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GEOGRAPHIC VARIATION IN RESPONSE OF PINE ENGRAVER, *Ips pini*, AND ASSOCIATED SPECIES TO PHEROMONE, LANIERONE

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Abstract—Lanierone strongly synergized the attraction of male and female *Ips pini* (Say) to ipsdienol in New York and Wisconsin. Synergy was only weakly significant in Montana and British Columbia and not significant in California. Catches of *I. pini* in ipsdienol-baited traps were increased 0% (i.e., nonsignificant) to 9942% by lanierone, with the highest increases in eastern North America. Lanierone had the least effect in California. The effects of lanierone on sex ratios of *I. pini* in trap catches varied significantly between regions. The addition of lanierone to ipsdienol-baited traps resulted in a general increase in male representation at nine of 12 sites. *Ips integer* (Eichhoff) was attracted to lanierone alone. Ipsdienol reduced the response of *I. integer*

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to lanierone. *Enoclerus lecontei* (Wolcott) (Cleridae) preferred traps baited with the combination of ipsdienol and lanierone. (*R*)-(−)-Ipsdienol was attractive to *E. sphegeus* (F.), *Thanasimus undatulus* (Say) (Cleridae), and *Temnochila chlorodia* (Mannerheim) (Trogositidae), while racemic ipsdienol was attractive to *E. nigrifrons* var. *gerhardi* Wolc. and *Thanasimus dubius* (F.). Lanierone had no effect on these species.

Key Words—*Ips pini*, *Ips integer*, Coleoptera, Scolytidae, aggregation pheromone, lanierone, ipsdienol, geographic variation, synergism, *Enoclerus lecontei*, Cleridae, kairomone.

INTRODUCTION

The pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), uses the enantiomers of ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) as aggregation pheromones (Stewart, 1975; Birch et al., 1980; Lanier et al., 1980). In New York, males produce both (*R*)-(−)- and (*S*)-(+)-ipsdienol, and both sexes prefer blends with roughly equal ratios of (*R*)-(−)- and (*S*)-(+)-ipsdienol over blends enriched with either enantiomer (Lanier et al., 1980; Teale, 1990; Teale and Lanier, 1991). Males in California produce primarily (*R*)-(−)-ipsdienol (Stewart, 1975; Birch et al., 1980; Miller et al., 1989a; Seybold, 1992; Seybold et al., 1995). Californian beetles are attracted to (*R*)-(−)-ipsdienol (Birch et al., 1980; Seybold, 1992). Attraction to (*R*)-(−)-ipsdienol is interrupted by (*S*)-(+)-ipsdienol. In southeastern British Columbia, males produce primarily (*R*)-(−)-ipsdienol as in California (Miller et al., 1989a, 1996; Seybold et al., 1995), but both sexes are attracted to a broader range of enantiomeric mixtures [98:2 to 20:80 (*R*)-(−):(*S*)-(+), inclusively] (Miller et al., 1996) than Californian beetles (Birch et al., 1980; Seybold, 1992). In contrast to most other western populations, males in southwestern British Columbia produce ipsdienol with a mean enantiomeric composition of 34:66 (*R*)-(−):(*S*)-(+) (Miller et al., 1989a, 1996) and a pooled composition of 39:61 (*R*)-(−):(*S*)-(+) (Seybold et al., 1995). In this area, both sexes are attracted to intermediate enantiomeric mixtures [70:30 to 20:80 (*R*)-(−):(*S*)-(+), inclusively] (Miller, 1990; Miller et al., 1996). Beetles in Wisconsin prefer an enantiomeric mixture of 25:75 (*R*)-(−):(*S*)-(+) (Raffa and Klepzig, 1989).

Lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) has been identified as a third male-produced aggregation pheromone for *I. pini* in New York (Teale et al., 1991). Attraction of both sexes to racemic ipsdienol is synergized by lanierone. However, the role of lanierone may not be the same throughout the broad transcontinental range of *I. pini* (Teale et al., 1991; Seybold et al., 1992).

The high degree of geographic variation in the use of ipsdienol enantiomers as pheromones by *I. pini* suggests that similar variation may also exist for lanierone. Lanierone was not detected in Porapak extracts from California (Seybold et al., 1992). Similarly, the effect of lanierone on the attraction of *I. pini* to ipsdienol is weaker in California than in New York (Seybold et al., 1992). Therefore we hypothesized that lanierone would not have the same effect on the response of *I. pini* to region-specific enantiomeric mixtures of ipsdienol throughout North America.

METHODS AND MATERIALS

Chemicals and Release Devices. Phero Tech Inc. (Delta, British Columbia) supplied the following types of polyvinyl, bubble-cap lures: (1) 1,3-butanediol (chemical purity, >98%); (2) racemic ipsdienol (chemical purity, 98%) in solution with 1,3-butanediol; (3) (*R*)-(−)-ipsdienol (chemical purity, 98%; optical purity, >97%) in solution with 1,3-butanediol; and (4) lanierone (chemical purity, 95%) in solution with 1,3-butanediol. The release rates of 1,3-butanediol, ipsdienol [racemic and (*R*)-(−)], and lanierone were approximately 2, 0.2, and 0.02 mg/day, respectively, at 24°C (determined by collection of volatiles on Porapak-Q). 1,3-Butanediol is not attractive to *I. pini* alone or in combination with ipsdienol (Miller, 1990).

