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ENANTIOSPECIFIC PHEROMONE PRODUCTION AND RESPONSE PROFILES FOR POPULATIONS OF PINE ENGRAVER, *Ips pini* (SAY) (COLEOPTERA: SCOLYTIDAE), IN BRITISH COLUMBIA

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Abstract-Analyses of the enantiomeric composition of ipsdienol produced by individual male pine engravers, *Ips pini* (Say), from six populations in British Columbia, support the hypothesis that New York and Idaho races of this species hybridize in southeastern British Columbia. Production profiles, expressed as frequency distributions of (+):(-) ipsdienol ratios [= ratio of (*S*)-(+)-ipsdienol to (*R*)-(-)-ipsdienol], were bimodal for four western British Columbia populations. The (+):(−) ratios ranged from 63:37 to 71:29, consistent with those previously found for the New York race. The profile for a southeastern population from Radium, British Columbia, was intermediate between those for the four western British Columbia populations and that from one population in Kimberley, British Columbia, just south of Radium. Males in the Kimberley population produce predominantly (*R*)-(-)-ipsdienol, typical of California and Idaho males. Response profiles of different individuals of *I. pini*, determined by captures of beetles in multiple-funnel traps baited with ipsdienol of 11 different (+):(-) ratios, were not consistent with production profiles. Populations in Williams Lake and Princeton, in western British Columbia, and Radium, in southeastern British Columbia, had response profiles with maximal attraction to ipsdienol over a broad range of (+):(−) ratios, falling off as enantiomeric purity was approached at either end of the

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spectrum. This type of response profile is consistent with that for the New York race, which has been shown to respond optimally to (+):(-) ratios ranging from 40:60 to 70:30. The response profile of the Kimberley population gradually declined from maximal attraction to ipsdienol with a (+):(-) ratio of 2:98 to the lowest response at a (+):(-) ratio of 98:2. The attraction of I. *pini* to chemical stimuli in California is interrupted by ipsdienol with a (+):(−) ratio $>$ 5:95, a pheromone of a host competitor, the California five-spined ips, *Ips paraconfusus* Lanier. We hypothesize that the Idaho race, which does not compete with *I. paraconfusus* due to geographical separation, is characterized by a Kimberley-type enantiomeric response profile, intermediate between those of the New York and California races.

Key Words-Ipsdienol, *Ips pini,* Scolytidae, aggregation pheromone, enantiomer, geographic variation, intmpopulation variation, speciation, competitive exclusion.

INTRODUCTION

The principal male-produced aggregation pheromone of the pine engraver, *Ips pini* (Say)(Coleoptera: Scolytidae), is ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol), a monoterpene alcohol with one asymmetric carbon center and two enantiomeric configurations (Seybold, 1993). Pioneering research on volatile extracts trapped from populations of *I. pini* disclosed that males from California (Stewart, 1975; Birch et al., 1980) and Idaho (Plummer et al., 1976) produce only (*R*)-(-)-ipsdienol, while males from New York produce a 65:35 blend of (*S*)-(+) and (*R*)-(-) enantiomers (Lanier et al., 1980).

Recently, pheromone production profiles were determined for populations of *I. pini* based on the enantiomeric ratios of ipsdienol produced by individual beetles (Slessor et al., 1985; Miller et al., 1989). Males in populations from Hat Creek, California, and Kimberley in southeastern British Columbia produce primarily (*R*)-(-)-ipsdienol, with mean (+):(-) ratios [= ratio of (*S*)-(+)-ipsdienol to (*R*)-(−)-ipsdienol] of 9:91 and 11:89, respectively. In each population, however, there are a few beetles that produce primarily the (+) enantiomer. Beetles from Newcomb, New York, are characterized by a bimodal frequency distribution, with respect to enantiomeric composition, with a mean (+):(−) ratio of 57:43. A population from Princeton in southwestern British Columbia is characterized by a similar, but slightly broader, bimodal enantiomeric production profile, with a mean (+):(-) ratio of 66:34.

Seybold et al. (1995a) determined enantiomeric compositions of ipsdienol in volatiles captured from logs infested by males from 35 populations of *I. pini*, representing the North American range of the species. These included one population from southwestern British Columbia and a second population from southeastern British Columbia, very close to the locations used by Miller et al. (1989), and several populations from Washington, Idaho, and Montana. Seybold et al.

