they found that the attraction of *I. avulsus* to traps baited with (\pm)-ipsdienol (50:50 blend of the two enantiomers) and lanierone was significantly higher than that to traps baited with ($-$)-ipsdienol and lanierone in Texas, Louisiana, and Florida.

Our objective was to assess the effects of (\pm)-ipsenol, (\pm)-ipsdienol, and lanierone alone and in all combinations, in trapping the principal southern pine engraver species *I. avulsus*, *I. grandicollis*, *I. calligraphus*, and *Ips pini* (Say) at various locations in the southeastern United States. A general lure combination would be a cost-effective tool in trapping these species at ports-of-entry in overseas countries as well as monitoring population levels in native forests of the southern United States. We also assessed the response of the following bark and ambrosia beetles commonly associated with southern pine engravers (USDA-FS 1985): *Dendroctonus terebrans* (Olivier), *Gnathotrichus materiarius* (Fitch), *Hylurgops rugipennis pinifex* (Fitch), *Hylastes salebrosus* Eichhoff, and *Hylastes tenuis* Eichhoff.

Materials and Methods

Semiochemical Release Devices. Phero Tech Inc. (Delta, British Columbia, Canada) supplied bubble-cap release devices for (\pm)-ipsenol (=racemic ipsenol, 50:50 mix of the two enantiomers), (\pm)-ipsdienol (=racemic ipsdienol, 50:50 mix of the two enantiomers), and lanierone (chemical purities >98%). The release rates for ipsenol, ipsdienol, and lanierone were \approx 0.2, 0.2, and 0.02 mg/d 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 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 (\pm)-ipsdienol and lanierone in a 10:1 ratio is used specifically as a lure for eastern populations of *I. pini* (Teale et al. 1991; Miller et al. 1997, 2003).

Experiments. Experiments were conducted in 2003–2004 to determine the response of *I. avulsus*, *I. grandicollis*, *I. calligraphus*, and *I. pini* and associated bark and ambrosia beetles to (\pm)-ipsenol, (\pm)-ipsdienol, and lanierone in the southeastern United States. The same experiment was conducted at each of the following four 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 mature mixed stands of longleaf, *Pinus palustris* Mill., and slash pine, *Pinus elliottii* Engelm., and mature loblolly and longleaf pine, respectively.

Stands at all four locations (Georgia, North Carolina, Florida, and Louisiana) had experienced some disturbance in the past year. The traps in North Carolina were located within an active infestation of *D. frontalis* 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, replicate blocks (four or six) of eight 8-unit multiple-funnel traps (Phero Tech Inc.) were set in grids of 2 by 4 or an eight-trap semicircular transect. Traps within blocks were spaced 10–15 m apart, whereas replicate blocks were spaced 15–500 m apart. 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 in 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 block of traps: 1) blank control, 2) (\pm)-ipsenol, 3) (\pm)-ipsdienol, 4) lanierone, 5) (\pm)-ipsenol + (\pm)-ipsdienol, 6) (\pm)-ipsenol + lanierone, 7) (\pm)-ipsdienol + lanierone, and 8) (\pm)-ipsenol + (\pm)-ipsdienol + lanierone. The number of replicates was six in Georgia, Florida, and Louisiana and four in North Carolina. 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–11 June 2004, and 28 April–22 June 2004, respectively.

Statistical Analyses. Data were analyzed using the SYSTAT (version 11.00.01) and the SigmaStat (ver-

Table 1. Effects of location (Florida, Georgia, Louisiana, and North Carolina) and semiochemical treatments on trap catches of bark beetles in multiple-funnel traps baited with ips pheromones in southeastern United States

Source	<i>I. avulsus</i>			<i>I. grandicollis</i>			<i>I. calligraphus</i>			<i>D. terebrans</i>		
	df	F	P	df	F	P	df	F	P	df	F	P
Location (L) ^a	3	73.32	<0.001	3	40.97	<0.001	2	7.35	0.001	1	35.59	<0.001
Treatment (T)	7	629.01	<0.001	7	915.17	<0.001	3	10.64	<0.001	7	2.31	0.039
L × T	21	6.80	<0.001	21	5.89	<0.001	6	10.20	<0.001	7	1.11	0.371
Rep (within L)	18	3.93	<0.001	18	2.21	0.006	5	1.20	0.323	8	1.89	0.080
Error	126			126			55			56		

