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EFFECTS OF HOST TREE SPECIES ON ATTRACTIVENESS OF TUNNELING PINE ENGRAVERS, *Ips pini*, TO CONSPECIFICS AND INSECT PREDATORS

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Abstract—The effect of host tree species on the attractiveness of tunneling *Ips pini* to flying beetles and their insect predators in Wisconsin was investigated. Tree species influenced the flight response of both predators and prey in the same rank order. *Ips pini* and its major predators, *Thanasimus dubius* and *Platysoma cylindrica*, were more attracted to *I. pini* males boring into bark–phloem disks of *Pinus strobus* L. than *Pinus banksiana* Lamb, and least attracted to *I. pini* males boring into bark–phloem disks of *Pinus resinosa*. Sources of within-tree, between-tree, and between-species variation in the degree of attraction elicited by tunneling beetles were quantified. A bioassay for evaluating host tree effects on pheromone based communication among bark beetles under conditions of controlled beetle entry was developed. Possible mechanisms of host species effects on the dynamics of predator and prey interactions in bark beetle ecology are discussed.

Key Words—*Ips pini*, Coleoptera, Scolytidae, aggregation pheromone, *Thanasimus dubius*, Cleridae, *Platysoma cylindrica*, Histeridae, kairomone, host attraction.

INTRODUCTION

Bark beetles (Coleoptera: Scolytidae) colonize the subcortical tissues of trees and release aggregation pheromones that attract both males and females once they have selected potential hosts (Vité and Renwick, 1968; D. L. Wood, 1982; Vanderwel and Oehlschlager, 1987; Miller, 1990; Seybold, 1992; Vanderwel,

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1994). Scolytid pheromones function in mating, reproductive isolation, habitat location, counteraction of host defenses, and resource partitioning (Lanier et al., 1972; Birch et al., 1980; D. L. Wood, 1982; Raffa and Berryman, 1983; Borden et al., 1986; Raffa et al., 1993). Pheromonal communication among conifer-infesting bark beetles has been closely linked to host tree chemistry, particularly terpenoids (Pitman and Vité, 1970; Vité and Renwick, 1971; Renwick and Vité, 1972; Billings et al., 1976; Borden, 1989; Miller and Borden, 1990; Seybold, 1993; Vanderwell, 1994).

The presence of host plant material may influence the production and release of aggregation pheromone directly or indirectly. For example, some bark beetles may convert host plant terpenes to oxygenated products that serve as aggregation pheromones (Hughes, 1973; Hendry et al., 1980; Byers, 1983; Fish et al., 1984; Pierce et al., 1987). Exposure to host monoterpenes may also stimulate de novo synthesis of pheromones (Seybold et al., 1995a). Synergistic or additive effects on attraction often occur when host kairomones are released in combination with insect-produced pheromones (Billings et al., 1976; Borden et al., 1982; Conn et al., 1983; Raffa and Berryman, 1983; Borden, 1985; Miller and Borden, 1990).

Host plant responses and compounds can also interfere with chemical communication by bark beetles. Raffa and Berryman (1983) observed that mountain pine beetles, *Dendroctonus ponderosae* (Hopkins), that were tunneling beneath the bark, but whose entrance sites were covered with liquid resin, often failed to elicit aggregation. Even in an area with high populations, only half of the trees that were entered first by solitary beetles, i.e., were not part of "switching" from a neighboring tree (Geiszler and Gara, 1978), became foci of attraction (Raffa and Berryman, 1983). Chemicals present in the foliage of host (Strom et al., 1994) or nonhost (Dickens et al., 1992; Borden et al., 1998; Deglow and Borden, 1998) trees can also inhibit the attraction of flying bark beetles to their aggregation pheromones.

Most bark beetles species are oligophagous but show preferences for certain tree species (S. L. Wood, 1982; Kirkendall, 1983). The role of host tree species in pheromonal communication among bark beetles and their predators is only partially understood. Seybert and Gara (1970) reported that *I. pini* prefer *Pinus resinosa* (Aitman) over *Pinus strobus* L. as host material. However, Piston and Lanier (1974) suggested *P. strobus* was superior for pheromone production.