(1995a) hypothesized that there are two, possibly three, geographically separate pheromone variants or races of *I. pini*. Males in the "California" race, with a range extending from Washington to Arizona and New Mexico, produce ipsdienol with (+):(−) ratios of 6:94 to 2:98. The eastern "New York" race is characterized by (+):(−) ratios of 68:32 to 44:56. This race ranges from southern Appalachia, north along the Atlantic coast, through the US Lake states, and across the boreal forest of Canada, extending south in British Columbia to the US border. The third "Idaho" race is located in southeastern British Columbia, Idaho, and Montana (and possibly further east, west, and south); its males produce ipsdienol with (+):(-) ratios ranging from 9:91 to 5:95. Seybold et al. (1995a) speculated that the Idaho race may represent a zone of hybridization between the New York and California races.

Responses to ipsdienol-baited traps by *I. pini* in California and New York appear to correspond to the enantiomeric composition of ipsdienol produced by the respective races. In California, *I. pini* are attracted by (*R*)-(-)-ipsdienol. The attraction is significantly interrupted by as little as 5 % of the antipode (Birch et al., 1980; Seybold, 1992). In New York, the (+):(−) ratio of ipsdienol eliciting maximal attraction of *I. pini* ranges from 70:30 to 40:60, inclusively (Lanier et al., 1980; Teale and Lanier, 1991; Teale et al., 1994). The enantiospecific response to (*R*)-(-)-ipsdienol in California may be driven by natural selection arising from competition with the California fivespined ips, ***Ips paraconfisus*** Lanier. Both species breed in ***Pinus ponderosae*** Laws. and ***P. jeffreyi*** Grev. & Balf. (Wood, 1982). The reproductive success of individuals of both species is reduced when they infest the same host material (Birch, 1978; Light et al., 1983). Male *I.* ***paraconfisus*** produce predominately (*S*)-(+)-ipsdienol as one component of their aggregation pheromone blend (Seybold, 1992; Seybold et al., 1995b). Attraction of *I. paraconfusus* to its pheromone is interrupted by the (-) enantiomer, to which *I. pini* is attracted (Light and Birch, 1977; Birch et al., 1980; Seybold, 1992).

We report the results of experiments in which four additional populations in southern British Columbia were characterized by their ipsdienol enantiomeric production profiles. We also tested different individuals from two of these new populations, as well as those from Princeton and Kimberley, British Columbia, for their field response to ipsdienol with enantiomeric (+):(-) ratios ranging from 2:98 to 98:2. Populations of *I. pini* have been tested previously in California and New York for their responses to ipsdienol over a broad range of enantiomeric ratios (Seybold, 1992; Teale et al., 1994).

METHODS AND MATERIALS

Production Profiles. Bolts of lodgepole pine, ***Pinus contorta*** var. ***latifolia*** Engelm., infested with live broods of *I. pini*, were collected from Osprey Lake, Pemberton, and Williams Lake, British Columbia, in 1986, and Radium, British Columbia, in 1987. Bolts were placed in rearing cages and beetles were collected after they emerged as mature adults. Using the gelatin-pill-capsule technique (Borden, 1967), adult males from each of the four populations were restrained on uninfested bolts of lodgepole pine collected near Princeton, British Columbia. They were allowed to bore into the bark and feed for 24-48 hr. Abdomens from individual males were removed and each was crushed in 150 μl of pentane containing racemic 3-octanol (4.1 ng/μl) as an internal standard. Extracts were analyzed by splitless, capillary gas chromatography using a Hewlett-Packard (HP) 5890 and a fused silica column (J&W Scientific, Folsom, California; 30 m x 0.25 mm ID, 0.25 μm DB-l), before and after derivatization to acetyl lactate diastereomers (Slessor et al., 1985). Only extracts containing > 10 ng of ipsdienol were derivatized. Retention times of ipsdienol and its two derivatives were determined with mcemic ipsdienol obtained from Borregaard Fine Chemicals, A.S. (Sarpsborg, Norway), and enantiomeric assignments were made according to Slessor et al. (1985). The identities and integrities of ipsdienol acetyl lactate diastereomers were verified by mass spectrometry using splitless, capillary gas chromatography (HP 5985B).

