

CHEMICALLY MEDIATED PREDATOR-FREE SPACE: HERBIVORES CAN SYNERGIZE INTRASPECIFIC COMMUNICATION WITHOUT INCREASING RISK OF PREDATION

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(Received October 20, 1999; accepted April 15, 2000)

Abstract—Natural enemies of herbivores often locate cryptic insects by responding to volatiles associated with the prey's feeding and mating. For example, predators of bark beetles (Coleoptera: Scolytidae) exploit the aggregation pheromones that their prey use to attract mates and secure hosts. Bark beetles are cryptic insects that feed and develop in the subcortical tissues of trees and spend all but a portion of their life history within this habitat. The pine engraver, *Ips pini*, produces the pheromone ipsdienol throughout its transcontinental range. Predators of *I. pini* exploit this chemical as a kairomonal cue. Eastern and Midwestern *I. pini* populations also produce lanierone, which synergizes their attraction to ipsdienol. We evaluated the effects of varying amounts of lanierone, in combination with a constant amount of racemic ipsdienol, on the relative attraction of *I. pini* and its major predators in Wisconsin. Higher numbers of *I. pini* were captured with increasing release rates of lanierone. In contrast, the numbers of the major predators, such as *Thanasimus dubius*, *Enoclerus nigrifrons*, *Platysoma cylindrica*, and *P. parallelum*, did not differ among different lanierone release rates. The response of *I. pini* but not their predators to lanierone at ecologically realistic release rates may be part of a coevolving interaction between predators and prey and offers new strategies for semiochemically based pest management by selectively removing pests and leaving predators.

Key Words—*Ips pini*, ipsdienol, lanierone, *Thanasimus dubius*, *Platysoma*, *Enoclerus nigrifrons*, kairomone, aggregation pheromone, synergism, Coleoptera, Scolytidae, Cleridae, coevolution, pest management.

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INTRODUCTION

Bark beetles comprise one of the most damaging groups of forest insects in North America and Europe (Wood, 1982). During host colonization, adults produce aggregation pheromones that attract large numbers of conspecifics and function in mate attraction, host procurement, and interspecific resource partitioning (Birch et al., 1980a,b; Lanier et al., 1980; Borden, 1982; Wood, 1982; Raffa and Berryman, 1983; Poland and Borden, 1998). Aggregation pheromones have complex biological activities that may vary with quantity (Lanier et al., 1980), season (Teale and Lanier, 1991), chirality (Silverstein, 1979; Seybold, 1993; Mori, 1998a,b), presence of host compounds (Chénier and Philogène, 1989; Erbilgin and Raffa, 2000), and/or synergistic components (Teale et al., 1991).

Ips pini (Say) is the principal bark beetle pest in northeastern and north central North American pine plantations (Schenk and Benjamin, 1969; Klepzig et al., 1991) and causes chronic mortality in western harvest operations (Borden et al., 1992). It produces the aggregation pheromone ipsdienol, which occurs as two enantiomers [(4*R*)-(-)- and (4*S*)-(+)-2-methyl-6-methylene-2,7-octadien-4-ol] (Miller et al., 1997). In western North America, *I. pini* respond primarily to (-)-ipsdienol (Miller et al., 1996). The only known exception is a population in southwestern BC, which responds to (+):(-) ratios of 66:34 (Miller et al., 1996) and may represent an introduction from the eastern range (Seybold et al., 1992). In New York, *I. pini* prefer (+):(-) ratios ranging from 70:30 to 40:60 (Lanier et al., 1980; Teale and Lanier, 1991; Teale et al., 1994). Wisconsin *I. pini* are similar to those in New York, preferring (+):(-) mixtures such as 75:25 and 50:50 ipsdienol (Raffa and Klepzig, 1989; Hems et al., 1991; Aukema et al., 2000a,b). Some *I. pini* also produce a synergistic pheromone component, lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Teale and Lanier, 1991). Lanierone activity varies across North America. It synergizes attraction of both sexes of *I. pini* to ipsdienol in New York and Wisconsin, but in California it is produced not at all or in extremely low quantities by a few individuals. In California, lanierone only weakly enhances attraction of *I. pini* to ipsdienol (Seybold et al., 1992; Miller et al., 1997).

Numerous predators of scolytids use bark beetle pheromones as kairomones (Bakke and Kvamme, 1981; Billings and Cameron, 1984; Payne et al., 1984; Raffa and Klepzig, 1989; Raffa and Dahlsten 1995; Ross and Daterman, 1995). Transcontinental variation in responses to *I. pini* pheromones also occurs among its major predators (Seybold et al., 1992). However, the geographic trends between eastern and western populations of *I. pini* versus its predators contradict each other, rather than coincide. That is, predators in California are relatively more attracted to pheromone plumes characteristic of *I. pini* populations in Wisconsin and vice versa (Raffa and Dahlsten, 1995). A predominant California predator, *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae), is attracted

to ipsdienol plus increasing amounts of lanierone in a dose-dependent manner (Seybold et al., 1992), while less abundant predators, such as *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogoitidae) and *Enoclerus sphaeus* (F.) (Coleoptera: Cleridae) show no additive or multiplicative response to lanierone in combination with ipsdienol. The predominant predators in Wisconsin, such as *Thanasimus dubius* (F.), *E. nigrifrons* var. *gerhardi* (Say) (Coleoptera: Cleridae), *Platysoma cylindrica* (Paykull), and *P. parallelum* (Say) (Coleoptera: Histeridae), also show no increased attraction to ipsdienol when low release rates of lanierone are added (Miller et al., 1997; Aukema et al., 2000a,b). This pattern suggests a coevolving system, in which pheromonal signals by the herbivore *I. pini* are modified through selective pressures exerted by predators, and predators adapt to *I. pini* shifts in pheromone production (Raffa, 1995).