Initial selection of the host plant is performed by individual beetles that arrest in response to visual (Shepherd, 1966; Groberman and Borden, 1981) or chemical (Hobson et al., 1993; Macías-Sámano et al., 1998) cues, and subsequently either enter or depart from the host based on short-range chemicals and tactile stimuli (Moeck et al., 1981; Raffa and Berryman, 1982). Pheromone production begins as beetles enter selected trees.

Monoterpenes vary among trees of the same species within a habitat and

among geographic regions (Mirov, 1961; Smith et al., 1969; Sturgeon, 1979; Byers and Birgersson, 1990). In addition, some bark beetle species show genetically based semiochemical variation over geographic regions (Anderson et al., 1983; Miller et al., 1989, 1997). Such differences could partly reflect underlying geographic and interspecific variation in the monoterpene composition of their conifer hosts. For example, sympatric populations of *D. ponderosae* vary genetically between host tree species (Stock and Amman, 1980). Moreover, Hobson et al. (1993) found that monoterpenes that are common to several pine species may differ in the ratios of stereoisomers present and that attraction by *Dendroctonus valens* LeConte to the resin volatiles of its host are strongly affected by the enantiomeric composition of the monoterpenes.

A major barrier to evaluating effects of host plant species on the ability of tunneling bark beetles to elicit attraction under natural conditions arises from the operational difficulties of working with trees. The most common methods are to remove infested tissues from trees undergoing colonization (Wood, 1962) or to manipulate controlled entries into logs (Piston and Lanier, 1974). However, the former method cannot provide control of beetle density, age, or duration in the host, and the latter method poses problems attaining adequate replicates for statistical analysis. Log-based assays are wasteful to the resource and can often necessitate reliance on unvalidated assumptions of independence of replicates. Moreover, the plant community in which a field experiment is conducted could conceivably affect beetle choice, a consideration that poses much greater operational difficulty when working with forest trees than annual crops. One of our objectives was to develop a more efficient system for assaying responses of bark beetles that is more controlled and less cumbersome than existing methods, has statistical independence, and allows superior replication. In developing this assay, we specifically tested the implications of within- and between-tree sources of variation to experimental design.

The test insect was the pine engraver, *Ips pini* (Say), a transcontinentally distributed species on *Pinus* throughout the coniferous forests of North America (Lanier, 1972). *Ips pini* has a relatively broad host range across its geographic distribution (S. L. Wood, 1982). In the Lake States region, *I. pini* primarily colonizes red pine, *P. resinosa* (Aitman), jack pine, *P. banksiana* Lamb, and white pine, *P. strobus* L. *Ips pini* can be an important pest under certain conditions (Schenk and Benjamin, 1969; Miller et al., 1989, 1990; Klepzig et al., 1991). During establishment within a suitable tree, adult males emit ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (Vité et al., 1972; Birch, 1978; Birch et al., 1980; Borden, 1982; Miller et al., 1989) and lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Teale et al., 1991). Lanierone synergizes the attraction of both sexes to ipsdienol (Teale et al., 1991). There is strong geographic variation in pheromone production and response among populations of *I. pini*. Western populations are attracted to (*R*)-(−)-ipsdienol, whereas eastern

and midwestern populations are more strongly attracted to 40–50% (−)-ipsdienol (Lanier et al., 1972, 1980; Birch et al., 1980; Raffa and Klepzig, 1989; Raffa, 1995; Seybold et al., 1995b). Likewise, the production of lanierone and its synergism of *I. pini* responses to ipsdienol show pronounced geographic variation, with effects predominant among eastern and midwestern, but not western, populations (Teale et al., 1991; Seybold et al., 1992).