Experimental Design. The same experiment was conducted at two sites in each of the following regions: (1) Syracuse, New York; (2) Madison, Wisconsin; (3) Missoula, Montana; (4) Kimberley, British Columbia; (5) Penticton, British Columbia; and (6) Hat Creek, California. At each site, 20 multiple-funnel traps (Lindgren, 1983) (Phero Tech Inc.) were set in five parallel lines of four traps per line. Each line of four traps constituted a replicate. Eight-unit funnel traps were used in California and New York, while 12-unit funnel traps were used in the remaining regions. Each trap was suspended by rope such that the bottom funnel of each trap was 0.5–1.0 m above ground level. No trap was within 1 m of any tree. Traps were set in the following types of stands: (1) lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, in British Columbia; (2) ponderosa pine, *P. ponderosa* Lawson, in Montana; (3) ponderosa and Jeffrey pines, *P. jeffreyi* Greville and Balfour, in California; and (4) red pine, *P. resinosa* Aiton, in New York and Wisconsin. Sites were at least 1 km apart while traps were spaced 10–15 m apart within sites.

The following treatments were randomly assigned within each replicate: (1) 1,3-butanediol control; (2) ipsdienol with 1,3-butanediol; (3) lanierone with 1,3-butanediol; and (4) ipsdienol and lanierone with 1,3-butanediol. (*R*)-(−)-Ipsdienol was used in California and southeastern British Columbia. Racemic ipsdienol was used in the remaining regions. For most regions, the choice of enantiomeric compositions for ipsdienol was based upon regional specificities in production and response by *I. pini* (Birch et al., 1980; Lanier et al., 1980;

Miller et al., 1989a, 1996; Raffa and Klepzig, 1989; Teale, 1990; Herms et al., 1991; Teale and Lanier, 1991; Seybold, 1992; Seybold et al., 1995). No previous studies had been conducted in Montana. We chose racemic ipsdienol, reasoning that populations in Montana would likely be similar to eastern populations.

The experiments were conducted in 1991 during the following periods: (1) July 18-31 in New York; (2) July 19-August 16 in Wisconsin; (3) July 12-29 in Montana; (4) June 27-July 11 in southeastern British Columbia; (5) July 3-August 17 in southwestern British Columbia; and (6) July 23-30 in California. Sexes of captured *I. pini* were determined, using declivital characters (Lanier and Cameron, 1969), for all beetles in small catches and for subsamples ($N = 30$-50) in large catches. Responses of associated beetle species were also recorded.

Statistics. Data were analyzed using the Systat statistical package ver. 5.02 (Systat, Inc., Evanston, Illinois). Trap catch data were transformed by $\ln(Y + 1)$ to remove heteroscedasticity and subjected to analysis of variance (ANOVA) using the following model factors: (1) replicate nested within site, (2) site, (3) ipsdienol, (4) lanierone, (5) site * ipsdienol, (6) site * lanierone, (7) ipsdienol * lanierone, and (8) site * ipsdienol * lanierone. For both male and female *I. pini*, differences in mean catches were determined using Tukey's HSD multiple-comparison test at $P = 0.05$ (experiment-wise). Proportional increases were calculated for each replicate by dividing the difference in catches between the two treatments by the catch in the trap baited with ipsdienol alone.

Synergism between lanierone and ipsdienol was indicated by satisfying three statistical conditions. First, synergism required a significant interaction between these two factors in the ANOVA, indicating that the proportional increases (not absolute increases) due to both factors were not additive. Secondly, one factor (lanierone) had to be benign while the second factor (ipsdienol) had to be active. Multiple comparison tests such as Tukey's HSD can affirm that one factor is benign and does not differ from the control and that a second factor is attractive relative to the control. Lastly, the combination of lanierone and ipsdienol had to result in significantly higher catches than ipsdienol alone.

Sex ratio data for *I. pini* captured in ipsdienol-baited traps were normalized by arcsine (Y), and analyzed by ANOVA using the following model factors: (1) replicate nested within site, (2) site, (3) lanierone, and (4) site * lanierone. Mean proportions of males in traps baited with ipsdienol were compared to those in traps with ipsdienol and lanierone using a two-sided t test. Differences in sex ratios among regions and among mean catches of other species were determined using Tukey's HSD multiple comparison test at $P = 0.05$ (experiment-wise).

RESULTS

Ips *Species.* In all regions, lanierone and ipsdienol had significant effects on trap catches of both sexes (all $P \leq 0.035$) (Table 1). The interaction between ipsdienol and lanierone had a significant effect on males in all regions except southeastern British Columbia. The interaction had no significant effect on females in California and southeastern British Columbia.

The effects of lanierone varied between regions (Figure 1), with the most pronounced effect apparent in New York and Wisconsin. In general, the preferred treatment for both sexes was the combination of ipsdienol and lanierone (Tables 2 and 3), with synergism apparent in most regions. Lanierone was not attractive in Montana, southwestern British Columbia, Wisconsin, and New York. However, when added to ipsdienol, lanierone increased trap catches 260–9942%. Lanierone did not increase catches of females in California. At one site in California, the addition of lanierone to ipsdienol resulted in a modest increase in trap catch of males.

