Role of Ipsdienol, Ipsenol, and *cis*-Verbenol in Chemical Ecology of *Ips avulsus*, *Ips calligraphus*, and *Ips grandicollis* (Coleoptera: Curculionidae: Scolytinae)

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ABSTRACT Stressed or damaged pine (*Pinus* sp.) trees in the southeastern United States are often colonized simultaneously by three southern *Ips* species (Coleoptera: Curculionidae: Scolytinae): small southern pine engraver, *Ips avulsus* (Eichhoff); sixspined ips, *Ips calligraphus* (Germar); and eastern fivespined ips, *Ips grandicollis* (Eichhoff). All three species mediate colonization of host material with volatile pheromones. All of the southern *Ips* produce *cis*-verbenol, and either ipsdienol or ipsenol, and electrophysiological studies have demonstrated that all three southern *Ips* are able to detect all three compounds. This study examined the role of ipsdienol, ipsenol, and *cis*-verbenol in the chemical ecology of the southern *Ips* in Georgia and Louisiana. The most attractive blends of pheromones, with the fewest number of components, were ipsdienol plus ipsenol for *I. avulsus*, *cis*-verbenol plus ipsdienol for *I. calligraphus*, and either *cis*-verbenol plus ipsenol or ipsdienol plus ipsenol for *I. grandicollis*. Cross-attraction of *I. grandicollis* to the pheromone blend most attractive to *I. avulsus* was observed. Although the presence of heterospecific pheromone reduced the catches of all three species (i.e., the tertiary blend captured fewer beetles than the most attractive binary blends) in both states (significantly in two cases), high numbers of all three species were still captured in traps baited with all three compounds. These results suggest that the pheromones *cis*-verbenol, ipsdienol, and ipsenol can be combined for monitoring all three species of the southern *Ips* simultaneously.

KEY WORDS *Ips*, aggregation pheromone, reproductive isolation, Scolytidae

Engraver beetles (Coleoptera: Curculionidae: Scolytinae: *Ips* DeGeer) spend most of their lives under bark in the trunk and larger branches of dead, dying, downed, or stressed pines (*Pinus* spp.) where adults mate and larvae feed and develop on phloem tissue (Furniss and Carolin 1977). Males are the pioneer sex and tunnel into the phloem, excavate a nuptial chamber, and release an aggregation pheromone to attract conspecifics. This pheromone-mediated mass attack behavior facilitates the rapid location and exploitation of available host material and the successful colonization of living pines.

Significant overlap exists in the niche requirements of small southern pine engraver, *Ips avulsus* (Eichhoff); sixspined ips, *Ips calligraphus* (Germar); and eastern fivespined ips, *Ips grandicollis* (Eichhoff), hereafter referred to as the "southern *Ips*." In addition to conspecifics, a diverse assemblage of insect associates responds to southern *Ips* pheromones, including congeners (Birch et al. 1980). In the southeastern United States, susceptible host material is often colonized simultaneously by the southern *Ips* (Birch and Svihra 1979, Svihra et al. 1980, Paine et al. 1981). *I. calligraphus* and *I. avulsus* generally rapidly colonize available host material, and their arrival is often synchronous (Birch and Svihra 1979, Dixon and Payne 1979, Svihra et al. 1980). Host colonization by *I. grandicollis* has been reported to both coincide with (Dixon and Payne 1979) and occur later than (Svihra et al. 1980) colonization by *I. calligraphus* and *I. avulsus.* Paine et al. (1981) dissected mass-attacked pines and determined the areas occupied by the southern *Ips.* They observed a general pattern of partitioning of the phloem tissue, although there was niche overlap between species pairs.

Interspecific interactions of bark beetles at host material can be mediated by host volatiles and bark beetle pheromones (Birch 1978, Birch et al. 1980,

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Svihra et al. 1980, Wood 1982a, Savoie et al. 1998) and can have inhibitory (e.g., pheromone-mediated deterrence, Lanier and Wood 1975) and attractive (e.g., pheromone-mediated attraction, Hedden et al. 1976) effects on the interacting species. Negative effects are typically attributed to reduced parental fecundity and progeny survival (e.g., Robins and Reid 1997) as a result of competition for a limited phloem resource (Berryman 1973, Anderbrandt et al. 1985). Positive effects could result from increased success of attacks, exploitation of material located by heterospecifics or predator swamping (Ayres et al. 2001). Species-specific pheromones have been hypothesized to be an important mechanism for reproductive isolation among sympatric species of *Ips* (Lanier and Burkholder 1974, Lanier and Wood 1975). For example, Birch and Wood (1975) used synthetic pheromone and infested host bolts to demonstrate that pheromones were involved in the reproductive isolation and resource partitioning of pine engraver, *Ips pini* (Say), and California fivespined ips, *Ips paraconfusus* Lanier.