Some predators utilize pheromones of their host bark beetles as kairomones to locate prey (Wood et al., 1968; Stephen and Dahlsten, 1976; Billings and Cameron, 1984; Mizell et al., 1984; Grégoire et al., 1992). The most abundant predators associated with midwestern *I. pini* populations that are known to respond to its pheromone are the beetles *Thanasimus dubius* (F.) (Cleridae) and *Platysoma cylindrica* (Paykull) (Histeridae), and to a lesser extent *Corticeus parallelus* (Melsh) (Tenebrionidae) and *Tenebroides collaris* (Sturm) (Tenebrionidae) (Raffa and Klepzig, 1989; Raffa, 1991; Raffa and Dahlsten, 1995). Secondary phloeophagous beetles, such as the red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae), the pine root weevils *Hylobius radicis* Buchanan, *Hylobius pales* (Herbst), and *Pachylobius picivorus* (Germar) (all Curculionidae), and the wood borer *Monochamus carolinensis* Oliver (Cerambycidae), are also attracted to ipsdienol (Klepzig et al., 1991; Raffa, 1991).

The purpose of this research is to determine effects of host tree species on attraction of flying *I. pini* and its associates, develop new bioassays for evaluating effects of host tree species, and quantify within-tree, between-tree, and between-species variation in beetle response.

METHODS AND MATERIALS

Study Site. Behavioral experiments were conducted from May 14 to June 18, 1998, in *P. resinosa* and *P. banksiana* forests in Sauk County (N43°11.78′, W90°11.15′), and Juneau County (N43°58.28′, W90°07.35′), Wisconsin, USA. Attention was taken to reduce site effects on insect populations by selecting stands with similar forest characteristics. Forty- to 50-year-old pine plantations with similar site indices were used throughout this study. All bark–phloem samples in which *I. pini* were allowed to tunnel were collected from live trees growing in a common site, the Mazomanie State Forest in Dane County (N43°13.53′, W89°47.50′). This forest consists of *P. resinosa*, *P. banksiana*, and *P. strobus* growing adjacent to each other.

Assay Preparation. The assay unit consisted of a 150-mm-diam. × 25-mm-high plastic Petri dish containing fresh bark–phloem. Bark–phloem samples were collected from stems in the lower 1–2.5 m of live trees by using a 8-cm-diam. round saw attached to a hand drill. Samples were brought to the laboratory and cut in a circular shape with a 150-mm-diam hole saw, and then placed in the

Petri dish in warm paraffin wax to minimize desiccation of the phloem. Seven 1-day-old *I. pini* from a laboratory colony in red pine maintained by using the methods of Raffa and Dahlsten (1995) were introduced onto this bark, which was then covered by mesh screen to keep the beetles from escaping. Beetles were allowed to tunnel into the bark–phloem disks for 24 hr at room temperature. The assay units were then taken to forested sites where they were suspended from multiple funnel traps (Lindgren, 1983). Treatment positions were rerandomized at collection date. The distance between treatments within each block was 10–15 m, and the distance between blocks was 45–55 m. Insect No-pest strips (Pest Strip, Loveland Industries, Inc. Greeley, Colorado) were placed in the collection jars to reduce predation. Insects were identified to species and tabulated. Arriving insects were sampled after four days, based on previous results with responses of flying *I. pini* and natural enemies to tunneling *I. pini* (Raffa and Dahlsten, 1995).

Evaluation of Bioassay. A preliminary experiment was conducted to determine whether *I. pini* can generate pheromonal attraction under the conditions provided by this assay unit. This experiment consisted of a comparison among *I. pini* entering *P. resinosa* bark–phloem, *P. resinosa* bark–phloem alone, and a blank control. This experiment was conducted in a mature red pine forest near Spring Green, Sauk County, Wisconsin (N43°11.78′,W90°11.15′). Ten replicates of each treatment were tested. After four days, all insects responding were collected and counted.