Traps baited with lanierone alone did not generally catch more *I. pini* than control traps (Tables 2 and 3). The exception was in southeastern British Columbia where significantly more males and females were captured in traps baited with lanierone alone than in control traps. The mean proportional increases ranged from 107% to 878%.

Lanierone, or the interaction between lanierone and site, had significant effects on the sex ratio of *I. pini* caught in ipsdienol-baited multiple-funnel traps in five of the six regions (Table 4). In California, southeastern British Columbia and New York, the mean proportion of males was greater in catches to traps baited with lanierone and epsdienol than in those to traps baited with ipsdienol alone (Table 5). The effect was weakly significant at site A in southwestern British Columbia and site B in Wisconsin.

Sex ratios varied between regions for catches to traps baited with either ipsdienol alone or ipsdienol and lanierone (Table 5). In nine of 12 sites, the sex ratio in catches to traps baited with ipsdienol alone was generally female-biased (mean proportions of males ranging from 0.19 to 0.40). In Montana, the sex ratio was male-biased (mean proportions of males were 0.63 and 0.71 for sites A and B, respectively). The sex ratios in catches of traps baited with ipsdienol and lanierone were generally close to 1 : 1. The exceptions were in Montana (male-biased) and southwestern British Columbia (female-biased).

Lanierone was attractive to *I. integer* (Eichhoff) in Montana (Figure 2). Significantly more beetles were caught in traps baited with lanierone alone than in those baited with any other treatment. The response to lanierone was strongly inhibited by racemic ipsdienol (ANOVA, $P < 0.001$, $df = 1{,}24$). The mean catches to traps baited with ipsdienol and lanierone were not significantly dif-

TABLE 1. SIGNIFICANCE LEVELS FOR ANALYSES OF VARIANCE (ANOVAs) ON TRAP CATCHES OF MALE AND FEMALE *Ips pini* IN MULTIPLE-FUNNEL TRAPS BAITED WITH IPSDIENOL AND/OR LANIERONE

Region	Sex	Site (S)	Ipsdienol (Id)[a]	Lanierone (L)	S * Id[a]	S * L	L * Id[a]	S * L * Id[a]
California	Female	0.000	0.000	0.035	0.013	0.497	0.795	0.084
	Male	0.000	0.000	0.016	0.002	0.235	0.002	0.708
British Columbia (SW)	Female	0.371	0.000	0.000	0.170	0.165	0.001	0.863
	Male	0.134	0.000	0.000	0.625	0.584	0.000	0.120
British Columbia (SE)	Female	0.335	0.000	0.000	0.447	0.726	0.603	0.188
	Male	0.309	0.000	0.000	0.526	0.513	0.327	0.102
Montana	Female	0.252	0.000	0.002	0.045	0.376	0.001	0.081
	Male	0.005	0.000	0.000	0.225	0.474	0.000	0.370
Wisconsin	Female	0.915	0.000	0.000	0.082	0.734	0.000	0.033
	Male	0.052	0.000	0.000	0.318	0.004	0.000	0.042
New York	Female	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Male	0.000	0.000	0.000	0.000	0.000	0.000	0.000

[a] (*R*)-(−)-Ipsdienol in California and southeastern British Columbia, and racemic ipsdienol in remaining regions.