Such disparities in behavioral responses to stereoisomers of ipsdienol and to lanierone can potentially provide novel pest management opportunities by affording the opportunity to selectively target pests, augment predators, and improve sampling estimates (Raffa and Klepzig, 1989; Raffa and Dahlsten, 1995; Aukema et al., 2000a,b). However, the responses by *I. pini* and its major predators to varying doses or release rates of lanierone in combination with ipsdienol are not known. Characterizing such dose-response curves is an important component for integrated pest management (Amman et al., 1991; Gibson et al., 1991; Bertram and Paine, 1994; Miller et al., 1995; Czokajlo and Teale, 1999). This experiment sought to further characterize the pheromone system of *I. pini* and its associates in Wisconsin. In particular, we studied insect responses to varying release rates of lanierone, especially at higher quantities than tested previously (Miller et al., 1997), in combination with a fixed release rate of racemic ipsdienol. Our objective was to determine whether previously reported relationships would be maintained at higher release rates and to characterize the nature of these relationships for different phloophagous and predator species.

METHODS AND MATERIALS

We conducted this experiment as a behavioral choice assay in a mature, 40-year-old, red pine (*Pinus resinosa* Aiton) plantation (latitude 43°34.61'N, longitude 89°52.30'W). The general design followed that of Aukema et al. (2000b). Three lines of five 12-funnel Lindgren traps (Lindgren, 1983) were deployed. The traps within a line were approximately 10 m apart, and the lines were at least 100 m apart.

Each trap received one treatment during each sample period. Four synthetic pheromone treatments dispensed from polyvinyl bubble cap pheromone lures (Pherotech Inc., Delta, British Columbia), and a blank control trap, were tested. Each pheromone treatment contained 20 mg (active ingredient) (+/-) (50/50)

ipsdienol, released at 110 $\mu\text{g}/\text{day}$ at 25°C. The pheromone treatments contained variable amounts of lanierone: 4, 8, 12, or 20 mg (a.i.) (release rates of 10, 20, 30, 100 $\mu\text{g}/\text{day}$ at 25°C, respectively). The amount of lanierone was altered by varying the number of lures. The lures used 1,3-butanediol as a carrier solvent, which is not attractive to *I. pini* (Miller, 1990).

A 3 \times 3-cm time-released 20% organophosphate insecticide strip (Pest Strip, Loveland Industries, Inc., Greeley, Colorado) was placed in each trap cup to prevent destruction of trap contents by responding predators. The trap catches were collected every four days for six equal sample periods within each 24-day trial. At each collection, treatments within each line were rerandomized. This experiment was performed 29 May–22 June (spring) and 14 July–03 August (summer), 1998, to correspond with the major flight periods of Wisconsin predators and *I. pini*. Five samples from the sample period 22 July–26 July were discarded due to an incorrect randomization in the field.

Trap catches were analyzed for herbivores, predators, and the parasitoid *Tomicobia tibialis* Ashmead (Hymenoptera: Pteromalidae). Population samples of 637 *Ips* specimens obtained during the same year in the same plantation with racemic ipsdienol plus 100 $\mu\text{g}/\text{day}$ lanierone revealed that 99.37% of the responding *Ips* spp. were *I. pini*: The remaining species were *I. grandicollis* (Eichhoff) (0.16%), which is not attracted to either ipsdienol or lanierone (Wood, 1982), and *I. perroti* Swaine (0.47%). Thus, we did not identify all of the captured individual *Ips* to species, as several thousand were caught. Given this preponderance of *I. pini* (>99%) responding to this blend, we subsequently refer to all *Ips* caught as *I. pini*. We grouped both *P. cylindrica* and *P. parallelum* as "*Platysoma* spp." for analysis purposes, as these species show similar preferences for ipsdienol and lanierone in Wisconsin (K. F. Raffa, unpublished data).

Statistical Analyses. An analysis of variance was performed with PROC MIXED (SAS Institute, 1996) on each species of insect caught. The experiment was conducted as a split plot and analyzed as a mixed model. Replication, line, and the interaction were used as blocking factors in the whole plot, with treatment, sample period, and the interaction in the subplot. Line, line \times treatment, and the interaction across the two replications were considered random effects. Least-squared means were used to adjust for all terms in the model. Raw means are used for data presentation. Standard errors were derived from averaging the insect collections over the four-day sample intervals, which were considered subsamples.