Profiles. For experiment 1, racemic ipsdienol (chemical purity > 95 %) was obtained from Borregaard Fine Chemicals, A.S. Two enantiomeric mixtures of ipsdienol [(+):(−) ratios of 98:2 and 2:98, respectively] were obtained from E. K. Czyzewska (Department of Chemistry, Simon Fraser University, Bumaby, British Columbia). For experiments 2-4, three enantiomeric mixtures [(+):(-) ratios of 98:2, 50:50, and 2:98, respectively] (chemical purities, 93, 98, and 83%, respectively) were obtained from Phero Tech Inc. (Delta, British Columbia).

In experiment 1, each lure consisted of 10 Microcap disposable pipettes (2 μl) (Drummond Scientific Co., Broomall, Pennsylvania), each sealed at one end and filled with ipsdienol, and placed in a polyethylene, microcentrifuge tube (1.8 ml) (Evergreen Scientific, Los Angeles, California). The release of ipsdienol with different enantiomeric ratios was achieved by adjusting the relative proportion of tubes filled with the different mixtures. The release rate of ipsdienol from each lure was approximately 0.1 mg/day at 24°C (determined by weight loss).

In experiments 2-4, each lure consisted of a lo-cm-length of C-flex tubing (ID = 1.6 mm; OD = 2.4 mm) (Concept Inc., Clearwater Florida), filled with an ethanol solution of ipsdienol (80 mg/ml). Solutions were prepared for each of 11 different enantiomeric ratios of ipsdienol. The release rate of ipsdienol from each lure was approximately 0.6 mg/day at 24°C (determined by collection of volatiles on Porapak-Q).

In all experiments, replicates of 12 eight-unit, multiple-funnel traps (Lindgren, 1983) (Phero Tech Inc.) were set in grids of 3 x 4 in stands of lodgepole pine. Replicate grids were placed at least 100 m apart, and traps were spaced 10–15 m apart within each replicate. Each trap was baited, and suspended such that the top of each trap was approximately 1.3–1.5 m above ground level. No trap was within 2 m of any tree.

Experiments 1-4 determined the effect of the enantiomeric composition of ipsdienol on the attraction of *I. pini* near Princeton, Williams Lake, Radium, and Kimberley, British Columbia, respectively. Ten replicates were set for experiments 1-3 during the period of May 22-June 9, 1986; July 5–September 6, 1987; and July 7-September 9, 1987, respectively. Eight replicates were set for experiment 4 during the period of July 13-September 6, 1989. The 12 treatments consisted of 11 different enantiomeric ratios of ipsdienol and a control, randomly assigned within each replicate. In experiment 1, the control traps did not have any lures while in experiments 2-4, the control traps were baited with C-flex tubing containing ethanol alone. All lures were replaced, and treatments rerandomized within each replicate, at intervals of 3 to 4 weeks. Trap catches were pooled at the conclusion of each experiment.

Statistical Analyses. Data were analyzed using the SAS statistical package ver. 5 .O (SAS Institute Inc., Cary , North Carolina). Quantities of ipsdienol from individual abdominal extracts from males were transformed by ln(Y + 1) and subjected to one-way analysis of variance (ANOVA). Scheffé's multiple comparison test was performed when $P < 0.05$. For each population, coefficients of variation (CV) were determined for quantity and enantiomeric composition of ipsdienol, normalized by ln(Y + 1) and $\arcsin \sqrt{Y}$, respectively (Schlyter and Birgersson, 1989). Distributions of the enantiomeric compositions of ipsdienol, including data sets for populations from Princeton and Kimberley, British Columbia (Miller et al., 1989), were compared by χ^2 tests.

Trap catch data, transformed by ln(Y + 1) to remove heteroscedasticity, were analyzed by three-way ANOVA using location, treatment, replicate nested within location, and the interaction between location and treatment as model factors. For each location, data were analyzed by two-way ANOVA using replicate and treatment as model factors, first with all treatments and then with only the ipsdienol treatments. Eleven and 10 orthogonal contrasts were conducted for the first and second ANOVA's for each location, respectively, comparing the control against each ipsdienol treatment separately in the first case and comparing the response to racemic ipsdienol against each of the remaining ipsdienol treatments separately in the second.