^a *I. avulsus*, *I. grandicollis*: four locations, eight treatments; *I. calligraphus*: three locations, four treatments; and *D. terebrans*: two locations, eight treatments.

sion 3.1) statistical packages (Systat Software Inc., Point 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 (two-four levels) and treatment (four 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 *I. avulsus*, *I. grandicollis*, *D. terebrans*, and *H. r. pinifex*. Only four levels of treatments were used in analyses of data for *I. calligraphus* because no beetles were captured in blank control traps and traps baited without ipsdienol in most locations, resulting in no variance for three or four treatments and a clear violation of the assumption of homoscedasticity (Cobb 1998).

Data for all species except *I. calligraphus* also were subjected to three-way ANOVA for each location by using the following model components: 1) replicate, 2) ipsenol, 3) ipsdienol, 4) lanierone, 5) ipsenol × ipsdienol, 6) ipsenol × lanierone, 7) ipsdienol × lanierone, and 8) ipsenol × ipsdienol × lanierone. Data for *I. calligraphus* were subjected to one-way ANOVA using two model components (replicate and treatment) because four treatments (blank control, lanierone, (±)-ipsenol, and (±)-ipsenol + lanierone) had zero variances. Data for *I. calligraphus* 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). The Holm-Sidak multiple comparison procedure (Systat Software Inc. 2004) was used to compare means within a location for each species when treatment effect was significant at $P < 0.05$ and power > 0.8 .

Results

Catches of *I. avulsus* were clearly affected by treatments at all four locations (Table 1) with a total capture of 151,720 beetles (Fig. 1). Data for each location were analyzed separately as there was a significant interaction between treatments and location (Table 1). At all four locations, trap catches of *I. avulsus* were affected by (±)-ipsenol, (±)-ipsdienol and lanierone

(Table 2). Traps baited with (±)-ipsenol and/or (±)-ipsdienol (with or without lanierone) caught more beetles than control traps at all four locations (Fig. 1). Catches in traps baited with (±)-ipsdienol alone were consistently greater than those in traps baited with (±)-ipsenol alone (Fig. 1). At all four localities, catches of *I. avulsus* in traps baited with both (±)-ipsenol and (±)-ipsdienol were greater than those in traps baited with (±)-ipsenol alone or (±)-ipsdienol alone (Fig. 1). Catches of *I. avulsus* to traps baited with (±)-ipsdienol were synergized by lanierone at all locations, although lanierone was unattractive by itself. In addition, lanierone synergized the attraction of beetles to traps baited with both (±)-ipsenol and (±)-ipsdienol at all four locations (Fig. 1).

The interactions between various treatments were not the same at all locations (Table 2). The interactions between lanierone and (±)-ipsdienol on catches of *I. avulsus* were significant in Florida, Georgia, and Louisiana but not North Carolina (Table 2). In Georgia, there were significant interactions between (±)-ipsenol and (±)-ipsdienol and between lanierone and (±)-ipsenol, whereas none were significant in Florida or Louisiana. In North Carolina, there was a significant interaction between (±)-ipsenol and (±)-ipsdienol but not between lanierone and (±)-ipsenol.

The consequence of these various interactions was that the response profile for catches of *I. avulsus* in Florida was most similar to that for North Carolina, whereas the profile for Georgia was most similar to that for Louisiana (Fig. 1). In Florida and North Carolina, catches of beetles in traps baited with lanierone and (±)-ipsdienol were not different from those in traps baited with (±)-ipsenol and (±)-ipsdienol (Fig. 1A and C). In contrast, catches of *I. avulsus* in traps baited with (±)-ipsenol and (±)-ipsdienol were significantly less than those for traps baited with lanierone and (±)-ipsdienol in both Georgia and Louisiana (Fig. 1B and D).