Only insects that demonstrated significant treatment effects over either the entire year or for a season at $P < 0.05$ were included in the analysis. Least-squared means were separated by pairwise *t* tests when significant treatment effects occurred ($P < 0.05$) (Carmer and Swanson, 1973). For means comparisons, all data were transformed by square root (y) to reduce heteroscedascity. Scedascity was judged by examination of residual plots. Four values of negative

data, incurred when generating selection curves, were changed to zero so square root transformations could be performed. This modification did not change the analysis significantly.

To investigate the relationship between the number of insects caught and the release rates of lanierone, we performed linear contrasts. A significant contrast on the data transformed by square root (y) indicated a linear correlation. A linear contrast was also performed on data that were transformed \log (release rate + 1) and \log (insect catch + 1), which also reduced heteroscedascity. This $\log(x)$ vs. $\log(y)$ transformation often transforms nonlinear, inverse exponential data of the function $y = \alpha x^\beta$ (for $0 < \beta < 1$) to a linear form $y' = \log \alpha + \beta x'$ (Daniel and Wood, 1980; Chatterjee and Price, 1991). A significant linear contrast on such a transformed data set can be used to infer that the proper x - y relationship is nonlinear and asymptotic according to the inverse exponential function. Other contrasts were performed on this data set to determine the proportion of variation in the treatment effect (excluding control) explained by the "linear" model, all other polynomial models, and the treatments relative to the control trap. When appropriate, Microsoft (1997) Excel was used to calculate a line of best fit for the inverse exponential model $y = c * \log(x) + b$. Raw averages of insects caught at each pheromone release rate other than the control were used for these calculations.

RESULTS

Nineteen species of insects were captured; all were coleopterans except for the parasitoid *T. tibialis* (Table 1). Most *I. pini* (81.0%) were trapped in the summer. In contrast, most predators (64.0%) were captured in the spring. The other predator species caught in sufficient numbers to study pheromone preferences were *T. dubius*, *Platysoma*, and *E. nigrifrons*. *E. nigrifrons* was much more abundant in the summer than in the spring.

Sources of variation in trap catch of each species are shown in Table 2. Insect behaviors were analyzed on a seasonal basis because significantly more *I. pini* were caught in the summer than in the spring, a significant season \times treatment interaction existed, and each predator species demonstrated statistically significant seasonal and pheromonal preferences at the time during which it was most abundant. Based on the seasonal numbers and pheromone responses, complexes of spring and summer predators were constructed. Predators of *I. pini* that are abundant in the spring included *T. dubius* and *Platysoma*. Predators that are abundant in the summer included *T. dubius* and *E. nigrifrons*.

The number of *I. pini* caught in traps baited with ipsdienol increased as the amount of lanierone present increased (Figure 1). There was a strong treatment effect both relative to the controls and among the four ipsdienol treatments con-

TABLE 1. TOTAL NUMBER OF INSECTS CAUGHT IN 1998 IN WISCONSIN IN BEHAVIORAL CHOICE ASSAY^a

Insect	Family	Spring (N = 90)	Summer (N = 85)	Total (N = 175)
Herbivores (92.9%)				
<i>Ips pini</i> (Say)	Scolytidae	1469	6263	7732
<i>Dendroctonus valens</i> LeConte	Scolytidae	2	4	6
<i>Hylastes</i> spp.	Scolytidae	1	0	1
Metallic wood borers	Buprestidae	3	0	3
Long-horned beetles ^b	Cerambycidae	24	5	29
Total herbivores		1499	6272	7771
Predators (6.8%)				
<i>Thanasimus dubius</i> (F.)	Cleridae	169	55	224
<i>Enoclerus muttkowski</i> Wolcott	Cleridae	0	1	1
<i>Enoclerus nigrifrons</i> (Say)	Cleridae	5	69	74
<i>Enoclerus nigripes</i> Say	Cleridae	17	3	20
<i>Enoclerus spegheus</i> (F.)	Cleridae	22	10	32
<i>Phlogistosternus dislocatus</i> (Say) ^c	Cleridae	0	24	24
<i>Zenodosus sanguineus</i> (Say)	Cleridae	6	1	7
<i>Platysoma cylindrica</i> (Paykull)	Histeridae	63	5	68
<i>Platysoma parallelum</i> (Say)	Histeridae	30	1	31
<i>Corticus parallelus</i> (Melsheimer)	Tenebrionidae	5	1	6
<i>Grynocharis quadrilineata</i> (Melsheimer)	Trogositidae	5	0	5
<i>Tenebroides</i> spp. ^d	Trogositidae	34	11	45
<i>Plochionus pallens</i> F.	Carabidae	5	5	10
Flat bark beetles	Cucujidae	4	20	24
Total predators:		365	271	571
Parasitoid (0.3%)				
<i>Tomicobia tibialis</i> Ashmead	Pteromalidae	14	8	22
Total insects		1878	6486	8364

^aN represents the number of collections from traps baited with ipsdienol and varying amounts of lanierone in a red pine plantation.

^bPrimarily *Monochamus carolinensis* Olivier and *Monochamus titillator* (F.).

^cNatural history undetermined. Likely a predator.