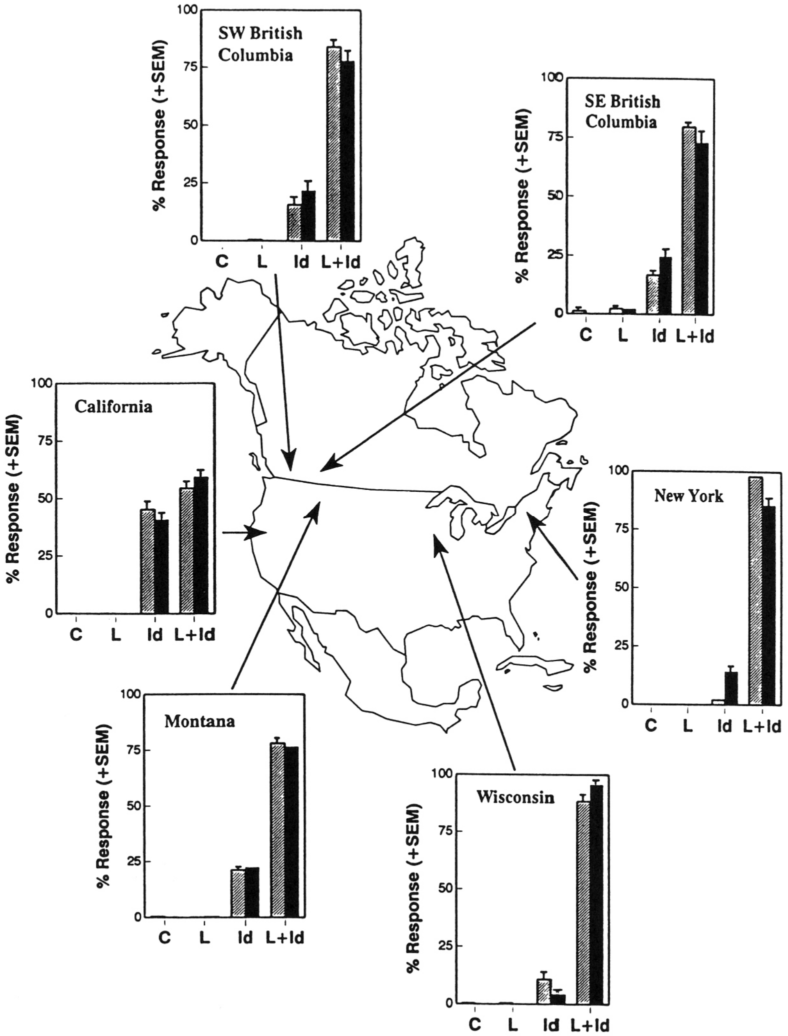

FIG. 1. Geographic variation in the response of *Ips pini* to multiple-funnel traps baited with lanierone (L) and/or ipsdienol (Id), relative to control traps (C). (*R*)-(−)-Ipsdienol was used in southeastern British Columbia and California. Racemic ipsdienol was used in the remaining regions. Data are presented as mean percentages of replicate catches for site A (striped bar) and site B (solid bar) in each region ($N = 5$).

TABLE 2. CATCHES OF MALE *Ips pini* IN MULTIPLE-FUNNEL TRAPS BAITED WITH IPSDIENOL AND/OR LANIERONE AT TWO SITES IN EACH OF SIX REGIONS IN NORTH AMERICA ($N = 5$)

	Mean (±SEM) number of male beetles[a]				
Region and site	Control	Lanierone	Ipsdienol[b]	Lanierone + Ipsdienol[b]	Increase (%)[c]
California					
A	0.4 ± 0.3 a	0.2 ± 0.2 a	129.9 ± 9.1 b	179.4 ± 5.6 b	
B	0.0 ± 0.0 a	0.0 ± 0.0 a	52.0 ± 19.8 b	94.2 ± 7.9 c	81
British Columbia (SW)					
A	0.0 ± 0.0 a	0.0 ± 0.0 a	10.9 ± 2.8 b	85.1 ± 23.1 c	681
B	0.0 ± 0.0 a	0.4 ± 0.3 a	17.1 ± 2.5 b	75.9 ± 13.9 c	344
British Columbia (SE)					
A	5.6 ± 2.6 a	13.8 ± 4.2 a	107.3 ± 15.1 b	714.0 ± 100.9 c	565
B	1.5 ± 0.5 a	12.2 ± 1.7 b	132.8 ± 30.1 c	542.7 ± 76.3 d	309
Montana					
A	3.9 ± 2.7 a	1.4 ± 0.4 a	188.0 ± 26.8 b	689.0 ± 37.2 c	266
B	4.3 ± 1.3 a	5.6 ± 1.4 a	252.9 ± 18.0 b	909.6 ± 87.3 c	260
Wisconsin					
A	1.2 ± 0.7 a	0.5 ± 0.2 a	19.5 ± 4.7 b	169.5 ± 34.9 c	769
B	0.0 ± 0.0 a	0.4 ± 0.3 a	6.4 ± 2.6 b	228.2 ± 32.3 c	3,466
New York					
A	0.2 ± 0.2 a	0.2 ± 0.2 a	83.3 ± 12.9 b	722.4 ± 132.7 c	767
B	0.0 ± 0.0 a	0.0 ± 0.0 a	2.4 ± 0.8 b	241.0 ± 22.3 c	9,942

[a] Means followed by the same letter within a row are not significantly different at $P = 0.05$ [Tukey's HSD multiple comparison test on data transformed by $\ln(Y + 1)$].

[b] (*R*)-(−)-Ipsdienol in California and southeastern British Columbia, and racemic ipsdienol in remaining regions.

[c] Percent increase of catches in traps baited with both ipsdienol and lanierone relative to those in traps baited with ipsdienol alone.

TABLE 3. CATCHES OF FEMALE *Ips pini* IN MULTIPLE-FUNNEL TRAPS BAITED WITH IPSDIENOL AND/OR LANIERONE AT TWO SITES IN EACH OF SIX REGIONS IN NORTH AMERICA ($N = 5$)

	Mean (±SEM) number of female beetles[a]				
Region and site	Control	Lanierone	Ipsdienol[b]	Lanierone + Ipsdienol[b]	Increase (%)[c]
California					
A	0.2 ± 0.2 a	0.8 ± 0.4 a	208.1 ± 16.7 b	219.8 ± 12.1 b	
B	0.0 ± 0.0 a	0.0 ± 0.0 a	95.6 ± 10.5 b	117.0 ± 4.0 b	
British Columbia (SW)					
A	0.0 ± 0.0 a	1.4 ± 0.8 a	27.7 ± 5.2 b	144.3 ± 29.8 c	421
B	0.2 ± 0.2 a	0.6 ± 0.3 a	41.1 ± 2.7 b	159.3 ± 28.1 c	288
British Columbia (SE)					
A	11.0 ± 6.9 a	22.8 ± 5.6 a	160.9 ± 18.7 b	576.0 ± 56.4 c	258
B	2.8 ± 1.0 a	17.6 ± 4.1 b	199.6 ± 33.0 c	472.9 ± 109.8 d	137
Montana					
A	2.7 ± 1.0 a	1.2 ± 0.4 a	104.0 ± 12.3 b	385.2 ± 14.5 c	270
B	3.3 ± 0.9 a	5.4 ± 1.6 a	102.1 ± 9.3 b	314.0 ± 68.9 c	208
Wisconsin					
A	0.4 ± 0.3 a	1.5 ± 0.4 a	23.3 ± 8.5 b	190.1 ± 25.9 c	716
B	0.0 ± 0.0 a	0.4 ± 0.3 a	17.4 ± 4.3 b	329.6 ± 33.3 c	1,794
New York					
A	0.0 ± 0.0 a	0.0 ± 0.0 a	7.8 ± 1.5 b	264.2 ± 28.9 c	3,287
B	0.0 ± 0.0 a	0.0 ± 0.0 a	138.1 ± 23.2 b	817.2 ± 200.6 c	492