Sex-ratio data [transformed by arcsin(Y)], for catches ≥ 10, were subjected to full-factorial two-way ANOVA. For each location, untransformed sex-ratio data (not means), for catches ≥ 10, were regressed against the enantiomeric composition of ipsdienol, using treatment as the only factor in a general linear model. Tests of homogeneity of slopes were performed by analysis of covariance (ANCOVA) using location, and the interaction between location and the covariate, enantiomeric composition of ipsdienol as model factors. One contrast was performed, comparing the slope for the population in Kimberley against the slope for the remaining populations. For each location, we determined the Pearson correlation coefficient between mean proportional responses to each of 11 enantiomeric ratios of ipsdienol and the associated mean proportion of males in populations producing the same enantiomeric ratio (± 5 %) as determined above.

RESULTS

Production Profiles. Male *I. pini* from the Pemberton population produced the lowest amounts of ipsdienol per male compared to those from the other three populations (Table 1). Pemberton males were the least vigorous of all populations with respect to rates of boring and feeding. Beetles from Radium were reared from logs with the thickest phloem, probably influencing their vigor and hence the high level of ipsdienol production (Table 1). The quantity of ipsdienol produced by individual males varied markedly within each population (Figure 1), with coefficients of variation ranging from 66.0 to 167.3% (Table 1). As found by Miller et al. (1989) in other populations of *I. pini,* most males contained low quantities of ipsdienol and relatively few contained large amounts.

Pronounced bimodal frequency distributions of the enantiomeric compositions of ipsdienol, previously found for populations from Princeton, British Columbia, and Newcomb, New York (Miller et al., 1989), were found in three additional British Columbia populations (Pemberton, Williams Lake, and Osprey Lake) (Figure 2). Males from all three of these populations produced more (*S*)-(+)-ipsdienol than (*R*)-(−)-ipsdienol with mean (+):(−) ratios ranging from 63:37 to 71:29 (Table 1). There were no significant differences among the distributions of enantiomeric compositions of ipsdienol from the four westernmost British Columbia populations (Pemberton, Princeton, Osprey Lake, and Williams Lake) (χ^2 test, $df = 27$, $P = 0.194$) (Figure 2). The distributions for these populations were significantly different from that for the population from Kimberley (χ^2 test, all $= 9$, all $P < 0.001$). In contrast, males from Radium produced almost equal amounts of both enantiomers (Table 1). The enantiomeric production profile for these males was significantly different from the profiles for males from the Kimberley population (χ^2 test, $df = 9$, $P < 0.001$) and the four western British Columbia populations (χ^2 test, all $df = 9$, all $P < 0.001$) (Figure 2).

Response Profiles. Ips pini showed considerable variation in attraction to ipsdienol-baited multiple-funnel traps as a consequence of enantiomeric composition (Table 2). In all populations, significantly fewer beetles were caught in traps baited with an ipsdienol (+):(-) ratio of 98:2 than in traps baited with racemic ipsdienol (Figure 3). Significantly fewer beetles were caught in all traps

TABLE 1. QUANTITIES AND ENANTIOMERIC COMPOSITIONS OF IPSDIENOL PRODUCED BY INDIVIDUAL MALE *Zpspini* (SAY) FROM 4 LOCALITIES IN BRITISH COLUMBIA

	Quantity of ipsdienol (ng)			Enantiomeric ratio of ipsdienol (S)-(+):(R)-(−)				Correlations between quantity and enantiomeric composition”	
Locality	N	Mean ± SE^a	CV (%)^b	N	Mean ratio^c	SE	CV (%)^d	*r*	*P*
Pemberton	68	47 ± 15a	167.3	14	65:35	4.9	30.4	-0.01	0.965
Williams Lake	75	158 ± 28 b	93.7	38	71:29	2.0	22.7	-0.02	0.8%
Lake Osprey	62	168 ± 34 b	74.8	35	63:37	2.7	25.8	-0.05	0.769
Radium	139	197 ± 21 b	66.0	87	52:48	2.5	32.7	+0.18	0.105

‘Means followed by the same letter are not significantly different at *P* = 0.05 [Scheffe’s multiple comparison test on data transformed by ln(*Y* + 1)].

[b] Data transformed by ln(*Y* + 1) prior to analysis.

‘Only for extracts containing > 10 ng of ipsdienol.

[d] Data, expressed as pmportion of (+) enantiomer in total amount of ipsdienol, transformed by arcsin $\sqrt{Y}$ prior to analysis.

‘Pearson correlation coefficient adjusted for degrees of freedom.