^d*Tenebroides* nr. *collaris* Sturm and other.

taining variable emission rates of lanierone (Table 2). *I. pini* did not respond in significant numbers to the blank control trap. The catch of *I. pini* increased in a statistically significant linear fashion with increasing quantity of lanierone, as evidenced by linear contrast values of $P < 0.012$ in the spring and $P < 0.015$ in the summer, based on \sqrt{y} -transformed data. However, the data in Figure 1, and the fact that pharmacological and toxicological relationships are rarely linear (Hayes, 1982; Tallarida et al., 1988; Hothorn, 1990) suggest that there may also be a nonlinear component. Therefore, we considered several other models, the results of which are shown in Table 3. Significant linear contrast based on log

TABLE 2. SEASON, TREATMENT, AND SEASON × TREATMENT INTERACTIONS WITH *I. pini* AND ASSOCIATES CAUGHT IN RESPONSE TO RACEMIC IPSIDIENOL AND LANIERONE, BY YEAR AND SEASON^a

Term	<i>I. pini</i>	<i>T. dubius</i>	<i>E. nigrifrons</i>	<i>Platysoma</i>	Total predators	
					Spring ^b	Summer ^c
Full year						
Season (spring to summer)						
<i>df</i>	1, 2	1, 2	1, 2	1, 2	1, 2	1, 2
<i>F</i>	55.73	3.31	13.49	11.74	6.81	0.18
<i>P</i>	0.0175	0.2104	0.0668	0.0756	0.1208	0.7150
Treatment						
<i>df</i>	4, 16	4, 16	4, 16	4, 16	4, 16	4, 16
<i>F</i>	144.64	11.35	5.52	6.04	20.04	17.45
<i>P</i>	0.0001	0.0001	0.0055	0.0037	0.0001	0.0001
Season × treatment						
<i>df</i>	4, 16	4, 16	4, 16	4, 16	4, 16	4, 16
<i>F</i>	22.24	1.93	3.87	3.88	3.75	0.83
<i>P</i>	0.0001	0.1551	0.0220	0.0218	0.0246	0.5262
Spring						
Treatment						
<i>df</i>	4, 8	4, 8	4, 8	4, 8	4, 8	n/a
<i>F</i>	41.21	7.58	0.52	6.25	16.55	n/a
<i>P</i>	0.0001	0.0079	0.7261	0.0139	0.0006	n/a
Summer						
Treatment						
<i>df</i>	4, 8	4, 8	4, 8	4, 8	n/a	4, 8
<i>F</i>	103.47	3.07	5.08	0.55	n/a	7.20
<i>P</i>	0.0001	0.0826	0.0247	0.7068	n/a	0.0092

^aTreatment effect includes the blank control trap in the analysis.

^bSpring predators include *T. dubius* and *Platysoma*.

^cSummer predators include *T. dubius* and *E. nigrifrons*.

($x + 1$) vs. $\log(y + 1)$ transformation shows that the variation among pheromone lures is nonlinear and can be approximated by an inverse exponential function (Chatterjee and Price, 1991). Figure 1 illustrates a simple line of best fit with Microsoft Excel (1997).

The trap catches of the major predators are shown in Figures 2 and 3 for spring and summer, respectively. The most abundant predators, *T. dubius*, *E. nigrifrons*, and *Platysoma*, also preferred pheromone lures, relative to the blank control traps (Table 2). However, there were no significant response differences among the varying release rates of lanierone from 10 to 100 $\mu\text{g}/\text{day}$ for any of the predators, individually or when grouped by spring and summer seasons