[a] Means followed by the same letter within a row are not significantly different at $P = 0.05$ [Tukey's HSD multiple comparison test on data transformed by $\ln(Y + 1)$].

[b] (R)-(−)-Ipsdienol in California and southeastern British Columbia, and racemic ipsdienol in remaining regions.

[c] Percent increase of catches in traps baited with both ipsdienol and lanierone relative to those in traps baited with ipsdienol alone.

TABLE 4. SIGNIFICANCE LEVELS FOR ANALYSES OF VARIANCE (ANOVAS) ON SEX RATIOS IN CATCHES OF *Ips pini* IN IPSDIENOL-BAITED MULTIPLE-FUNNEL TRAPS IN SIX REGIONS OF NORTH AMERICA

Region	Site (S)	Lanierone (L)	S * L
California	0.287	0.001	0.495
British Columbia (SW)	0.886	0.051	0.328
British Columbia (SE)	0.866	0.001	0.800
Montana	0.033	0.562	0.567
Wisconsin	0.007	0.235	0.042
New York	0.017	0.001	0.023

TABLE 5. PROPORTION OF MALE *Ips pini* IN IPSDIENOL-BAITED MULTIPLE-FUNNEL TRAPS AT TWO SITES IN EACH OF SIX REGIONS IN NORTH AMERICA ($N = 5$)

	Mean (± SEM) proportion of males[a]		*t* test[b]	
Region and site	Ipsdienol[c]	Lanierone + ipsdienol[c]	*df*	*P*
California				
A	0.38 ± 0.02 abcd	0.45 ± 0.02 abc	7.8	0.015
B	0.35 ± 0.02 abcd	0.44 ± 0.02 abc	7.9	0.007
British Columbia (SW)				
A	0.26 ± 0.04 abc	0.36 ± 0.03 ab	7.5	0.068
B	0.29 ± 0.02 abcd	0.32 ± 0.02 a	7.6	0.258
British Columbia (SE)				
A	0.40 ± 0.02 c	0.55 ± 0.02 cd	7.6	.001
B	0.38 ± 0.03 c	0.55 ± 0.04 cd	7.1	0.017
Montana				
A	0.63 ± 0.06 ef	0.64 ± 0.02 de	4.7	0.996
B	0.71 ± 0.01 f	0.75 ± 0.05 e	4.2	0.456
Wisconsin				
A	0.50 ± 0.06 cde	0.46 ± 0.04 abc	7.5	0.517
B	0.23 ± 0.08 abcd	0.41 ± 0.03 abc	5.2	0.079
New York				
A	0.19 ± 0.06 a	0.48 ± 0.02 abc	5.1	0.003
B	0.38 ± 0.02 abcd	0.48 ± 0.02 abc	7.9	0.004

[a] Means followed by the same letter within a column are not significantly different at $P = 0.05$ [Tukey's HSD multiple comparison test on data transformed by arcsine(Y)].

[b] Two-sided test comparing proportions of males in traps baited with ipsdienol alone to those in traps baited with the combination of ipsdienol and lanierone.

[c] (R)-(−)-Ipsdienol in California and southeastern British Columbia, and racemic ipsdienol in remaining regions.

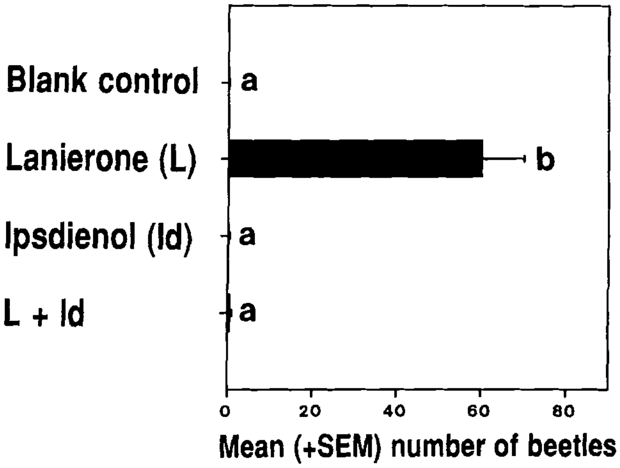

FIG. 2. Responses of *Ips integer* to multiple-funnel traps baited with lanierone and/or racemic ipsdienol in Missoula, Montana, from July 19 to 29, 1991 (N = 10). Means followed by the same letter are not significantly different at P = 0.05 [Tukey's HSD multiple comparison test on data transformed by $\ln(Y + 1)$].

ferent from the control traps (Figure 2). Racemic ipsdienol alone was not attractive. *Ips integer* were not caught at any other location.