Evaluation of Host Tree Effects. Three experiments were conducted to evaluate the effects of host tree species on the attractiveness of tunneling *I. pini* to flying *I. pini*, predators, and other associates. The first experiment was conducted to determine whether several bark–phloem sections from an individual tree could be used, as opposed to the more wasteful and destructive approach of using a separate tree for each bark–phloem section. More specifically, this was an explicit test of whether multiple bark–phloem samples from one tree would constitute pseudoreplication, or whether between-tree, within-species variance was insignificant. Nine trees each of *P. resinosa*, *P. banksiana*, and *P. strobus* were sampled. Three bark–phloem disks from each tree were collected to provide subsamples. Each block consisted of three subsamples from one tree of each species. There were nine blocks. The position of each treatment within a block was assigned randomly. Assays were conducted in *P. resinosa* plantations in Juneau County, Wisconsin. Numbers of *I. pini* and associated insects were recorded after four days.

In the second experiment, traps were deployed in two mature *P. resinosa* stands in Sauk and Juneau Counties, as described above. Treatments were assigned randomly within each of 10 blocks. There were seven blocks in Sauk County and three blocks in Juneau County. Insects were collected at four-day intervals over eight days, providing 20 replicates per treatment. Bark–phloem

samples were obtained from the same trees in the Mazomanie State Forest that were used to evaluate within- and between-tree variation. Based on the observation that there was no between-tree variation within a species (see Results), more samples could be obtained from each tree. Based on the significant differences we observed in the validation experiment between *I. pini* tunneling in bark vs. either bark–phloem alone or blanks (see Results), all treatments included *I. pini*. Treatments consisted of *P. strobus* with *I. pini*, *P. banksiana* with *I. pini*, and *P. resinosa* with *I. pini*.

Beetle Tunneling Distance. To determine whether differences in beetle arrival might be due to differences in tunneling length by *I. pini*, the gallery of each beetle was measured in the bark–phloem samples. The same 60 bark–phloem samples from the evaluation of host tree effect (experiment 2) were used. The average tunneling distance of the seven bark beetles per dish was used to provide one replicate, as the Petri dish provides the experimental unit. Percent entrance was measured by counting the number of entrance holes and measuring gallery length from each hole. Insects that tunneled less than 1 cm were not considered to be successful colonizers of the bark sample.

Statistical Analyses. Data were analyzed by using analysis of variance. Each variable was tested to satisfy assumptions of normality and homogeneity of variances (Zar, 1996) by graphical analysis of residuals (Neter et al., 1983). If the variance was nonhomogeneous, variables were transformed to $\log_{10}(x + 1)$, which provided distributions that satisfied these assumptions in all cases. Sex ratio data for *I. pini* were transformed by arcsin $\sqrt{Y}$. Dependent variables were analyzed as a split plot, with randomized block design, treating sites as blocks (PROC MIX; SAS Institute, 1996). For each variable, covariance parameter estimates (REML) for block and block × treatment were calculated in order to reveal whether there is any variability due to block or block × treatment. In all experiments, blocks were accepted as a random factor, and if the covariance parameter of block was equal to 0, then the block term was eliminated from the random statement in the model. If it was different from 0, the −2 residual log likelihood values of the model with random block and the model without random block were compared by chi-square analysis ($df = 1$) at $P < 0.05$. If chi-square analysis revealed any significance, then block was included in the random statement. An additional blocking factor for collection time was included for experiments with two collection periods. A protected LSD test was used for multiple comparison of means.

RESULTS

Evaluation of Bioassays. Ips pini boring in bark and phloem samples attracted more *I. pini* than host tissue alone (12×) or blank controls (34×)

TABLE 1. RESPONSE OF FLYING *I. pini* TO MALE *I. pini* TUNNELING IN *Pinus resinosa* BARK–PHLOEM SAMPLES[a]

Treatment	*I. pini* (mean ± SEM)[b]
P. resinosa with male *I. pini* tunneling	10.30 ± 4.94 a
P. resinosa alone	0.900 ± 0.23 b
Control	0.300 ± 0.21 b
F	9.902
P	0.0007

[a] Means followed by the same letter in a column are not significantly different at $P < 0.05$, based on protected LSD test. Data transformed by $\log_{10}(x + 1)$ for analysis. Nontransformed means are reported.
[b] Mean catch per trap per four-day sampling period.