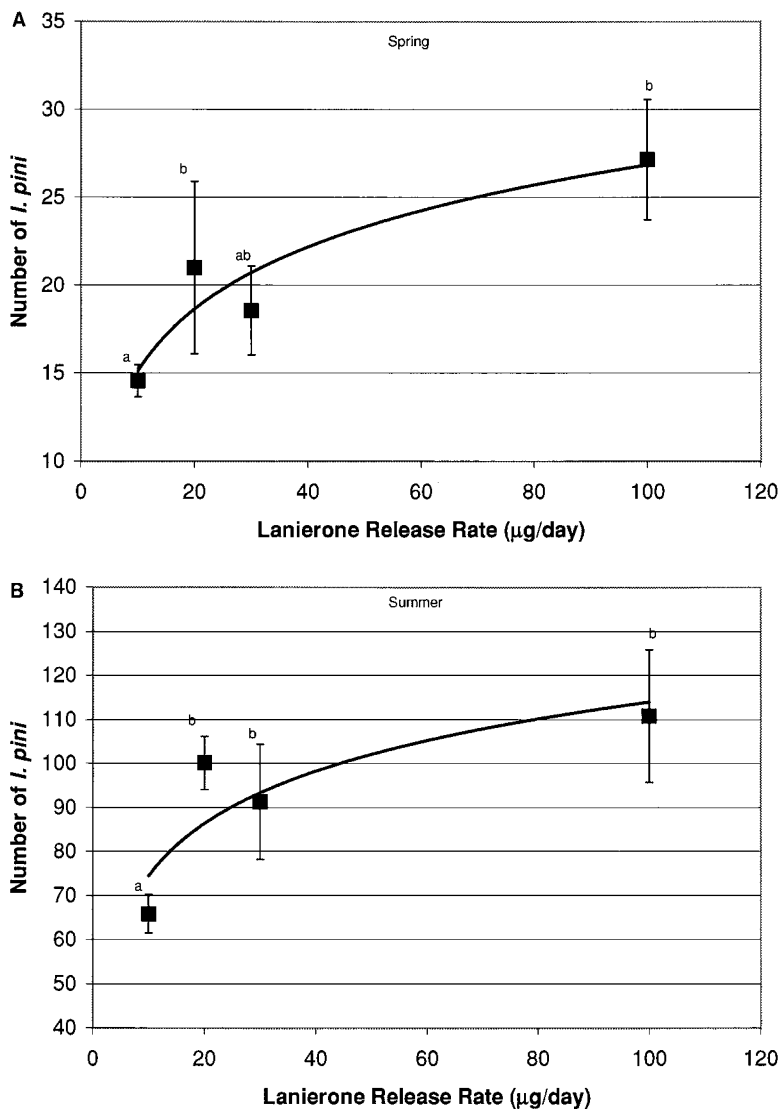


FIG. 1. Number of *I. pini* responding to combinations of racemic ipsdienol with varying release rates of lanierone per 4-day sample period in field trials in red pine plantation in Wisconsin, USA, 1998. The blank control trap attracted no insects and is not graphed. Different letters indicate different responses at $P < 0.05$. (A) Spring; line of best fit: $y = 5.110\text{Ln}(x) + 3.322$. (B) Summer; line of best fit: $y = 17.201\text{Ln}(x) + 34.803$.

TABLE 3. MODELS THAT EXPLAIN SOURCES OF VARIATION IN DATA FOR TESTS OF ATTRACTION OF *I. pini* AND ASSOCIATE PREDATORS TO IPSDIENOL AND LANIERONE LURES IN RED PINE PLANTATION IN WISCONSIN, USA, 1998^a

	Sqrt (y) vs. x			Log (x + 1) vs. log (y + 1)								
	Linear ^b			Linear ^c			Other models ^d			Control vs. lures ^e		
	df	F	P	df	F	P	df	F	P	df	F	P
Spring												
<i>I. pini</i>	1	10.30	0.0124	1	8.77	0.0181	2	1.46	0.2870	1	233.54	<0.0001
<i>T. dubius</i>	1	2.49	0.1531	1	1.70	0.2285	2	1.18	0.3542	1	26.57	0.0009
<i>Platysoma</i> spp.	1	0.02	0.8827	1	0.01	0.9167	2	1.52	0.2747	1	20.70	0.0019
<i>T. dubius</i> and <i>Platysoma</i> spp.	1	1.85	0.2104	1	1.32	0.2840	2	1.67	0.2477	1	65.22	<0.0001
Selectivity curve ^f	1	12.87	0.0071	1	15.58	0.0043	2	1.48	0.2849	1	165.83	<0.0001
Summer												
<i>I. pini</i>	1	9.53	0.0150	1	12.13	0.0083	2	3.18	0.0961	1	1,376.70	<0.0001
<i>E. nigrifrons</i>	1	0.01	0.9218	1	0.00	0.9996	2	0.50	0.6215	1	17.91	0.0029
<i>T. dubius</i> and <i>E. nigrifrons</i>	1	0.02	0.8921	1	0.01	0.9296	2	0.05	0.9515	1	26.61	0.0009
Selectivity curve ^g	1	9.75	0.0142	1	12.32	0.0080	2	3.39	0.0861	1	1,352.75	<0.0001

^aSources of variation are listed for spring and summer experiments for two transformations of the data set. For log (x + 1) vs. log (y + 1) transformation, total variation in the treatment effects (significant at $P < 0.05$) is separated into different models. All tests use 8 df in the denominator, and only the release rates of lanierone at 10, 20, 30, and 100 μg are tested except in the contrast which tests the control trap (0 μg lanierone).

^bLinear contrast with this transformed data set tests positive linear correlation between insect catch and release rate.

^cSignificant linear contrast with this transformed data set indicates trend is non-linear and asymptotic according to an inverse exponential function (Chatterjee and Price, 1991).

^dVariation explained by pooled quadratic and cubic models.

^eContrast of insect catches of blank control trap versus traps containing pheromone lures.

^fSelectivity curve reflects the number of *Ips pini* captured minus the number of spring predators.

^gSelectivity curve reflects the number of *Ips pini* captured minus the number of summer predators.