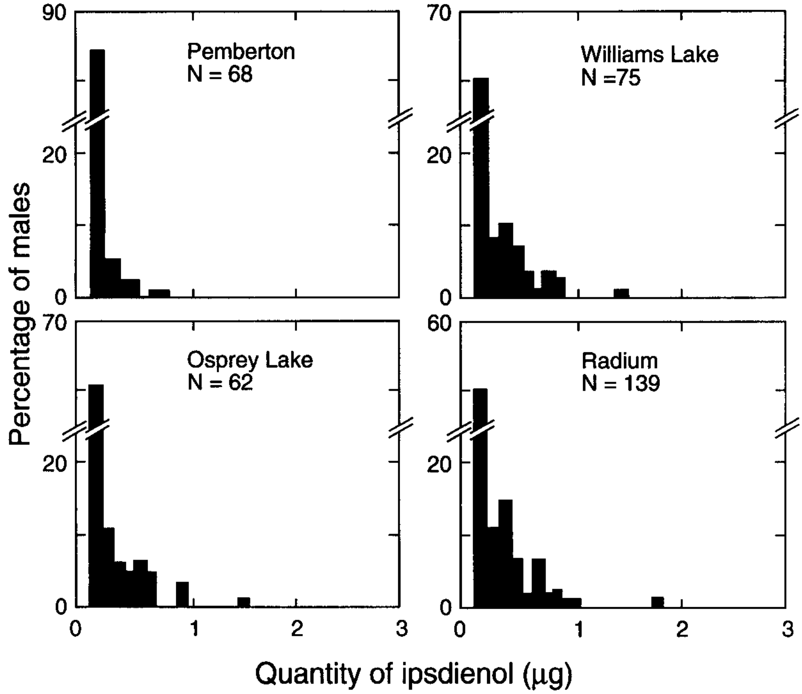

FIG. 1. Frequency distributions of the quantities of ipsdienol produced by individual male *Ips pini* from four populations in British Columbia.

baited with a (+):(−) ratio of 2:98 than in traps baited with racemic ipsdienol in Williams Lake, Radium, and Princeton. Except for one contrast, significantly more beetles were caught in traps baited with ipsdienol than in control traps (orthogonal contrasts, ANOVA, all $P < 0.029$). The exception was in Kimberley, where there was a weakly significant increase of catches in traps baited with a (+):(-) ipsdienol ratio of 98:2 relative to those in traps baited with ethanol alone (orthogonal contrast, ANOVA, $P = 0.079$.

The enantiospecific response profiles varied significantly between locations ($P < 0.001$; Table 2). The most obvious differences were related to the attraction of *I. pini* to (+):(-) ipsdienol ratios of 2:98 and 10:90. For both ratios, catches were low in Williams Lake and Princeton but high in Kimberley (Figure 3). In Radium, catches to traps baited with (+):(-) ratio of 10:90 were high but low to those baited with a (+):(-) ratio of 2:98.

The sex ratio of captured *I. pini* varied among locations and enantiomeric treatments (Table 2). As in California (Seybold, 1992), the proportion of males caught in ipsdienol-baited traps increased as the proportion of (*S*)-(+)-ipsdienol