($P < 0.0007$) (Table 1). There was no difference between host tissue alone and blank controls.

Effects of Host Tree Species. In the first experiment, the insects that were attracted to funnel traps baited with *I. pini* boring in host tissue included *I. pini*, *T. dubius*, *P. cylindrica*, and *Corticeus* sp. The mean numbers of these insects caught in multiple funnel traps did not vary among trees within a species (*F* statistics in Table 2). Covariance parameter estimates revealed no significant variation among bark–phloem samples within a species, and no significant block effects.

Tree species had an effect on trap catches of *I. pini* and its major predators (*F* statistics in Table 3). Male *I. pini* tunneling in *P. strobus* attracted more *I. pini* than male *I. pini* in either *P. banksiana* or *P. resinosa* ($P < 0.007$). The proportion of males in trap catches of responding *I. pini* (mean ± SE = 0.40 ± 0.011) was not affected by the tree species ($F = 1.32$, $P = 0.562$). *Thanasimus dubius* ($P < 0.03$), *P. cylindrica* ($P < 0.0001$), and *Corticeus* sp. ($P < 0.02$) all showed a similar response pattern. Only a few (18) *Enoclerus sphegeus* (F.) were captured, and although these did not appear to differ among various tree species ($P > 0.3$), the small sample size may be responsible. The range of responses was higher for predators than for the prey. For example, the ratios of *T. dubius*, *P. cylindrica*, and *Corticeus* sp. in *P. strobus* to *P. resinosa* were 4.8, 9.0, and 3.0, respectively, compared to 2.3 for *I. pini*. Covariance parameter estimates revealed that there was insignificant variation among bark–phloem samples within a species among blocks for *I. pini* (block <0.01) and *Corticeus* sp. (block < 0.06 and block × treatment < 0.06) (covariance parameter estimates in Table 3).

In the second experiment, *I. pini*, *T. dubius*, *P. cylindrica*, and other associated insects also showed significant differences among various host tree species (Table 4). As in the previous assay, male *I. pini* boring in *P. strobus* attracted more *I. pini* than male *I. pini* boring in *P. banksiana* or *P. resinosa*. The sex

TABLE 2. RESPONSE OF *I. pini* AND ITS MAJOR PREDATORS, *T. dubius*, *P. cylindrica*, AND *Corticeus* sp. TO MALE *I. pini* TUNNELING IN *P. strobus*, *P. banksiana*, AND *P. resinosa* BARK–PHLOEM SAMPLES TO REVEAL BETWEEN-TREE, WITHIN-HOST SPECIES VARIATION[a]

Host tree	Statistical summary											
		I. pini			*T. dubius*			*P. cylindrica*			*Corticeus* sp.	
	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P
P. strobus	26	46.9	2.0	0.1	2.3	1.4	0.2	5.0	0.7	0.6	4.2	1.5	0.2
P. banksiana	26	29.5	0.2	0.9	0.5	0.7	0.7	1.6	1.9	0.1	—	—	—
P. resinosa	26	4.7	1.1	0.3	2.3	0.4	0.8	0.0	1.5	0.2	1.1	0.4	0.8
	Covariance parameter estimates (REML)												
P. strobus													
Block		0			0			0			0		
Block × treatment		0			0			0			0		
P. banksiana													
Block		0			0			0					
Block × treatment		0			0			0					
P. resinosa													
Block		0			0			0			0		
Block × treatment		0			0			0			0		

[a] Nine samples from each of 3 trees within a species. Data transformed by $\log_{10}(x+1)$ for analysis. A dash indicates that there were an insufficient number of insects for analysis. Within species summary statistics (mean + SE) are not shown because replicates at the species level is only three trees and is inadequate for between-species comparisons. For one of the white pines, only eight samples were available for analysis (one lost).

ratio (males: mean ± SE = 0.62 ± 0.05) in trap catches of responding *I. pini* was not affected by the tree species ($F = 0.96$, $P = 0.760$). Likewise, male *I. pini* boring in *P. strobus* attracted more of the predators, *T. dubius* and *P. cylindrica* than male *I. pini* boring in either *P. resinosa* or *P. banksiana*. There were no differences in the number of *E. sphegeus* and *P. parallelum* captured among treatments, although the sample sizes of these species were very small. Covariance parameter estimates for block and block × treatment revealed that there was no or small variation among samples within a species among blocks (Covariance Parameter Estimates in Table 4).