Catches of *I. grandicollis* were affected significantly by treatments at all four locations (Table 1) with a total capture of 58,337 beetles (Fig. 2). Because there was a significant interaction between treatments and location (Table 1), data for each location were analyzed separately. At all four locations, catches of *I. grandicollis* were affected by (±)-ipsenol and (±)-ipsdienol but not lanierone (Table 3). Traps baited with (±)-ipsenol, (±)-ipsdienol (with or without lanierone), or a combination caught more beetles than

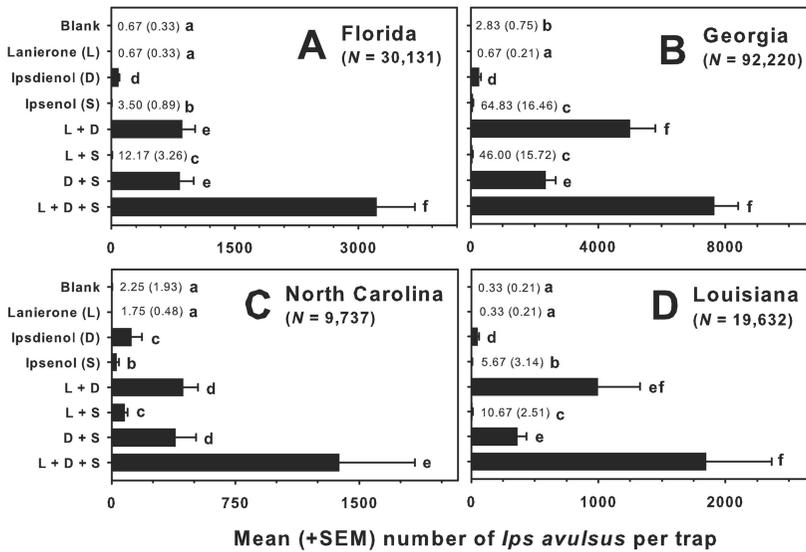


Fig. 1. Effects of (±)-ipfenol, (±)-ipsdienol, and lanierone on trap catches of *I. avulsus* for Florida (A) and Louisiana (C) in 2004 and Georgia (B) and North Carolina (D) in 2003. Means followed by the same letter within a figure are not significantly different at $P = 0.05$ (Holm-Sidak test). Mean (SEM) trap catches are given for bars with magnitudes that are difficult to discern in the figure.

control traps at all four locations (Fig. 2). Catches of beetles in traps baited with (±)-ipfenol (with or without lanierone) were consistently greater than those in traps baited with (±)-ipsdienol (with or without lanierone) (Fig. 2).

Although there was a significant interaction between treatment and location in catches of *I. grandicollis* (Table 1), the interactions between various treatments were similar (but not identical) at all locations (Table 3). The interaction between ipfenol and ipsdienol was significant at all locations, whereas the interaction between lanierone and ipfenol was significant only in North Carolina.

The response profile for catches of *I. grandicollis* varied between locations (Fig. 2). The profiles for Georgia, North Carolina, and Louisiana were the most similar with catches in traps baited with (±)-ipfenol (with or without lanierone) no different from those in traps baited with both (±)-ipfenol and (±)-ipsdienol (with or without lanierone) (Fig. 2B–D). The profile

for Florida was distinct from the other profiles in that catches of *I. grandicollis* in traps baited with both ipfenol and ipsdienol (with or without lanierone) were greater than those baited with ipfenol (with or without lanierone) (Fig. 2A). There were no significant differences in mean trap catches of *I. grandicollis* among these treatments at the other three locations (Fig. 2B–D).

The total number of *I. calligraphus* caught in Louisiana, Georgia, and Florida was 332 beetles; none were caught in North Carolina (Fig. 3). No beetles were captured in blank control traps or in traps not baited with (±)-ipsdienol (except for traps baited with (±)-ipfenol and lanierone in Louisiana). Data for these four treatments were not included in the following analyses because of a lack of variance.

In all three localities, catches of *I. calligraphus* in traps baited with (±)-ipsdienol (with or without other components) were significantly greater than zero (Table 4). There was a significant treatment ef-

Table 2. Significance levels for ANOVAs on trap catches of *I. avulsus* in multiple-funnel traps baited with ips pheromones in Georgia, Florida, Louisiana, and North Carolina