Predators. Ipsdienol and or lanierone were attractive to six species of bark beetle predators. The preferred treatments for *Enoclerus lecontei* (Wolcott) (Cleridae) were the combination of lanierone and (*R*)-(−)-ipsdienol in California and southeastern British Columbia, and the combination of lanierone and racemic ipsdienol in Montana (Table 6). The attraction was synergistic in California (ANOVA, $P < 0.001$, $df = 1{,}24$) but not in southeastern British Columbia and Montana (ANOVA; $P = 0.616$ and $P = 0.554$, respectively; $df = 1{,}24$ and $df = 1{,}24$, respectively). (*R*)-(−)-Ipsdienol was attractive to *E. sphegeus* (F.) and *Temnochila chlorodia* (Mannerheim) (Trogositidae) in California and to *Thanasimus undatulus* (Say) (Cleridae) in southeastern British Columbia (Table 6). Similarly, *E. nigrifrons* var. *gerhardi* Wolc. and *Thanasimus dubius* (F.) in Wisconsin were attracted to racemic ipsdienol. None of these five species were affected by lanierone.

DISCUSSION

Our results are consistent with those of Teale (1990), Teale et al. (1991), and Seybold et al. (1992). Lanierone generally synergized the attraction of both male and female *I. pini* to the principal pheromones, (*R*)-(−)- and (*S*)-(+)-

TABLE 6. RESPONSES OF BANK BEETLE PREDATORS TO MULTIPLE-FUNNEL TRAPS BAITED WITH IPSDIENOL AND/OR LANIERONE

	Mean (±SEM) number of beetles[a]			
Species and region	Control	Lanierone	Ipsdienol[b]	Lanierone + ipsdienol[b]
Enoclerus lecontei				
California[c]	0.0 ± 0.0 a	0.2 ± 0.1 a	0.6 ± 0.2 a	6.3 ± 1.6 b
British Columbia (SE)[d]	0.8 ± 0.6 a	1.5 ± 0.3 ab	2.3 ± 0.4 b	6.9 ± 1.4 c
Montana[e]	8.6 ± 2.1 a	24.2 ± 4.9 b	76.2 ± 6.6 cd	156.2 ± 23.9 d
Enoclerus sphegeus				
California[c]	0.3 ± 0.2 a	0.4 ± 0.2 a	8.2 ± 1.6 b	6.3 ± 1.8 b
British Columbia (SE)[f]	2.0 ± 0.8 a	2.0 ± 1.1 a	6.2 ± 1.5 a	5.4 ± 1.8 a
Enoclerus nigrifrons				
Wisconsin[g]	0.1 ± 0.1 a	0.0 ± 0.0 a	2.8 ± 0.7 b	2.8 ± 1.4 b
Thanasimus dubius				
Wisconsin[g]	0.0 ± 0.0 a	0.0 ± 0.0 a	3.6 ± 1.7 b	3.2 ± 1.1 b
Thanasimus undatulus				
British Columbia (SE)[f]	1.6 ± 0.3 a	1.4 ± 0.4 a	6.4 ± 1.8 b	7.0 ± 1.1 b
Temnochila chlorodia				
California[c]	0.8 ± 0.5 a	1.3 ± 0.4 a	14.2 ± 0.9 b	11.4 ± 1.2 b

[a] Means followed by the same letter within a row are not significantly different at $P = 0.05$ [Tukey's HSD multiple comparison test on data transformed by $\ln(Y + 1)$].

[b] (*R*)-(−)-Ipsdienol in California and southeastern British Columbia, and racemic ipsdienol in remaining regions.

[c] Collected between July 23 and 30, 1991 ($N = 10$).

[d] Collected between June 27 and July 11, 1991 ($N = 10$).

[e] Collected between July 12 and 29, 1991 ($N = 10$).

[f] Collected between June 27 and July 11, 1991 ($N = 5$).

[g] Collected between July 19 and August 16, 1991 ($N = 10$).

ipsdienol. By itself, lanierone was not very attractive. However, there were significant regional differences in the effects of lanierone on the responses of male and female *I. pini*.

Firstly, there was geographical variation in the mean proportional increases in catches to ipsdienol-baited, multiple-funnel traps due to the presence of lanierone. Synergism was most pronounced in both of the eastern regions. The mean proportional increases ranged from 492% to 9942% in eastern North America compared to a range of 0–681% in western regions. Lanierone had the least effect in California.

Secondly, southeastern British Columbia differed from other regions with respect to the effect of lanierone alone, and the interaction between ipsdienol and lanierone. This was the only region where lanierone was significantly attractive to *I. pini* by itself. The mean proportional increases in catches between control traps and those baited with lanierone alone ranged from 107% to 713%. Further, southeastern British Columbia was the only region where the interaction between ipsdienol and lanierone was not significant ($P = 0.603$ and $P = 0.327$ for females and males, respectively). The lack of statistical significances associated with the interaction terms for males and females indicate that the proportional increases in trap catches due to the presence of lanierone was the same with and without ipsdienol. This was not true of most of the other sites, which clearly demonstrated synergism between ipsdienol and lanierone in the attraction of *I. pini*.