Beetle Tunneling Distance. Host tree species had some effect on tunneling distance by *I. pini* ($F = 10.60$, $df = 56$, $P = 0.0001$). Male *I. pini* tunneled 1.9× more in *P. banksiana* and 1.7× more in *P. strobus* than in *P. resinosa* (Table 5). There was no statistical difference in the tunneling distance of *I. pini* between *P. banksiana* and *P. strobus*. There was little variability among bark–phloem samples within plant species.

TABLE 3. RESPONSE OF *I. pini* AND ITS MAJOR PREDATORS, *T. dubius*, *P. cylindrica*, AND *Corticeus* sp. TO MALE *I. pini* TUNNELING IN *P. strobus*, *P. banksiana*, AND *P. resinosa* BARK–PHLOEM SAMPLES

	Insects (mean ± SEM)[b]				
Host tree	*I. pini*	Sex ratio (M/F)	*T. dubius*	*P. cylindrica*	*Corticeus* sp.
P. strobus	8.73 ± 1.61 a	1.02	1.77 ± 0.50 a	1.62 ± 0.33 a	2.31 ± 0.59 a
P. banksiana	6.59 ± 1.77 b	1.04	1.12 ± 0.27 ab	0.41 ± 0.11 b	0.85 ± 0.26 b
P. resinosa	3.85 ± 0.72 b	1.01	37 ± 0.11 b	0.18 ± 0.09 b	0.78 ± 0.22 b
F	5.23		3.68	15.71	5.02
P	0.007		0.03	0.0001	0.02
	Covariance parameter estimates (REML)				
Block	0.01		0	0	0.06
Block × treatment	0		0	0	0.06

[a] Means followed by the same letter in a column are not significantly different at the 0.05 probability level, based on protected LSD test. Data transformed by $\log_{10}(x+1)$ for analysis. Nontransformed means are reported.
[b] Mean catches per trap per four-day sampling period.

DISCUSSION

These results indicate that host plant species can affect the relative attractiveness of tunneling male *I. pini* to flying beetles. The major predators are also affected by host plant species, in the same rank order as their prey (Figure 1). Responses to *P. strobus* were higher for *I. pini*, *T. dubius*, and *P. cylindrica*, and responses to *P. banksiana* were higher than for *P. resinosa*. Our results show some similarity with those of Piston and Lanier (1974), who found that *I. pini* exhibited a preference for *P. strobus* over *P. resinosa* as host material. However, predators in that study did not show any preference based on host tree species. The present study obtained larger sample sizes of predators than were reported in Piston and Lanier (1974), and more fully accounted for intra- and interspecies sources of variation, which may partially explain this difference. The high correspondence between the response of *I. pini* and its major predators to chemical signals from male *I. pini* in different host species (Figure 1) differs from the disparities between predators and prey observed in response to enantiomeric composition of ipsdienol, lanierone content, and spatial and temporal factors (Raffa and Klepzig, 1989; Raffa, 1991; Raffa and Dahlsten, 1995; Miller et al., 1997).