The literature on the chemical ecology of the southern *Ips* is incomplete. Empirical work has included field trapping studies using intercept traps of two types: traps baited with synthetic copies of attractants and traps baited with infested host material. Vité et al. (1964) baited traps with infested bolts and reported that none of the southern *Ips* were attracted to bolts infested with heterospecifics. Birch et al. (1980) examined the responses of the southern *Ips* to host material infested with each species and observed inconsistent results (cross-attraction was observed in some tests and not in others). Although both studies provide support for the hypothesis that reproductive isolation among the southern *Ips* is chemically mediated, neither study provides any information on specific mechanisms.

Several studies have attempted to identify specific mechanisms of mate location among the southern *Ips* by using synthetic copies of pheromones (Vité and Renwick 1971; Renwick and Vité 1972; Hedden et al. 1976; Vité et al. 1976, 1978; Birgersson et al. 1995; Strom et al. 2003; Miller et al. 2005). In general, these studies reported that the most attractive blend for the southern *Ips* involves one or more of ipsenol, ipsdienol, or *cis*-verbenol. The results of electrophysiological studies support the hypothesis of interspecific olfactory communication among the southern *Ips*, i.e., both sexes of all three southern *Ips* species can detect ipsdienol, ipsenol, and *cis*-verbenol (Smith et al. 1988, Ascoli-Christensen et al. 1993). Chemical analyses of all three southern *Ips* documented the production of *cis*- and *trans*-verbenol by all three species, production of ipsdienol by *I. avulsus* and *I. calligraphus,* and that only *I. grandicollis* produced ipsenol (Vité and Renwick 1971, Renwick and Vité 1972, Vité et al. 1972, Hughes 1974).

The binary and the tertiary combinations of the compounds ipsdienol, ipsenol, and *cis*-verbenol have not all been tested. The objective of this study was to assess the effects of ipsdienol, ipsenol, and *cis*-verbenol alone and in all combinations to evaluate their potential to catch *Ips* beetles in Georgia and Louisiana. Specific objectives were the identification of the most attractive blend of compounds for each species and determination of whether these compounds could be combined to simultaneously monitor populations of all three species.

Materials and Methods

Semiochemical Release Devices. Bubble cap lures loaded with (±)-ipsdienol (=racemic ipsdienol, 50:50 mix of the plus and minus enantiomers), (±)-ipsenol (=racemic ipsenol, 50:50 mix of the plus and minus enantiomers), or *cis*-verbenol (=13:87 mix of the plus and minus enantiomers) were purchased from Contech Enterprises Inc. (Victoria, BC, Canada). The chemical purity for all three pheromones was >98% (Contech Enterprises Inc.). Release rates were estimated to be 0.1–0.2 mg/d at 25°C for ipsdienol and ipsenol and 0.3–0.6 mg/d at 22°C for *cis*-verbenol (all release rates were supplied by the manufacturer).

Field Experiments. Two identical experiments were conducted to examine the effect of ipsdienol, ipsenol, and *cis*-verbenol on the attraction of the southern *Ips.* Both experiments used the same design of 48 funnel traps deployed in a linear array of six replicate blocks of eight traps per block by using black eight-unit multiple-funnel traps (Contech Enterprises Inc.). In each experiment, the following treatments were assigned randomly within each replicate block: 1) unbaited control, 2) ipsdienol, 3) ipsenol, 4) *cis*-verbenol, 5) ipsdienol plus ipsenol, 6) ipsdienol plus *cis*-verbenol, 7) ipsenol plus *cis*-verbenol, and 8) ipsdienol, ipsenol plus *cis*-verbenol.