Lastly, the differences in sex ratios in catches to traps baited with ipsdienol and lanierone, relative to those in traps baited with ipsdienol alone, were clearly significant in three regions. In California, New York, and southeastern British Columbia, proportionally more males than females were attracted to traps baited with the binary mixture, resulting in a reduction in female bias. Yet lanierone had little effect on catches of males and females in California. Previous results in New York demonstrated that an increase in the proportion of lanierone resulted in an increase in the proportion of males (Teale et al., 1991). In a separate trial in California, Seybold et al. (1992) found that sex ratio of *I. pini* caught in ipsdienol-baited funnel traps was not affected by lanierone. In the three sites in this study where the sex ratio was either 1 : 1 or slightly male biased, there were no significant differences in sex ratio between the two ipsdienol treatments. Further, the increase in male representation in trap catches varied between sites in eastern regions but not in western ones.

Presently, we cannot fully explain all these observed variations. However, the following factors may be important. Firstly, geographic variation in the use of (*R*)-(−)- and (*S*)-(+)-ipsdienol as a pheromone by *I. pini* is known to occur between populations in California and New York. Beetles in California produce and respond primarily to (*R*)-(−)-ipsdienol (Birch et al., 1980; Seybold, 1992).

Attraction to (*R*)-(−)-ipsdienol is interrupted by (*S*)-(+)-ipsdienol. The sympatric species *I. paraconfusus* Lanier uses (*S*)-(+)-ipsdienol as one of its pheromones (Silverstein et al., 1966; Wood et al., 1968). The pheromones of *I. pini* and *I. paraconfusus* are mutually inhibitory in California, presumably to ensure reproductive isolation (Birch and Wood, 1975; Birch and Light, 1977; Birch, 1978; Light and Birch, 1979; Birch et al., 1980). *Ips paraconfusus* is not present east of Oregon and California (Wood, 1982) and eastern *I. pini* use both enantiomers of ipsdienol as pheromones (Stewart, 1975; Lanier et al., 1980; Teale and Lanier, 1991).

The lack of a strong increase in attraction of *I. pini* to ipsdienol-baited traps in California, when lanierone is added, may be a consequence of similar species specificity in the use of pheromones to ensure reproductive and/or ecological separation. The role of lanierone in the aggregation behavior of *I. paraconfusus* has not been studied. Seybold et al. (1992) could not detect lanierone in another potential competitor, *Dendroctonus brevicomis* LeConte. *Ips integer* was strongly attracted to lanierone in Montana but not detected in California or British Columbia, even though both regions are well within its range (Wood, 1982).

Either lanierone is not important as a pheromone to *I. pini* in California or only a specific mixture of lanierone and (*R*)-(−)-ipsdienol is active. Evidence by Seybold et al. (1992) seems to support the first hypothesis. However, they suggest that selection pressure from predation by *E. lecontei* may have favored *I. pini* that no longer used lanierone as a pheromone, similar to the model proposed for differential chiral and seasonal responses between *I. pini* and its major predators in Wisconsin (Raffa and Klepzig, 1989; Raffa, 1991). Yet, in southeastern British Columbia and Montana both *E. lecontei* and *I. pini* responded strongly to the combination of ipsdienol and lanierone.

Regional differences in population levels may explain some of the variation. The mean replicate catches of *I. pini* per site were correlated with the mean proportion of males in catches to traps baited with ipsdienol alone and the mean proportion of males in catches to traps baited with ipsdienol and lanierone ($r = 0.623$ and $r = 0.781$, respectively; $P = 0.031$ and $P = 0.003$, respectively). In contrast, the mean replicate catches of males and females per site were not correlated with the mean proportional increases in catches of males and females, respectively, in ipsdienol-baited traps due to the presence of lanierone ($r = 0.220$ and $r = 0.249$, respectively; $P = 0.491$ and $P = 0.436$, respectively). We should note, however, that the mean replicate catches of beetles may not be a good estimator of population size since the regions varied in trapping period and duration, stand structure, and temperature regime. Unfortunately, we do not have a better estimator.

Regional differences in the timing of life history activities relative to the trapping periods might also explain some of the variation. In California, responses of male and female *I. pini* to extracts of male frass were lowest during the winter months, presumably due to diapause-related decreased receptiveness and/or decreased pheromone production (Birch, 1974). In New York and Wisconsin, most *I. pini* respond to synthetic ipsdienol late in the season (Teale, 1990; Raffa, 1991; Teale and Lanier, 1991). However, in Wisconsin in 1990, catches of beetles in ipsdienol-baited funnel traps were as high in April as they were in June and August (Raffa, 1991).

We should expect changes in the operational sex ratio (Emlen and Oring, 1977) during the course of an attack as well. The sex ratio among *Dendroctonus ponderosae* Hopkins landing on lodgepole pine changes during the colonization period, with the proportion of females declining over time (Raffa and Berryman, 1983). In this study, the operational sex ratio is defined as the ratio of active, searching males to available, unattached females, thereby omitting those beetles that are occupied in activities under the bark such as mating or egg laying. Males initiate the attacks and then produce pheromones while they wait for females. This results in local depletions of males available for capture in pheromone-baited traps. *Ips pini* is a polygynous species, with males having three to four females per harem (Thomas, 1961). Once harems are fully established, the operational sex ratio should become male biased with two to three times as many females as males under the bark. If males exhibit defensive behaviors by remaining in the gallery after females have left, then once again we would expect female bias in the operational sex ratio. Therefore, variation in sex ratios between regions may be due to variation in sampling periods relative to the sequence of behaviors during attack. Beetles in some regions may have only begun to attack new host material while beetles in other regions may have been well into the last stages of the behaviors associated with attacks.