Relatively little is known about the underlying mechanisms by which host tree species can affect the attraction of bark beetles and predators to tunneling bark beetles. Some possible explanations include greater tunneling by beetles in the phloem of certain tree species, larger amounts of pheromone produced,

TABLE 4. RESPONSE OF *I. pini* AND ITS MAJOR PREDATORS, *T. dubius*, *P. cylindrica*, AND *Corticeus* sp. TO MALE *I. pini* TUNNELING IN *P. strobus*, *P. banksiana*, AND *P. resinosa* BARK–PHLOEM SAMPLES[a]

	Insects (mean ± SEM)[b]					
Host tree	*I. pini*	Sex ratio (M/F)	*T. dubius*	*P. cylindrica*	*P. parallelum*	*E. sphegeus*
P. strobus	18.3 ± 3.46 a	1.01	16.9 ± 4.44 a	4.95 ± 1.11 a	0.90 ± 0.25 a	0.30 ± 0.13 a
P. banksiana	9.60 ± 2.14 b	1.03	.95 ± 0.94 b	3.15 ± 0.87 b	0.90 ± 0.37 a	0.60 ± 0.31 a
P. resinosa	4.35 ± 1.00 c	1.05	3.95 ± 0.77 b	2.15 ± 0.61 b	0.40 ± 0.17 a	0.60 ± 0.27 a
F	14.47		7.49	5.78	1.28	0.42
P	0.000		0.004	0.005	0.28	0.66
	Covariance parameter estimates (REML)					
Block	0.002		0.00001	0.002	0.0001	0.0001
Block × treatment	0		0.0011	0	0	0

[a] Means followed by the same letter in a column are not significantly different at 0.05 probability level, based on protected LSD test. Data transformed by $\log_{10}(x + 1)$ for analysis. Nontransformed means are reported.
[b] Mean catches per trap per four-day sampling period.

TABLE 5. TUNNELING DISTANCE OF MALE *I. pini* IN *P. resinosa*, *P. banksiana*, AND *P. strobus* BARK–PHLOEM SAMPLES[a]

Host tree	Distance (cm, Mean ± SEM)[b]
P. strobus	2.77 ± 0.17 b
P. banksiana	3.02 ± 0.17 b
P. resinosa	1.62 ± 0.11 a
F	10.60
P	0.0001

[a] Means followed by the same letter in a column are not significantly different at 0.05 probability level, based on protected LSD test. Data transformed by $\log_{10}(x+1)$ for analysis. Nontransformed means are reported. Covariance parameter estimates of block and block × time are 0.05 and 0, respectively.

[b] Mean trap catches per trap per four-day sampling period.

or altered enantiomeric composition of pheromones produced in certain trees, and differences in the attraction to, or synergism of beetle pheromones by, host compounds.

Although tunneling length by male *I. pini* differed among tree species (Table 5), the rank order did not correspond to the host preference results (Figure

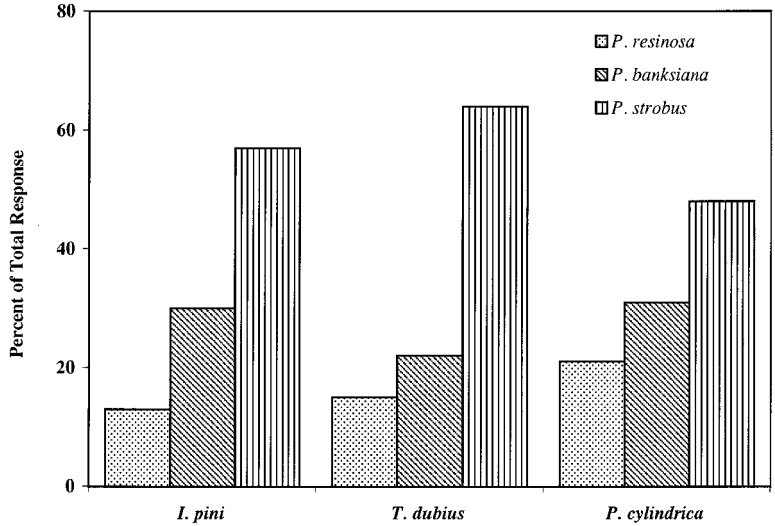

FIG. 1. Proportionate responses of *I. pini* and its major predators, *T. dubius*, and *P. cylindrica*, to male *I. pini* tunneling in bark-phloem samples of *P. resinosa*, *P. banksiana*, and *P. strobus* in Wisconsin. This summary represents the mean of assays that included all three tree species.