Source	df	Florida		Georgia		Louisiana		North Carolina	
		F	P	F	P	F	P	F	P
Replicate	5 ^a	51.66	0.171	4.90	0.002	2.51	0.048	8.49	0.001
(±)-Ipsdienol (D)	1	1243.30	<0.001	1655.73	<0.001	875.41	<0.001	321.71	<0.001
(±)-Ipsenol (S)	1	115.91	<0.001	292.76	<0.001	90.57	<0.001	99.67	<0.001
Lanierone (L)	1	60.84	<0.001	30.77	<0.001	67.44	<0.001	30.53	<0.001
S × D	1	1.52	0.226	36.41	<0.001	0.66	0.422	15.98	0.001
L × S	1	0.03	0.876	9.01	0.005	0.70	0.409	0.94	0.343
L × D	1	19.73	<0.001	113.50	<0.001	31.91	<0.001	2.25	0.149
S × D × L	1	10.246	0.003	19.84	<0.001	11.55	0.002	3.34	0.082
Error	35 ^a								

^a df for replicate and error terms in North Carolina were 3 and 21, respectively.

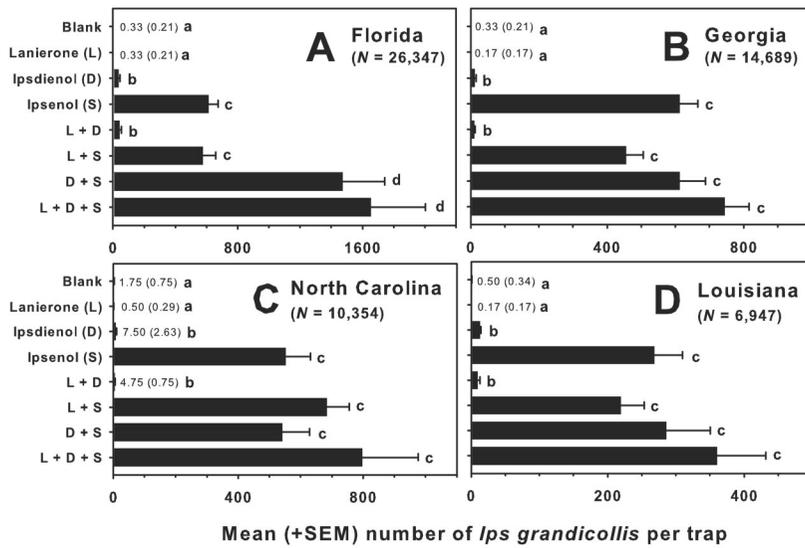


Fig. 2. Effects of (±)-ipfenol, (±)-ipsdienol, and lanierone on trap catches of *I. grandicollis* for Florida (A) and Louisiana (C) in 2004 and Georgia (B) and North Carolina (D) in 2003. Means followed by the same letter within a figure are not significantly different at $P = 0.05$ (Holm-Sidak test). Mean (SEM) trap catches are given for bars with magnitudes that are difficult to discern in the figure.

fect among the four treatments containing ipsdienol with a significant interaction between these treatments and location (Table 1). In Florida, catches of *I. calligraphus* in (±)-ipsdienol-baited traps were increased by both (±)-ipfenol and lanierone (Fig. 3A). In Louisiana, lanierone interrupted catches of beetles to traps baited with (±)-ipsdienol, whereas (±)-ipfenol had no effect (Fig. 3C). In both Louisiana and Florida, catches of beetles were less in traps baited with both (±)-ipfenol and (±)-ipsdienol (Fig. 3A and C). Separation of mean trap catches of *I. calligraphus* in Georgia was not possible because of weak treatment effect ($F = 3.05$; $df = 3, 15$; $P = 0.061$) and low power (0.54).

Catches of *I. pini* in North Carolina were significantly affected by (±)-ipsdienol, (±)-ipfenol, and lanierone treatments (Table 5); *I. pini* were not captured at any other location. Catches of beetles in traps baited with (±)-ipsdienol alone were greater than

those not baited with (±)-ipsdienol (Fig. 4A). Attraction of *I. pini* to (±)-ipsdienol-baited traps was interrupted by (±)-ipfenol. Lanierone was not attractive by itself but synergized attraction of *I. pini* to (±)-ipsdienol and nullified the interruptive effect of ipfenol (Fig. 4A).