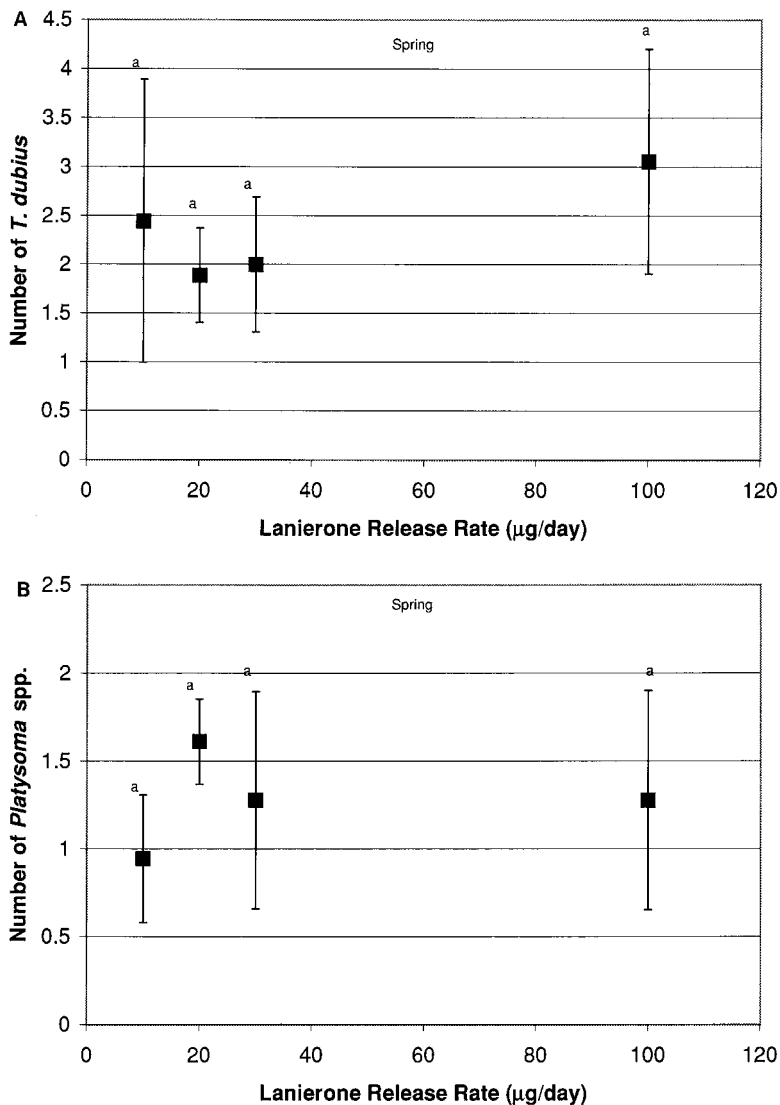


FIG. 2. Most abundant predators in spring trial responding to racemic ipsdienol with varying release rates of lanierone per 4-day sample period in field trials in red pine plantation in Wisconsin, USA, 1998. The blank control trap attracted no insects and is not graphed. Different letters indicate different responses at $P < 0.05$. (A) *T. dubius*; (B) *Platysoma* spp., (C) combined *T. dubius* and *Platysoma* spp.

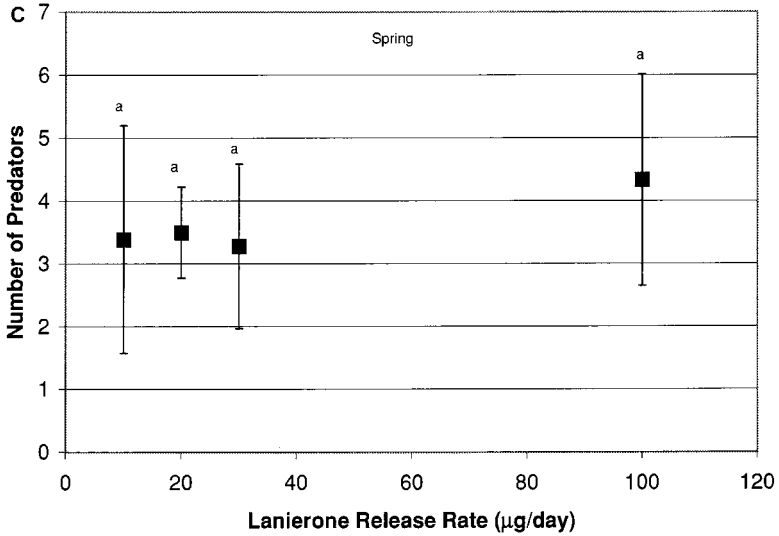


FIG. 2. Continued.

(Table 3). The variation in numbers of predatory insects caught could not be explained by either a linear or inverse exponential model, so no lines of best fit are shown in Figures 2 or 3. There is no relationship between the amount of lanierone released with ipsdienol and the total number of predators captured.

By graphing the differences in numbers between the average numbers of *I. pini* and seasonally abundant predators, we constructed selectivity curves for spring and summer across the different release rates of lanierone when combined with ipsdienol (Figure 4). Similar to the number of *I. pini* caught, the selectivity curve appears nonlinear and can be described by an inverse exponential function (Table 3). The line of best fit (generated by Microsoft Excel software) shows that more *I. pini* can be removed in the spring than in the summer by these lure combinations (Figure 4).