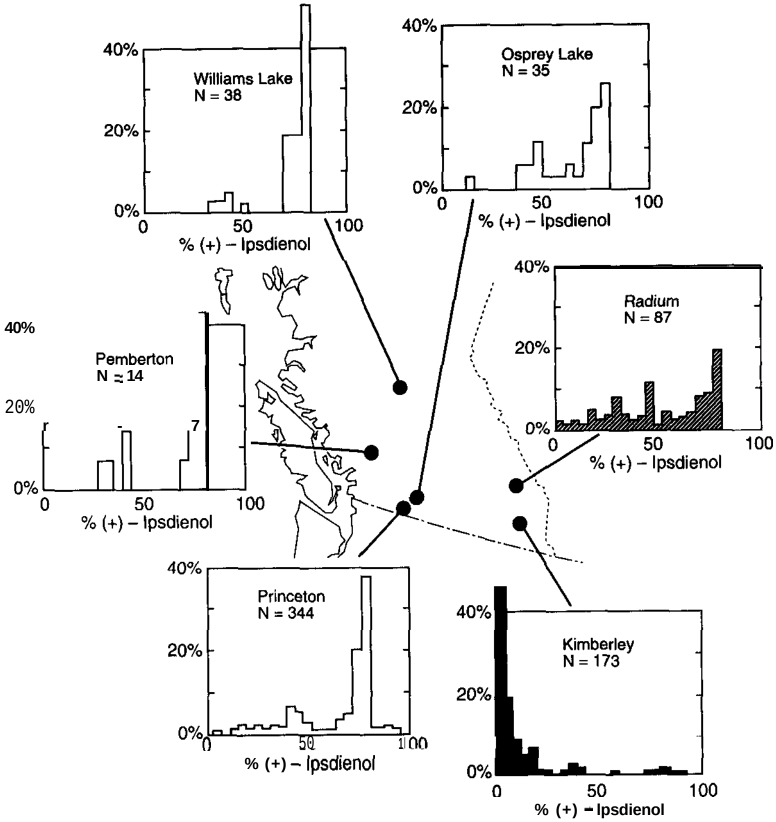

FIG. 2. Frequency distributions of the enantiomeric compositions of ipsdienol produced by individual male *Ips pini* from six populations in British Columbia. Data for Princeton and Kimberley are reproduced from Miller et al. (1989). Histograms with different shading patterns are significantly different (see text).

increased (Figure 4). The slope of the regression line for the Kimberley population was significantly different from that of the other three populations (orthogonal contrast, ANCOVA, $P = 0.003$). Accordingly, the effect of the interaction between location and enantiomeric composition of ipsdienol was not significant when the Kimberley population was omitted from the analysis. When Kimberley was included, the effect was significant ($P = 0.021$; Table 2).

The association between enantiospecific production and response profiles differed between locations. In Radium and Princeton the correlations between mean (+):(-) ipsdienol ratios produced by males within the population and the respective enantiospecific response profile were significantly different from zero

TABLE 2. ANALYSIS OF VARIANCE OF EFFECTS OF LOCATION (WILLIAMS LAKE, RADIUM, PRINCETON, AND KIMBERLEY, BRITISH COLUMBIA], ENANTIOMERIC COMPOSITION OF IPSDIENOL [11 DIFFERENT (+) : (-) RATIOS], INTERACTION BETWEEN LOCATION AND ENANTIOMERIC COMPOSITION, AND REPLICATE (N = 8 OR 10) NESTED WITHIN LOCATION ON NUMBER AND SEX RATIO OF *Ips pini* (SAY) CAPTURED IN IPSDIENOL-BAITED MULTIPLE-FUNNEL TRAPS

	Trap catch”			Proportion of males[b]		
Source	*df*	*F*	*P*	*df*	*F*	*P*
Location (A)	3	**86.95**	<0.001	3	309.81	<0.001
Enantiomeric composition (B)	10	**33.98**	<0.001	10	11.67	<0.001
Replicate nested within location (C)	34	15.81	<0.001	34	**4.45**	<0.001
$A * B$	30	**5.77**	<0.001	28	1.68	0.021
Error	**319**			**260**		

“Data transformed by $\ln(Y + 1)$ prior to analysis.

“Data transformed by $\arcsin(Y)$ prior to analysis.

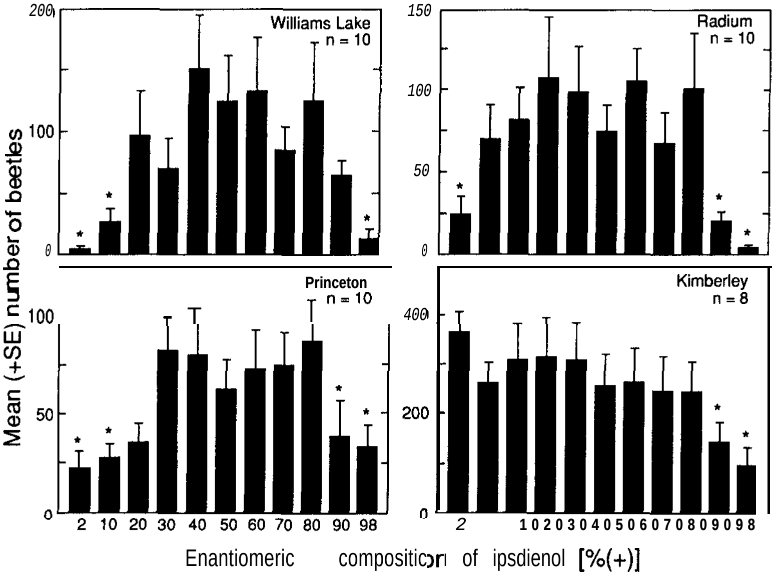

FIG. 3. Effect of the enantiomeric composition of ipsdienol on the capture of ***Ips pini*** in multiple-funnel traps at four locations in British Columbia. Asterisks indicate significant difference in trap catches relative to those in traps baited with racemic ipsdienol, orthogonal contrasts, $P < 0.08$.