In total, 166 *D. terebrans* were captured in North Carolina and Florida with a significant treatment effect (Table 1); none were caught in Georgia and Louisiana. There was a significant treatment effect in Florida ($F = 3.924$; $df = 7, 35$; $P = 0.003$) but not in North Carolina ($F = 0.628$; $df = 7, 21$; $P = 0.728$). In Florida, more *D. terebrans* were captured in traps baited with ipfenol and ipsdienol than in traps baited with lanierone (with or without ipfenol) (Fig. 4B). The mean ± SEM trap catch of *D. terebrans* in North Carolina was 3.6 ± 0.5 .

G. materiarus, *H. salebrosus*, and *H. tenuis* were only captured in North Carolina. Catches of *G. materiarus* were affected by both (±)-ipfenol and (±)-ipsdienol

Table 3. Significance levels for ANOVAs on trap catches of *I. grandicollis* in multiple-funnel traps baited with ips pheromones in Georgia, Florida, Louisiana, and North Carolina

Source	df	Florida		Georgia		Louisiana		North Carolina	
		F	P	F	P	F	P	F	P
Replicate	5 ^a	3.41	0.013	2.91	0.027	1.27	0.298	1.70	0.198
(±)-Ipsdienol (D)	1	389.09	<0.001	111.77	<0.001	75.04	<0.001	18.31	<0.001
(±)-Ipsenol (S)	1	2069.83	<0.001	2048.15	<0.001	919.07	<0.001	1276.16	<0.001
Lanierone (L)	1	0.07	0.798	0.48	0.493	0.75	0.392	0.17	0.689
S × D	1	125.59	<0.001	70.13	<0.001	50.58	<0.001	16.40	0.001
L × S	1	0.01	0.950	0.04	0.845	1.44	0.238	5.77	0.026
L × D	1	0.40	0.533	0.51	0.479	0.19	0.662	0.61	0.444
S × D × L	1	0.10	0.759	2.58	0.118	1.43	0.241	0.15	0.702
Error	35 ^a								

^a df for replicate and error terms in North Carolina were 3 and 21, respectively.

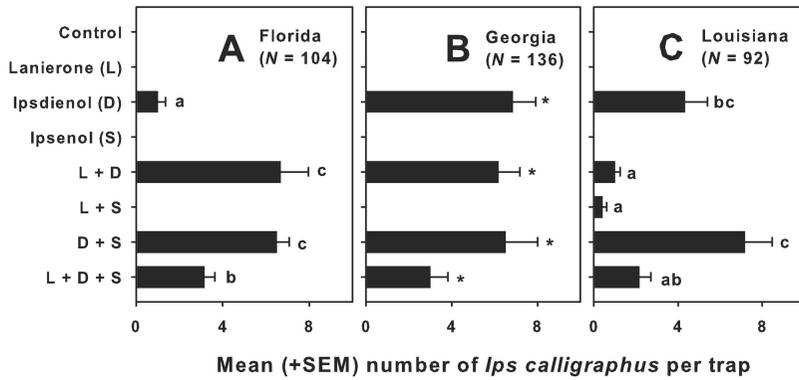


Fig. 3. Effects of (±)-ipfenol, (±)-ipfenol, and lanierone on trap catches of *I. calligraphus* for Florida (A) and Louisiana (C) in 2004 and Georgia (B) in 2003. Means followed by an asterisk or a letter are significantly different from zero (see Table 4). Means followed by the same letter within a figure are not significantly different at $P = 0.05$ (Holm-Sidak test).

with a significant interaction between the two factors (Table 5). However, separation of mean trap catches of *G. materiarus* was not possible because of low power (0.45) (Fig. 4C). There was no significant treatment effect on catches of *H. salebrosus* and *H. tenuis* in North Carolina ($F = 0.92$; $df = 7, 21$; $P = 0.513$ and $F = 0.188$; $df = 7, 24$; $P = 0.985$, respectively) where we captured totals of 93 and 1,053 beetles, respectively, with mean \pm SEM catches of 2.9 ± 0.6 and 32.9 ± 5.3 beetles per trap, respectively.

Similarly, there was no significant treatment effect on catches of *H. rugipennis pinifex* in Georgia and North Carolina ($F = 0.869$; $df = 7, 40$; $P = 0.539$ and $F = 0.956$; $df = 7, 24$; $P = 0.484$, respectively) with mean \pm SEM trap catches of 2.4 ± 0.4 and 5.1 ± 0.5 , respectively, and total numbers of captured beetles of 113 and 164, respectively; none were captured in Florida and Louisiana.