DISCUSSION

Increasing concentrations of lanierone generate increasing attraction by *I. pini* to racemic ipsdienol in Wisconsin. In contrast, response of local predators to ipsdienol is not enhanced by any concentration of lanierone. Thus, production of lanierone by *I. pini* improves intraspecific communication without increasing attraction and exposure to natural enemies. Although the ability of *I. pini* to exploit the subcortical tissues of stressed trees can be restricted by natural

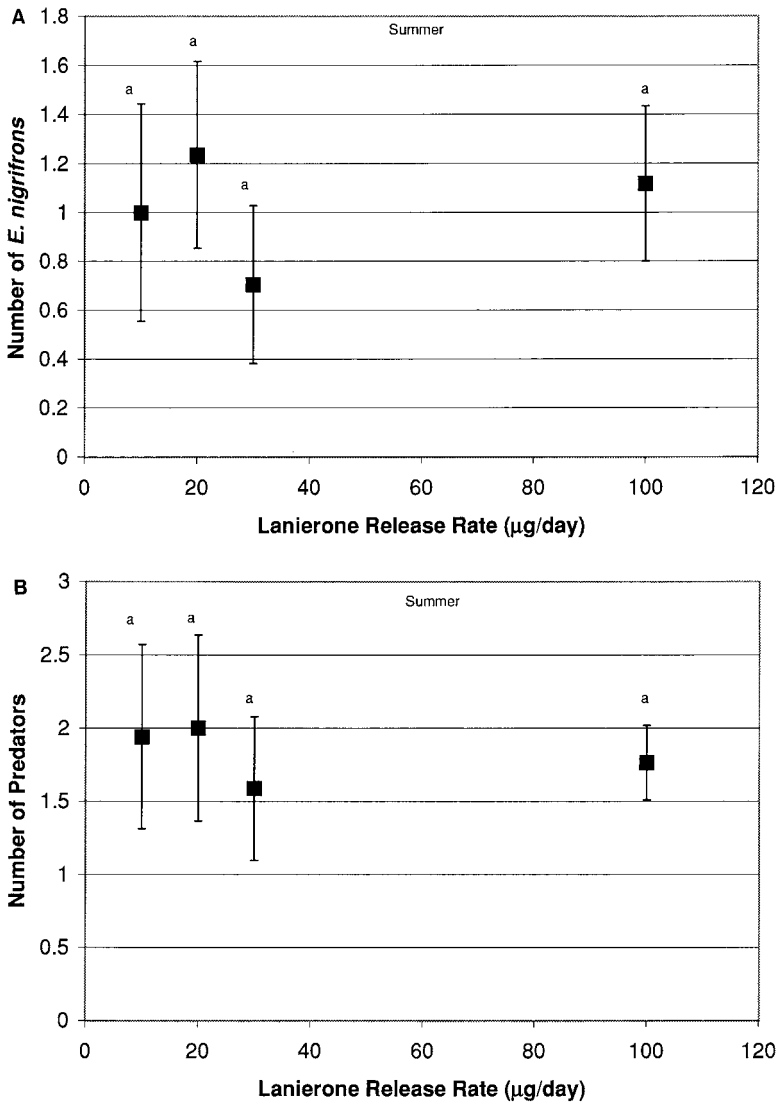


FIG. 3. Most abundant predators in summer trial responding to racemic ipspdienol with varying release rates of lanierone per 4-day sample period in field trials in red pine plantation in Wisconsin, USA, 1998. The blank control trap attracted no insects and is not graphed. Different letters indicate different responses at $P < 0.05$. (A) *E. nigrifrons*; (B) combined *T. dubius* and *E. nigrifrons*.