There are three additional factors that may contribute to regional differences in the operational sex ratio. Firstly, attacks by bark beetles on suitable hosts are sequential. Activities at one gallery may not be synchronous with activities in galleries farther up the trunk of a tree (see reviews in Coulson, 1979; Berryman, 1982). Secondly, if males have a propensity to disperse prior to attack, then this would result in additional depletion of males. The sex ratio among *I. pini* attacking new host material is generally female biased at 2 females/male (Schenk and Benjamin, 1969; Schmitz, 1972). Lastly, the male bias detected in Montana may have resulted from the use of racemic ipsdienol in this region. Past studies in British Columbia and California have demonstrated that the proportion of males captured in ipsdienol-baited traps is correlated with the proportion of (*S*)-(+)-ipsdienol used in the lures (Miller, 1990; Seybold, 1992). Males in Montana produce ipsdienol with an enantiomeric composition of 91:9 to 95:5 (*R*)-(−):(*S*)-(+) (Seybold et al., 1995). Male bias in trap catches might have been reduced if (*R*)-(−)-ipsdienol had been used instead of racemic ipsdienol.

Examples of geographic variation in the use of pheromones have commonly been reported for Lepidoptera (Roelofs, 1980; Cardé and Baker, 1984). The European corn borer, *Ostrinia nubilalis* (Hübner) (Pyralidae), uses 11-tetradecenyl acetate (11–14:OAc) as a sex pheromone (Klun, 1968; Klun and Brindley, 1970; Klun and Robinson, 1971). Geographic variation is based on the relative proportion of the *E* and *Z* isomers of 11–14:OAc (Klun et al., 1973; Kochansky et al., 1975). Most populations in Europe and North America respond to a 3:97 *E*:*Z* ratio of 11–14:OAc, while populations in Italy, the Netherlands, and parts of northeastern United States respond preferentially to a 97:3 *E*:*Z* blend (Klun and Cooperators, 1975). Some areas, such as New York state, have discrete populations using only the 3:97 *E*:*Z* blend as well as hybrid populations (Roelofs et al., 1985). In California, at least three different populations of the western avocado leafroller, *Amorbia cuneana* (Walsingham) (Tortricidae), differ in the production of *E*:*Z* blends of the sex pheromone, (*E*,*E*/*Z*)-10,12-tetradecadien-1-ol acetate. Two populations respond to blends close to 1:1, while the third prefers blends with a higher *E*:*Z* ratio (Bailey et al., 1986). In New Zealand, brown-headed leafrollers, *Ctenopseustis obliquana* (Walker) (Tortricidae), exhibit two different pheromone population types. One uses an 80:20 mix of (Z)-8-tetradecenyl and (Z)-5-tetradecenyl acetates, while the other uses only (Z)-5-tetradecenyl acetate (Foster and Roelofs, 1987).

Our results and those of others (Birch et al., 1980; Lanier et al., 1980; Miller et al., 1989a, 1996; Raffa and Klepzig, 1989; Teale, 1990; Teale et al., 1991; Seybold, 1992; Seybold et al., 1992, 1995) with *I. pini* support the need for tests over its full geographical range. Pheromone blends differ substantially between areas, necessitating the use of regionally specific lures for pest management. Our results indicate that a blend of racemic ipsdienol and lanierone is optimal for most regions while (*R*)-(−)-ipsdienol by itself is sufficient for use in California. Regional pheromone specificity, and the need for tests throughout geographic ranges, may be important for other scolytid species as well. In laboratory bioassays, the southern pine beetle, *Dendroctonus frontalis* Zimmerman, collected from Georgia, Texas, and Virginia, showed marked preferences for pheromones from their respective regions (Berisford et al., 1990). A standard lure of frontalin, *trans*-verbenol, and turpentine was as attractive as the regional blends in Georgia and Texas, but not in Virginia.

Bark beetle pheromones are used as kairomones by predators (Borden, 1982; Dahlsten, 1982; Miller et al., 1989b; Payne, 1989). *Temnochila chlorodia*, *Enoclerus sphegeus*, *E. nigrifrons*, *Thanasimus undatulus*, and *T. dubius* were all attracted to ipsdienol. These results are consistent with those of Vité and Gara (1962), Wood et al. (1968), Furniss and Livingston (1979), Raffa and Klepzig (1989), Miller and Borden (1990), and Seybold et al. (1992). Similar research has demonstrated that *E. lecontei* is also attracted to ipsdienol (Wood et al., 1968; Miller and Borden, 1990). Our results further show attraction of *E. lecontei* to ipsdienol and lanierone in three different regions. As found by

Seybold et al. (1992), synergism occurred between ipsdienol and lanierone in attracting *E. lecontei* in California. Synergism did not occur in British Columbia or Montana. We suggest that synergism may reflect differential benefits for *E. lecontei* in California, compared to *E. lecontei* in British Columbia and Montana, resulting in a greater measure of prey specificity in California, relative to other regions.

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