Discussion

The combination of (±)-ipfenol, (±)-ipfenol, and lanierone commercial lures was very effective in trapping large numbers of *I. avulsus*, *I. grandicollis*, and *I. pini* in the southeastern United States (Figs. 1, 2, and 4A). Our results with *I. avulsus* are consistent with those of Hedden et al. (1976), who found that both ipfenol and ipfenol were attractants for *I. avulsus* in Texas as well as those of Miller et al. (2003), who found that lanierone significantly increased catches of *I. avulsus* to ipfenol in North Carolina. We clearly demonstrated that the three-component lure is better than any other combination that we tested (Fig. 1).

Similarly, our results with *I. grandicollis* are consistent with those of Vité and Renwick (1971) and Vité et al. (1976a), who found that ipfenol was attractive to *I. grandicollis* in Texas. Our studies demonstrate that attraction of *I. grandicollis* to ipfenol-baited funnel traps is enhanced by ipfenol in Florida but not Louisiana, Georgia, or North Carolina (Fig. 2). Fortunately, attraction of *I. grandicollis* to ipfenol-baited traps was not interrupted by ipfenol or lanierone in any of the four localities. Therefore, the use of the three-component lure would be sufficient in trapping *I. grandicollis* from the southern United States without any loss in efficiency in trapping *I. avulsus*.

Our results with *I. pini* in North Carolina are consistent with those of Miller et al. (2003), who found that attraction of *I. pini* to ipfenol-baited traps was enhanced by lanierone in North Carolina. As in British Columbia (Borden et al. 1992), we found that attraction of *I. pini* to ipfenol-baited traps was interrupted by ipfenol (Fig. 4A) However, addition of lanierone negated the interruption of attraction by ipfenol, i.e., catches of *I. pini* in traps baited with lanierone, ipfenol, and ipfenol were no different from those in traps baited with lanierone and ipfenol (Fig. 4A). Therefore, the use of the three-component lure would still be effective for *I. pini* without any loss of efficiency in trapping *I. avulsus* or *I. grandicollis*. The use of a two-component lure consisting of ipfenol and lanierone would be effective for *I. avulsus* (Fig. 1) and *I. pini* (Fig. 4A) but ineffective for *I. grandicollis* (Fig. 2).

Consistent with results by Renwick and Vité (1972) and Vité et al. (1976b), we found that *I. calligraphus*

Table 4. Significance levels (Bonferroni adjusted) for multiple *t*-tests on trap catches of *I. calligraphus* in multiple-funnel traps baited with (±)-ipfenol in southeastern United States ($H_0: \mu = 0$; $H_A: \mu > 0$)

Treatment	Florida			Georgia			Louisiana		
	df	<i>t</i>	<i>P</i>	df	<i>t</i>	<i>P</i>	df	<i>t</i>	<i>P</i>
(±)-Ipsdienol (D)	5	2.94	0.064	5	10.10	<0.001	5	6.79	0.002
D + Lanierone (L)	5	11.89	<0.001	5	9.57	<0.001	5	4.45	0.013
D + (±)-Ipsenol (S)	5	28.31	<0.001	5	7.70	0.001	5	13.22	<0.001
D + L + S	5	12.41	<0.001	5	3.35	0.041	5	4.64	0.011

Table 5. Significance levels for ANOVAs on trap catches of *I. pini*, *D. terebrans*, and *G. materiarus* in multiple-funnel traps baited with ips pheromones in Florida and North Carolina

Source	df	<i>I. pini</i>		<i>D. terebrans</i>				<i>G. materiarus</i>	
		North Carolina		Florida		North Carolina		North Carolina	
		F	P	F	P	F	P	F	P
Replicate	3 ^a	4.09	0.020	1.92	0.116	1.86	0.168	10.07	<0.001
(±)-Ipsdienol (D)	1	407.22	<0.001	22.78	<0.001	0.22	0.642	8.18	0.009
(±)-Ipsenol (S)	1	18.21	<0.001	1.51	0.228	0.86	0.365	3.30	0.083
Lanierone (L)	1	67.04	<0.001	2.27	0.141	0.21	0.653	0.28	0.604
S × D	1	9.98	0.005	0.67	0.419	0.65	0.429	4.46	0.047
L × S	1	6.79	0.017	0.17	0.685	1.21	0.284	0.62	0.439
L × D	1	36.68	<0.001	0.08	0.783	1.05	0.317	0.01	0.944
S × D × L	1	13.79	0.001	<0.01	1.000	0.20	0.663	<0.01	0.981
Error	21 ^a								