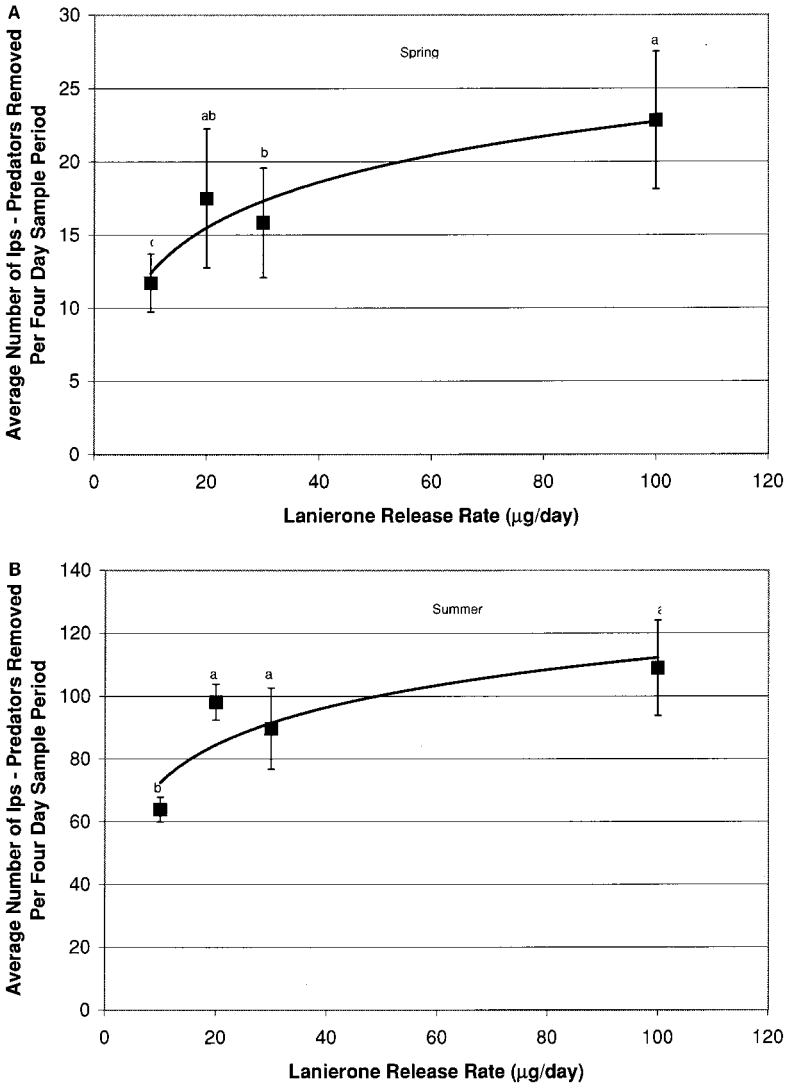


FIG. 4. Selectivity curves showing average number of *I. pini* minus predators caught at varying release rates of lanierone in combination with racemic ipsdienol per four day sample period in field trials in red pine in Wisconsin, USA, 1998. The blank control trap attracted no insects and is not graphed. Different letters indicate different responses at $P < 0.05$. (A) Spring (predators: *T. dubius* and *Platysoma* spp.); line of best fit: $y = 4.5062\text{Ln}(x) + 1.9836$. (B) Summer (predators: *T. dubius* and *E. nigrifrons*); line of best fit: $y = 17.298\text{Ln}(x) + 32.657$.

enemies, this restriction can be alleviated by variation in its pheromone signals. Our results suggest that the ecological factors that contribute to an herbivore's "enemy-free space" (Denno et al., 1990), such as location, time, and host plant volatiles, may include a pheromonal dimension as well.

These differences in communication between bark beetles and predators may be used to improve pest management. Selectivity curves that quantify the differences between the number of herbivores and predators responding to a pheromone can indicate the optimal dose at which the benefits of semiochemically based trap-out can be maximized. Inadvertent attraction and removal of predators is a serious problem that reduces utility of semiochemically based pest management programs (DeMars et al., 1986). More *I. pini* can be removed in the summer than spring, which is consistent with other work in red pine plantations in Wisconsin (Aukema et al., 2000a,b). The maximum difference between numbers of *I. pini* and predators captured with ipsdienol is achieved at a release rate of 20 $\mu\text{g}/\text{day}$ lanierone. Above this amount of lanierone, net removal is not improved substantially.

Approximately 20 $\mu\text{g}/\text{day}$ of lanierone can achieve maximum separation between *I. pini* and its predators responding to racemic ipsdienol. This is ecologically significant because it approximates emission from a naturally colonized tree. Schenk and Benjamin (1969) reported colonization densities of *I. pini* in jack pine (*Pinus banksiana* Lamb) with an average diameter of 12.7 cm that correspond to approximately 444 males/6-m section. Likewise, Robins and Reid (1997) reported natural colonization densities of *I. pini* to be 4.5–9.0 females/100 cm^2 in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) with diameters of approximately 13.3 cm. Taking the mid-range and assuming 3 females/male, then the average *P. resinosa* in our study with a utilizable trunk of 6 m \times 15 cm average diameter would yield 636 attacking males. Because each male produces approximately 33.5 ng lanierone/day (Teale et al., 1991), each tree would emit 14.9–21.3 $\mu\text{g}/\text{day}$, assuming attack density and pheromone production does not differ significantly between the common hosts. This corresponds to the emission rates at which selectivity between *I. pini* and its predators approaches the maximum.

The occurrence of this disparity between herbivore and predator responses to prey signals at ecologically relevant concentrations supports the view that they reflect coevolutionary interactions. Such disparity may be especially important to *I. pini* because its major predators are highly efficient at tracking semiochemical differences associated with the colonization of various host trees (Erbilgin and Raffa, 2000). Coevolutionary change requires both a close association between the prey and predator and a strong genetic component to traits affecting their success (Janzen, 1980). *T. dubius* arrives synchronously with bark beetles at attacked trees (Dixon and Payne, 1979). *Ips pini* is known to demonstrate pheromone-based assortative mating (Teale et al., 1994), but the genetics of its communi-

cation system remain largely unknown. Further investigation on the heritability of the predators' preferences for various prey, their numerical impacts, and the degree of plasticity in prey searching is needed to help elucidate this interaction (Kudon and Berisford, 1980; Mizell et al., 1984).

Acknowledgments—This study was supported by National Science Foundation grants DEB 9408264 and DEB 9629776, US Department of Agriculture USDA NRI AMD 96 04317, S. C. Johnson and Sons Foundation, the Wisconsin Department of Natural Resources, and the University of Wisconsin-Madison, College of Agricultural and Life Sciences. Dr. M. K. Clayton, Department of Statistics, UW-Madison, provided statistical advice. Mr. S. Krauth, Insect Research Collection, Department of Entomology, UW-Madison, and Mr. K. Katovich, Department of Entomology, UW-Madison, aided in insect identification. Field assistance by Mr. J. Gruber, Department of Entomology, UW-Madison is greatly appreciated. We thank Mr. P. Pingrey, Private Forestry Specialist, Wisconsin Department of Natural Resources, for providing the study site. We thank Pherotech Inc., Delta, British Columbia, for donating the funnel traps. We thank D. Mahr and D. Hogg, UW-Madison, and two anonymous reviewers for their critical reviews of this manuscript.

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