Experiment 1 was conducted in the Bob R. Jones-Idlewild Research Station, LSU AgCenter, near Clinton, LA (30.8049°N, 90.9740°E; 64 m) from 12 June to 7 August 2009, whereas experiment 2 was conducted in the Oconee National Forest, near Eatonton, GA (33.4045°N, 83.4258°E; 154 m) from 21 April to 30 June 2009. The stands used for both experiments were predominantly loblolly pine (*Pinus taeda* L.), and each had experienced a prescribed burn within the 12 mo preceding trap deployment. Traps were suspended individually on rope strung between two trees such that the trap was ≥2 m from any tree and the collection cup of each trap was 0.5–1.5 m above ground level. All traps were equipped with a wet collection cup with 150–200 ml of a solution of polypropylene glycol and water and were spaced ≈15 m apart within and between blocks. Trap catches were collected every 2–3 wk. Species of *Ips* were identified using differences in morphology, especially those of the elytral declivities (Wood 1982b).

Statistical Analyses. Experimental designs were identical for both experiments (six randomized complete blocks with eight treatments), so data were analyzed similarly. Both experiments had four collection dates, which were summed for analysis. Total catch per trap of each species was analyzed using a blocked multiresponse permutation procedure (MRBP; McCune et al. 2002). Insect trap count

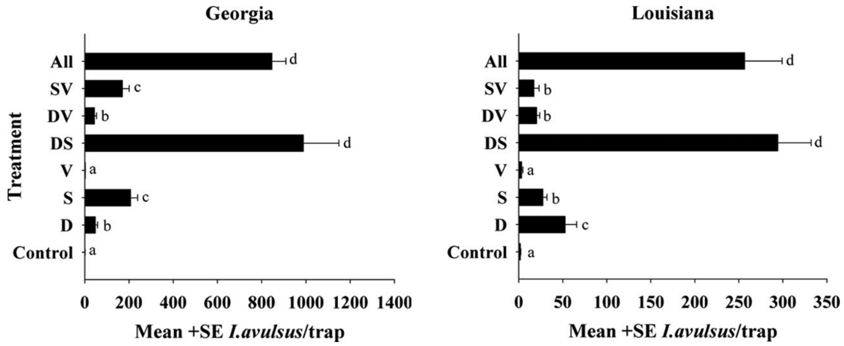

Fig. 1. Effects of *cis*-verbenol (V), ipsdienol (D), and ipsenol (S) on trap catches of *I. avulsus* in Georgia and Louisiana in 2009. Number of replicates per treatment is 6. Means followed by the same letter within a figure are not significantly different at $P = 0.05$.

data are often non-normal and frequently transformations cannot be found to meet the assumptions of normal theory statistics. MRBP has the benefit that assumptions regarding the distribution of dependent variables are relaxed. All analyses were conducted with PC-ORD 6.0 (MjM Software Design, Gleneden Beach, OR) using Euclidean distances to construct the distance matrix with blocks aligned before analysis (McCune et al. 2002). To control the multiplicity effect, researchers typically attempt to control the probability of committing any type I error in families of comparisons under simultaneous consideration (e.g., Bonferroni method). The limitations of this approach include a substantial loss of power with increasing treatments (Garcia 2004). Benjamini and Hochberg (1995) present an alternative approach that controls the false discovery rate (hereafter, step-up FDR). Step-up FDR is equivalent to the family-wise error rate when all hypotheses are true but is smaller otherwise. As a result, use of step-up FDR can have substantially more power than traditional methods (Benjamini and Hochberg 1995), particularly when the number of tests is large (Garcia 2004). This study used step-up FDR to control the FDR when "n" (28 in this study) hypotheses were simultaneously tested (Benjamini and Hochberg 1995, Garcia 2004).

Results

In Georgia, mean total catch of southern *Ips* per trap ranged from 0 to 985.5 depending on the species, with *I. avulsus* being the most abundant (Figs. 1–3). Univariate (i.e., by species) analyses of mean total trap catches indicated that there was a treatment effect for *I. avulsus* ($T = -10.56, P < 0.0001$), *I. calligraphus* ($T = -10.76, P < 0.0001$), and *I. grandicollis* ($T = -10.8, P < 0.0001$) in Georgia. In Louisiana, mean total catch of southern *Ips* per trap ranged from 0.2 to 802.5 depending on the species, with *I. grandicollis* being the most abundant (Figs. 1–3). Univariate analyses indicated that there was a treatment effect for *I. avulsus* ($T = -10.05, P < 0.0001$), *I. calligraphus* ($T = -11.16, P < 0.0001$), and *I. grandicollis* ($T = -10.47, P < 0.0001$).