^a df for replicate and error terms in Florida were 5 and 35, respectively.

was attracted by ipsdienol (Fig. 3), although treatment effects varied among locations. Because low numbers of captured beetles, our results are insufficient to determine an optimal lure blend that would be effective for *I. calligraphus* as well as the other three pine engraver species.

One possible explanation for the low catches and variation in effects for *I. calligraphus* may be that population levels were considerably lower for *I. calligraphus* than for the other species. An alternate explanation may relate to a missing pheromone component. Renwick and Vité (1972) found that verbenol with a *cis:trans* ratio of 11:1 enhanced attraction to ipsdienol by 88-fold; verbenol with a *cis:trans* ratio of 1:16 also had a modest effect on trap catches. Enantiomeric composition of ipsdienol also may be an issue in explaining our low trap catches for *I. calligraphus*. Vité et al. (1978) found that attraction of *I. calligraphus* to *cis*-verbenol and (R)-(-)-ipsdienol was interrupted by (S)-(+)-ipsdienol. Enantiomeric composition will likely be an important issue in future tests with verbenols as well. Vité et al. (1976b) found that there was a greater increase in catches of *I. calligra-*

phus to ipsdienol with (S)-(-)-*cis*-verbenol than with (R)-(+)-*cis*-verbenol. Further work is clearly required in developing a cost-effective lure for *I. calligraphus*.

Similar issues of enantiospecificity with respect to ipsenol and ipsdienol are known for *I. avulsus* and *I. grandicollis* in Texas (Hedden et al. 1976; Vité et al. 1976a, 1978). However, Strom et al. (2003) found that attraction of *I. avulsus* to lanierone-baited traps in Texas, Louisiana, and Florida was greater with racemic ipsdienol than with (R)-(-)-ipsdienol. The large numbers of beetles captured in our study suggest that enantiomeric composition may not be an important issue for trapping *I. grandicollis* as well. Although racemic ipsenol and racemic ipsdienol may be cost-effective for a monitoring program, the issue of enantiomeric composition may be important in understanding the semiochemical ecology of *I. avulsus* and *I. grandicollis* and requires further investigation.

We found evidence of geographic variation in the responses of *I. avulsus* and *I. grandicollis* (Figs. 1 and 2). The response profile for *I. avulsus* in Florida was most similar to that in North Carolina with the tertiary

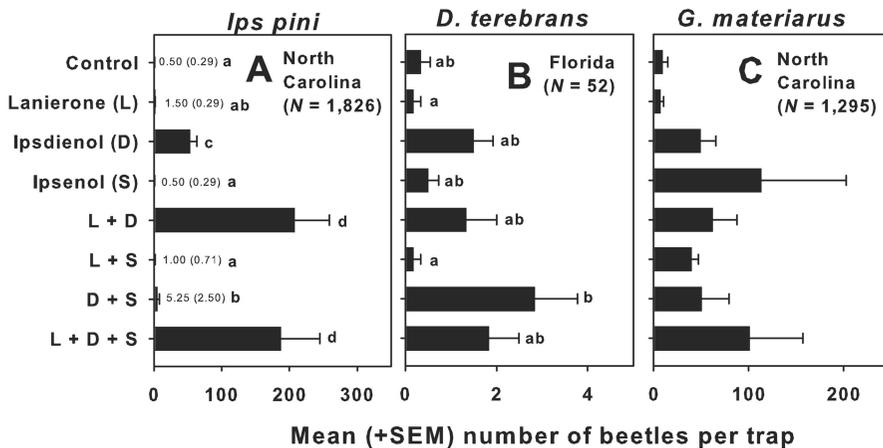


Fig. 4. Effects of (±)-ipsenol, (±)-ipsdienol, and lanierone on trap catches of *I. pini* (A) and *G. materiarus* (C) for North Carolina in 2003 and *D. terebrans* (B) for Florida in 2004. Means followed by the same letter within a figure are not significantly different at $P = 0.05$ (Holm-Sidak test). Mean (SEM) trap catches are given for bars with magnitudes that are difficult to discern in the figure.