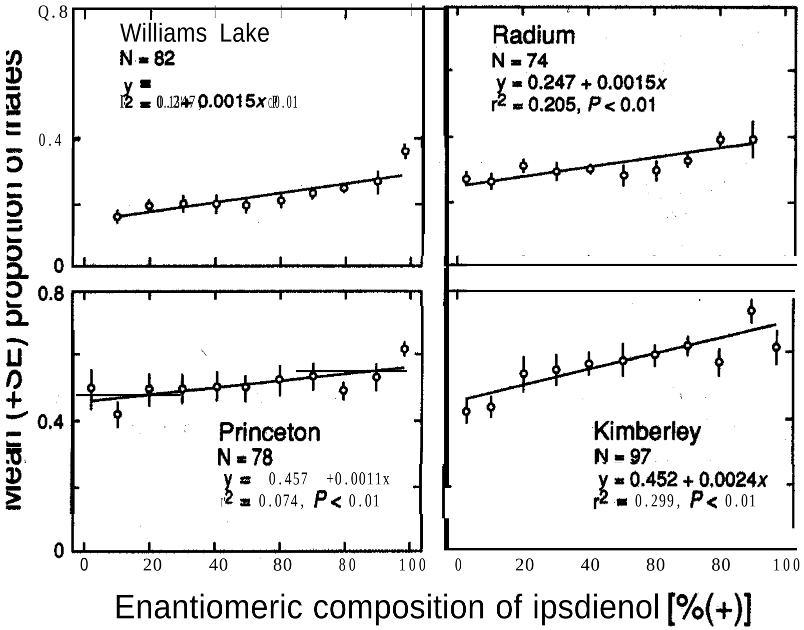

FIG. 4. Effect of the enantiomeric composition of ipsdiendl on ratio of *Ips pini* captured in multiple-funnel traps at four locations in British Columbia. Slope of the regression line for Kimberley is significantly different from those for the other three populations (see text).

(Table 3). The correlation was only weakly significant for the population from Kimberley and not significant for Williams Lake. In no case did the variation in one variable explain more than 50% of the variation in the other variable (all $r^2 < 0.475$).

DISCUSSION

The similarity of enantiospecific ipsdienol production profiles for males from the four western-most British Columbia populations examined (Figure 2) to that previously examined from Newcomb, New York (Miller et al., 1989) supports the hypothesis that the New York race ranges across the boreal forest in Canada and extends southward into British Columbia (Seybold et al., 1995a). The similarity of response profiles for populations from Williams Lake and Princeton to that for a population from Syracuse, New York (Teale et al., 1994) further supports this hypothesis, although the distribution was narrower for the

TABLE 3. CORRELATIONS BETWEEN ENANTIOSPECIFIC IPSDIENOL PRODUCTION PROFILES FOR MALE *Ips sini* (SAY) AND ENANTIOSPECIFIC RESPONSE PROFILES OF MALE AND FEMALE *I. pini* IN 4 LOCALITIES IN BRITISH COLUMBIA

Locality	Pearson correlation coefficient (*r*)	*P*
Williams Lake	0.356	0.283
Kimberley	0.538	0.088
Princeton	0.624	0.040
Radium	0.689	0.019

Syracuse population. The dissimilarity of the response profile for the Kimberley population to those for the other three British Columbia populations (Figure 2) is consistent with dissimilarities in production profiles previously reported between Kimberley and Princeton populations (Miller et al., 1989). The Kimberley population has previously been identified as part of the Idaho race (Seybold et al., 1995a). In our study, this is the only British Columbia population in which I. *pini* showed a considerable attraction to ipsdienol with a (+):(-) ratio of 2:98 (Figure 2), a preferred ratio for the California race (Birch et al., 1980; Seybold, 1992).