Catches of *I. avulsus*. Mean total trap catch of *I. avulsus* ranged from 0.8 to 985.5 and from 1.8 to 292 in Georgia and Louisiana, respectively (Fig. 1). In both states, unbaited control traps captured the fewest *I. avulsus* and traps baited with ipsdienol plus ipsenol captured the most. Overall, the pattern of mean total trap catches was very similar for *I. avulsus* in Georgia and Louisiana. In both states, traps baited with ipsdienol plus ipsenol or the tertiary blend captured significantly more *I. avulsus* than all other trap treatments. Similarly, there was no difference in the mean

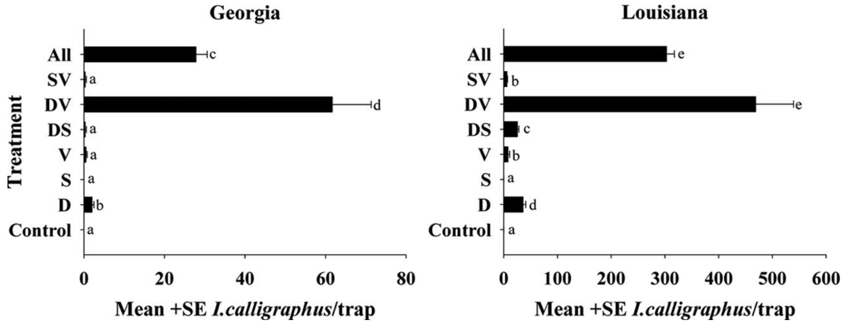

Fig. 2. Effects of *cis*-verbenol (V), ipsdienol (D), and ipsenol (S) on trap catches of *I. calligraphus* in Georgia and Louisiana in 2009. Number of replicates per treatment is 6. Means followed by the same letter within a figure are not significantly different at $P = 0.05$.

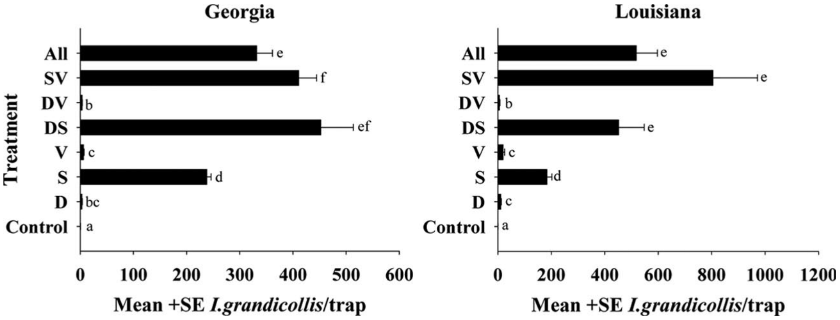

Fig. 3. Effects of *cis*-verbenol (V), ipsdienol (D), and ipsenol (S) on trap catches of *I. grandicollis* in Georgia and Louisiana in 2009. Number of replicates per treatment is 6. Means followed by the same letter within a figure are not significantly different at $P = 0.05$.

number of *I. avulsus* captured in unbaited control traps and in traps baited with *cis*-verbenol; both captured significantly fewer *I. avulsus* than all other trap treatments in both Georgia and Louisiana. In both states, traps baited with only ipsdienol or ipsenol, ipsdienol plus *cis*-verbenol, or ipsenol plus *cis*-verbenol all captured significantly more *I. avulsus* than unbaited controls and traps baited with *cis*-verbenol only, although there were some differences in the trap catches among these treatments between Georgia and Louisiana (Fig. 1).

Catches of *I. calligraphus*. Mean total trap catches of *I. calligraphus* ranged from 0 to 62 and from 0.2 to 468.8 in Georgia and Louisiana, respectively (Fig. 2). In both states, traps baited with ipsenol or unbaited control traps captured the fewest *I. calligraphus* and traps baited with *cis*-verbenol plus ipsdienol captured the most. The overall pattern of trap capture was very similar for *I. calligraphus* in Georgia and Louisiana. In both states, traps baited with *cis*-verbenol plus ipsdienol or the tertiary blend captured significantly more beetles than all other treatments; however, traps baited with the binary combination captured significantly more *I. calligraphus* than traps baited with the tertiary combination in Georgia (but not Louisiana). Similarly, traps baited only with ipsdienol captured more *I. calligraphus* than traps baited with all other treatments except those baited with *cis*-verbenol plus ipsdienol, and the tertiary blend, in both Georgia and Louisiana. Catches of *I. calligraphus* in traps baited with ipsenol, *cis*-verbenol, ipsdienol plus ipsenol, and ipsenol plus *cis*-verbenol were low in both Georgia and Louisiana. In Georgia, catches of beetles in traps baited with these treatments did not differ from unbaited controls, whereas in Louisiana catches in traps baited with all but the ipsenol only treatment captured significantly more *I. calligraphus* than unbaited control traps.