combination clearly better than any other treatment (Fig. 1A and C). In contrast, the tertiary blend was no better than the combination of (\pm)-ipsdienol and lanierone in attracting *I. avulsus* in Georgia and Louisiana (Fig. 1B and D). Similarly, the response profile for *I. grandicollis* in Florida was distinct from those of the other locations in that attraction of *I. grandicollis* to traps baited with ipsenol and ipsdienol (with or without lanierone) was greater than attraction to any other treatment (Fig. 2A). In the other locations, catches of *I. grandicollis* were unaffected by the presence of (\pm)-ipsdienol (Fig. 2B–D).

Geographic variation in pheromone responses of bark beetles is not unusual. For example, considerable variation in enantiospecificity and pheromone composition has been demonstrated for *I. pini* in North America with possible causal factors ranging from postglaciation colonization events to interspecific competition and predation (Seybold et al. 1992; Raffa and Dahlsten 1995; Miller et al. 1996, 1997). Variation in the responses of *I. avulsus* and *I. grandicollis* may be related to variation in host pines and species composition of pine engravers within stands of pines. *Ips pini* is common in the mountains of western North Carolina but not in other regions of the southern United States, whereas the opposite is true for *I. calligraphus* (unpublished data). Shortleaf pine and eastern white pine are common in western North Carolina, whereas loblolly pine dominates through most of the piedmont region; slash and longleaf dominate in the coastal region. Further research on the effects of host pine species and interspecific competition will be required to address the issue of regional differences in pheromone responses by *I. avulsus* and *I. grandicollis*.

We determined that the combination of (\pm)-ipsenol, (\pm)-ipsdienol, and lanierone is an effective lure in catching reasonable and consistent numbers of *I. avulsus*, *I. grandicollis*, and *I. pini* from the southeastern United States. This tertiary combination may have broad applicability for quarantine issues as well as being considerably less expensive than combinations using lures of high enantiopurity. Associated species such as *I. calligraphus*, *D. terebrans*, and *G. materiarus* also may be detected albeit at lower numbers than the principal species of southern pine engravers. As with most lures in quarantine programs, true efficacy of lures is unknown because population levels of target species are generally unknown. The key assumption in using lures in areas such as ports-of-entry is that, unlike natural forest situations, there are few, if any, competing sources of attractants.

In addition, the three-component lure is also effective in trapping the southern sawyer beetle, *Monochamus titillator* (F.) (Coleoptera: Cerambycidae), as well as other large bark and wood-boring beetles: *Acanthocinus obsoletus* (Olivier) (Cerambycidae), *Pachylobius picivorus* (Germar) (Curculionidae), and *Chalcophora virginiana* (Drury) (Buprestidae) (Miller and Asaro 2005). These various species can cause significant degrade losses to lumber and mortality to pine seedlings (USDA–FS 1985). Trapping *M.*

titillator is critical because of quarantine issues arising from its association with the pine wood nematode.

The three-component lure of ipsenol, ipsdienol, and lanierone could be used in native stands in the southeastern United States as well. Baited traps could be used to monitor population changes of beetles associated with silvicultural activities, such as thinning and prescribed fire. Such information could help in the interpretation of changes in stand dynamics resulting from silvicultural activities (Hanula et al. 2002). In addition, the three-component lure could be used to bait felled trees after attacks by *D. frontalis* to examine the effect of competition by pine engravers on the reproductive success of *D. frontalis*. If competition is deemed to have a significant impact on *D. frontalis* populations then the possibility exists that the three-component baits could be used in conjunction with other operational activities, such as cut-and-leave or cut-and-top (Billings 1980, Clarke 2003), to increase the abundance of pine engravers as competitors against *D. frontalis*. In British Columbia, Rankin and Borden (1991) and Safranyik et al. (1998) found that baiting lodgepole pines attacked by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, the primary insect pest of lodgepole pine (Furniss and Carolin 1980), with ips pheromones induced attacks by *I. pini* and resulted in reduced survival and emergence of *D. ponderosae*.

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