1). Thus, gallery length might provide a partial explanation for the responses of flying insects, but it does not describe clearly the role of host effects on attraction. One possibility that cannot be discounted is that potential differences in phloem thickness could affect relative attraction.

The quantity of aggregation pheromone produced by bark beetles may reflect the levels of precursors in the host tissue. For example, Byers (1981) and Birgersson et al. (1984) reported that the production of *cis*-verbenol by male *Ips paraconfusus* Lanier, and *cis*-verbenol, *trans*-verbenol, and myrtenol by *Ips typographus* (L.), increased with the concentrations of α-pinene in the host. Likewise, Miller et al. (1989) found substantial variation in the quantity of ipsdienol produced by *I. pini* and suggested that environmental factors, such as host species and levels of precursors, could be important. Exposure of *I. paraconfusus* to the two optical isomers of α-pinene led to production of different verbenols, (+)-*trans*-verbenol from (*R*)-(+)-α-pinene and (+)-*cis*-verbenol from (*S*)-(−)-α-pinene (Renwick et al., 1976), and host species may affect the enantiomeric composition of ipsdienol produced by *I. pini* (Seybold et al., 1995b). Thus, differences in the quantity or quality of ipsdienol and/or lanierone could possibly explain some of our results. However, as with gallery length, pheromone synthesis seems unlikely to fully explain the differences in Figure 1. For example, the extent to which *Ips* spp. depend on host monoterpenes as precursors to aggregation pheromone is not clear. Recent results demonstrate de novo biosynthesis by male *I. pini* and *I. paraconfusus* (Ivarsson et al., 1997; Seybold et al., 1995a). Moreover, midwestern populations of *I. pini*, *T. dubius*, and *P. cylindrica* are known to prefer different optical isomers of ipsdienol (Raffa and Klepzig, 1989; Raffa, 1995; Raffa and Dahlsten, 1995), so any differences in enantiomeric composition resulting from different host species would generate dissimilar responses among these insects, as opposed to the common pattern seen in Figure 1. Attraction is also likely to vary with the host species from which emerging adults developed (Piston and Lanier, 1974).

When boring activity is initiated by *I. pini*, host trees may emit kairomones that act synergistically with beetle pheromones (Borden et al., 1986). Although the three tree species used in this experiment share some common monoterpenes, relatively small changes in the proportions of cooccurring compounds can have large effects on bark beetle feeding or flight responses (Tømmerås and Mustaparta, 1987; Tømmerås, 1989). The major differences among these species are that *P. strobus* has a relatively lower percent composition of α-pinene, and relatively higher percent composition of β-pinene, myrcene, 3-carene, and β-phellandrene (e.g., Bridgen et al., 1979; Klepzig et al., 1995, 1996; Raffa and Smalley, 1995; Wallin and Raffa, 1999). However, there are no monoterpenes for which the rank order of composition corresponds either directly or inversely to our trap catches. The possibility that different ratios of host volatiles/pheromones among tree species differentially influence the attraction

of bark beetles and predators cannot be excluded. The most likely explanation is that a combination of the above mechanisms is involved.

Several sources of variation in pheromone production by *I. pini* have been identified (Miller et al., 1989). Our results show that the extent of intrapopulation variation can also be affected by host species. Between-tree variation in responding beetles was substantially lower for *I. pini* males entering *P. resinosa* than *P. banksiana* or *P. strobus*. This is consistent with the reported low genetic variation in *P. resinosa* (Fowler and Lester, 1970) compared to *P. strobus* and *P. banksiana* (Wright, 1970; Rudolph and Yeatman, 1978) and with the lower variation in monoterpenes in *P. resinosa* than *P. strobus* (Klepzig et al., 1995, 1996; Raffa and Smalley, 1995; Wallin and Raffa, 1999).

The modified assay system described here for evaluating responses of bark beetle and natural enemy populations to tunneling beetles is more controlled and less cumbersome and allows superior replication than previous methods that used logs. Additional economy can be achieved by obtaining multiple samples from individual trees, in those systems where insignificant intraspecific variation is validated.

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