Catches of *I. grandicollis*. In Georgia and Louisiana, mean total trap catch ranged from 0.5 to 451.7 and from 0.5 to 802.5 *I. grandicollis*, respectively (Fig. 3). In both states, the unbaited control traps captured the fewest individuals. Traps baited with *cis*-verbenol plus ipsenol captured the most *I. grandicollis* in Louisiana, whereas traps baited with ipsdienol plus ipsenol captured the most in Georgia. Like the other two southern *Ips,* the overall pattern of trap capture was very similar for *I. grandicollis* in Georgia and Louisiana. In both Georgia and Louisiana, unbaited control traps captured significantly fewer beetles than all other treatments. The three trap treatments of *cis*-verbenol plus ipsenol, ipsdienol plus ipsenol, and the tertiary blend all captured significantly more individuals than all other trap treatments in both Georgia and Louisiana. Although there were no differences among the trap captures of these three treatments in Louisiana, traps baited with ipsenol plus *cis*-verbenol captured significantly more *I. grandicollis* than traps baited with the tertiary blend in Georgia. Traps baited with ipsenol only were significantly less attractive than traps baited with ipsenol plus *cis*-verbenol, ipsenol plus ipsdienol, or the tertiary blend, but were significantly more attractive than all other trap treatments in both Georgia and Louisiana. The treatments ipsdienol only, *cis*-verbenol only, and ipsdienol plus *cis*-verbenol all captured few *I. grandicollis* and had similar patterns of relative attractiveness.

Discussion

We examined the effect of ipsdienol, ipsenol, and *cis*-verbenol on the attraction of the southern *Ips.* The literature examining semiochemical-based interactions among the southern *Ips* is enigmatic, with results inconsistent within and between some studies. For example, some studies have observed cross-attraction to infested host material (Birch et al. 1980, Svihra 1982), whereas others have not (Vité et al. 1964, Birch et al. 1980). This is not surprising given the challenges associated with standardizing qualitative and quantitative parameters of the volatile blends emitted from naturally infested host material. Subsequent studies attempted to overcome these challenges by using traps baited with synthetic pheromones, demonstrating some general patterns as well as some variation between studies.

We observed that the most attractive pheromone treatments (with the fewest number of components) were ipsdienol plus ipsenol for *I. avulsus*, *cis*-verbenol plus ipsdienol for *I. calligraphus,* and either ipsenol plus *cis*-verbenol or ipsenol plus ipsdienol for *I. grandicollis* (Figs. 1–3). Previous studies have reported attraction of *I. avulsus* to blends of ipsdienol [(*R*)-(−)-, (*S*)-(+)- or racemic] and *cis*- and *trans*-verbenol (Smith et al. 1990) and racemic ipsdienol or (*R*)-(−)-ipsdienol plus (*S*)-(−)-ipsenol (Hedden et al. 1976, Vité et al. 1978). Other trapping studies have reported attraction of *I. calligraphus* to blends of racemic ipsdienol and *cis*- and *trans*-verbenol (Smith et al. 1990) and (−)-ipsdienol and *cis*-verbenol (Renwick and Vité 1972, Vité et al. 1978). Finally, ipsenol alone (Vité and Renwick 1971, Vité et al. 1976) or combined with *cis*- and *trans*-verbenol (Smith et al. 1990) has been reported attractive to *I. grandicollis.*