The population from Radium showed characteristics suggesting a combination of traits of the New York race and the Idaho or California races. The enantiospecific production profile was broad (Figure 1), with the highest coefficient of variation (Table 1). The Radium profile lacked both bimodality, common to the New York race, and a sharp peak at a (+):(-) ratio of 2:98, common to the Idaho and California races (Miller et al., 1989; Seybold et al., 1995a). The response profile for the Radium population was also broader than for populations from Williams Lake and Princeton (Figure 3), showing an attraction to a (+):(-) ratio of 10:90. However, beetles in the Radium population were not highly attracted to a (+):(-) ratio of 2:98, as was evident in the Kimberley population. These data suggest that the Radium population lies within an intergradation zone of the New York race and the Idaho or California races.

Our results demonstrated significant variation in the attraction of *I. pini* to ipsdienol for all four populations in British Columbia (Figure 3). In no case did we find evidence of a narrow range of enantiospecific responses to ipsdienol as shown by *I. pini* in California (Birch et al., 1980; Seybold, 1992). The intrapopulational variation in attraction of *I. pini*, with respect to variation in enantiomeric composition of ipsdienol, should reflect the relative benefits gained by the responding individuals. The broad range of equal levels of attraction in all British Columbia populations examined (Figure 3) should, therefore, reflect similar fitnesses in the responding individuals. However, initial preferences shown by individuals may not be associated with subsequent preferences by the same individuals. Cardt et al. (1976) showed that initial preferences by individual Oriental fruit moths, *Grapholita molesta* (Busk), were not associated with their subsequent preferences, yet the response profiles for the population were the same on both occasions. Such probability functions may be determined, in part, by age and vigor, as well as by genetics. The benefits may accrue from the average of repeated choices among individuals rather than specific choices.

The enantiospecific responses with respect to sex ratio (Figure 4) should reflect differential benefits to males and females. In Kimberley, females showed the strongest preference for ipsdienol when proportions of the (+) enantiomer were lowest. This trend is consistent with the production of predominantly (*R*)-(-)-ipsdienol by males (Figure 2) and the declining profile of total response in the population as the proportion of (*S*)-(+)-ipsdienol increased in the bait stimulus (Figure 3). However, it is not clear why this trend, *albeit* at a lower intensity, should be evident in the other three populations. It is possible that it is a residual sex-linked trait from other selection pressures or, possibly, a trait that cannot vary in a nonlinear fashion due to genetic constraints.

Our results show that the population profile for the response of bark beetles to a pheromone signal may not be predicted necessarily by the population profile for the production of the signal. The broad response profiles for beetles in Kimberley and Williams Lake differed from their narrow production profiles (Figures 2 and 3). The correlations between production and response were not strongly significant in either location (Table 3). In Princeton and Radium, only 39% and 47 % of the variation in response was explained by the variation in production (Table 3).

We can only speculate on the composition underlying the response profiles. Populations may consist of generalists with the population response profile equating to the probability profile for response by an individual beetle. Alternatively, populations may have structure through a diverse collection of individuals, each with a narrow response range. Our correlations of population profiles are not necessarily indicative of genetic correlations within individuals.

Our results suggest that pheromone-mediated behavioral separation may not be necessarily a premating isolation mechanism leading to speciation. Two distinct strains of the European corn borer, *Ostriniu nubilalis* (Hübner), occur in Europe and North America, differing in the relative use of (*E*)- and (Z)-1 1-tetradecenyl acetates as pheromones (Kochansky et al., 1975; Klun and Cooperators, 1975; Anglade et al., 1984; Barbattini et al., 1985; Peña et al., 1988; Löfstedt, 1990). The two strains hybridize readily where they are sympatric (Roelofs et al., 1985; Cardé, 1986; Klun and Huettel, 1988). In a similar fashion, *I. pini* in the population from Kimberley showed a lack of enantiospecificity to ipsdienol even though males in the population were very enantiospecific in the production of ipsdienol. The population from Radium provides evidence of hybridization between two, possibly three, races of *I. pini*, presumbly due to plasticity in behavioral responses.

A complete understanding of the use of pheromones by *I. pini* should also consider the effect of a second pheromone, lanierone (Teale et al., 1991). Attraction of males and females to ipsdienol is synergized by lanierone in New York, Wisconsin, Montana, and British Columbia, yet is unaffected in California (Seybold et al., 1992; Miller et al., 1996).

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