Paine et al. (1981) observed that both *I. avulsus* and *I. grandicollis* colonized less area of phloem in host trees in the presence of the other southern *Ips* species than would be expected if colonization were independent of interspecific effects (this was not observed in *I. calligraphus*). The observed interspecific effects could be mediated pre- or postalightment on host material. If the interspecific effects are mediated prealightment by pheromones, heterospecific pheromone should inhibit attraction of *I. avulsus* and *I. grandicollis.* In general, the available literature (including this study) does not support the hypothesis of pheromone-mediated heterospecific inhibition prealightment in the southern *Ips.* Although heterospecific inhibition has been reported in *I. calligraphus* and *I. grandicollis,* enhancement was observed in *I. avulsus* and *I. calligraphus* in the same study (Birch et al. 1980). Similarly, interspecific attraction of all three southern *Ips* to host material infested with heterospecific southern *Ips* species has been observed previously (Birch et al. 1980, Svihra 1982). We did observe a reduction in trap catches associated with the addition of heterospecific pheromone components (Figs. 1–3). In Georgia, the addition of ipsenol to traps baited with ipsdienol and *cis*-verbenol or ipsdienol to traps baited with ipsenol and *cis*-verbenol significantly reduced the trap catches of *I. calligraphus* and *I. grandicollis,* respectively (Figs. 2 and 3). Despite the reduction in trap catches, traps baited with all three components still captured large numbers of *I. calligraphus* and *I. grandicollis.* Our results suggest that ipsdienol, ipsenol, and *cis*-verbenol can be combined to create a lure capable of simultaneously monitoring the southern *Ips.*

Lanier and Wood (1975) hypothesized that specificity of pheromone response was important for maintaining reproductive isolation among sympatric *Ips* species and that lack of specificity among some species may prohibit introgression of their ranges. Our study does not support this hypothesis (Figs. 1–3). Rather, it is consistent with those studies (Hedden et al. 1976, Symonds and Elgar 2004) that concluded that specificity of pheromones in sympatric *Ips* species is not an important mechanism in maintaining reproductive isolation. It is possible that additional compounds not tested in this study could mediate reproductive isolation among the southern *Ips.* For example, the addition of lanierone to traps baited with ipsdienol and ipsenol can significantly increase the number of *I. avulsus* captured in multiple-funnel traps (Miller et al. 2005). In addition, all three of the compounds tested in this study are chiral and several studies have demonstrated that bark beetle responses to aggregation pheromones are not independent of chirality (e.g., Vité et al. 1978). Chemical analyses are needed to quantify the range of enantiomeric ratios produced by each species and determine if differences in enantiomeric ratios could function as an isolating mechanism between species of the southern *Ips.*

There is evidence for isolating mechanisms that function postalightment in *Ips* beetles. Lanier and Wood (1975) reported that although *Ips cibricollis* (Eichhoff) females were attracted to Arizona fivespined ips, *Ips lecontei* Swaine, nuptial chambers, they did not enter the nuptial chambers. Numerous reproductive isolating mechanisms have been proposed or demonstrated in bark beetles (Lanier and Burkholder 1974, Sturgeon and Mitton 1982). Among these, differences in courtship behavior (e.g., stridulatory signals) could maintain reproductive isolation among sympatric species with cross-attractive pheromones (Barr 1969). Female *I. avulsus, I. calligraphus,* and *I. grandicollis* all have stridulatory organs on their heads (Wilkinson 1962). Female *I. calligraphus* stridulate at the entrance of male *I. calligraphus* nuptial chambers, and only once a female stridulates is she allowed entrance to the nuptial chamber (Wilkinson et al. 1967). It is not known whether females of the three southern *Ips* produce species-specific stridulatory signals. Additional evidence demonstrating that males only accept the stridulatory signals of conspecific females would be necessary to confirm that stridulatory signals were an isolating mechanism. For example, Lewis and Cane (1992) studied a group of sympatric *Ips* [pinyon ips, *Ips confusus* (LeConte); *I. paraconfusus;* and *Ips hoppingi* Lanier] with cross-attractive pheromones. Females of all three species stridulate as they attempt to enter male nuptial chambers; however, despite the existence of species-specific signals, males readily accepted some (but not all) heterospecific females.

In summary, some cross-attraction of the southern *Ips* species to heterospecific pheromone was observed and this was most pronounced in *I. grandicollis* (Fig. 3). It has been hypothesized that *I. grandicollis* is most responsive to heterospecific pheromone because of low niche overlap with the two other southern *Ips* (Birch et al. 1980, Smith et al. 1990). Although our results are consistent with this hypothesis, empirical support for this hypothesis (Paine et al. 1981) is limited and further work is needed. This study also observed that the presence of heterospecific pheromone does not strongly inhibit attraction of southern *Ips* species (Figs. 1–3). This strongly suggests that in the southern *Ips* the aggregation pheromones ipsdienol, ipsenol, and *cis*-verbenol do not confer reproductive isolation prelanding on host material and that additional (e.g., additional compounds, enantiomeric ratios, stridulatory signals) mechanisms may exist or that these compounds are active postlanding. More studies are needed in this and other systems to determine the general applicability of these findings to reproductive isolation in bark beetles.

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