Journal of Chemical Ecology, Vol. 15, No. 1, 1989

INTER- AND INTRAPOPULATION VARIATION OF THE PHEROMONE, IPSDIENOL PRODUCED BY MALE PINE ENGRAVERS, *Ips pini* (SAY) (COLEOPTERA: SCOLYTIDAE)

D.R. MILLER,[1] J.H. BORDEN,[1] and K.N. SLESSOR[2]

[1]*Centre for Pest Management, Department of Biological Sciences*
[2]*Department of Chemistry*
Simon Fraser University
Burnaby, British Columbia, Canada V5A 1S6

(Received September 1, 1987; accepted November 10, 1987)

Abstract—We determined the chirality of ipsdienol in individual male pine engravers, *Ips pini* (Say), from New York, California, and two localities in British Columbia (BC). Both quantity and chirality of ipsdienol varied significantly between and within populations of *I. pini*. Beetles from California and southeastern BC produced primarily (*R*)-(−)-ipsdienol with mean ratios of (*S*)-(+):(*R*)-(−) of 9:91 and 11:89, respectively, while beetles from New York produced primarily (*S*)-(+)-ipsdienol with a mean (*S*)-(+):(*R*)-(−) ratio of 57:43. A population from southwestern BC was unlike any other known western population, producing primarily (*S*)-(+)-ipsdienol with a mean (*S*)-(+):(*R*)-(−) ratio of 66:34. In contrast to the unimodal chirality profiles for ipsdienol production in populations from California and southeastern BC, the profiles of the populations from southwestern BC and New York were bimodal, with a common mode at approximately 44:56 (*S*)-(+):(*R*)-(−). Bimodality in the profiles of ipsdienol chirality in two populations of *I. pini* and remarkably high levels of intrapopulation variation in pheromone chirality in all four populations suggest that evolutionary change in pheromone channels of communication could occur, possibly in response to artificial selection pressures such as mass trapping.

Key Words—*Ips pini*, Coleoptera, Scolytidae, aggregation pheromone, ipsdienol, geographic variation, intrapopulation variation, speciation.

0098-0331/89/0100-0233$06.00/0 © 1989 Plenum Publishing Corporation

INTRODUCTION

Pine engravers, *Ips pini* (Say) (Scolytidae: Coleoptera), are common and ubiquitous bark beetles found throughout North America. They breed primarily in the phloem tissue of the boles and branches of pines and can be a serious pest in stands of lodgepole, *Pinus contorta* var. *latifolia* Engelmann, and ponderosa pines, *P. ponderosae* Dougl. ex Laws. (Furniss and Carolin, 1980). Male *I. pini* are polygamous with harems of three to four females, on average. Each male excavates a nuptial chamber in the phloem of the host. Females in his harem then construct egg tunnels that radiate from the nuptial chamber, resulting in a characteristic X- or Y-shaped gallery, often engraved in the sapwood. The larvae feed in the surrounding phloem, pupate at the end of their feeding tunnels, and mature adults bore out through the bark and disperse to new hosts (Chamberlin, 1958; Bright and Stark, 1973; Bright, 1976; Furniss and Carolin, 1980; S.L. Wood, 1982).

Like many scolytids, *I. pini* aggregate rapidly and in large numbers to a suitable host (Anderson, 1948). Both sexes of *I. pini* are attracted to a terpene alcohol, ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (Vité et al., 1972; Stewart, 1975). Only male *I. pini* produce ipsdienol, presumably from the host monoterpene, myrcene, as shown for male *I. paraconfusus* (Hughes, 1974; Byers et al., 1979; Hendry et al., 1980; Byers, 1981; Fish et al., 1984). Female *I. pini* are not known to produce any pheromone.

Geographic variation in the use of ipsdienol as a pheromone is known (Lanier, 1972). Ipsdienol exists as two optical isomers or enantiomers (Figure 1), differing only in the absolute configuration around the chiral center. Males from California (Stewart, 1975; Birch et al., 1980) and Idaho (Plummer et al., 1976) produce only (*R*)-(−)-ipsdienol while beetles from New York produce a 65:35 mixture of (*S*)-(+) and (*R*)-(−) enantiomers (Lanier et al., 1980). California beetles are attracted by (*R*)-(−)-ipsdienol but are repelled by (*S*)-(+)-ipsdienol (Birch et al., 1980), while New York beetles respond best to a racemic mixture (equal quantities of (*S*)-(+)- and (*R*)-(−)-ipsdienol) (Lanier et al., 1980).

Pheromones are important in speciation and community structure in many Coleoptera and Lepidoptera, particularly in the families Scolytidae and Tortricidae, respectively (Lanier and Burkholder, 1974; Roelofs and Cardé, 1974; Cardé and Baker, 1984). In many Tortricidae, specificity in the use of pheromones is based on the ratio of *E* and *Z* isomers (Cardé and Baker, 1984), comparable to the specificity shown by bark beetles for enantiomeric ratios (Birch, 1984).

In order to understand if and how natural selection structures the use of pheromones, estimates of intrapopulation variation and heritability in pheromone traits are first required (Lanier and Burkholder, 1974; Collins and Cardé,

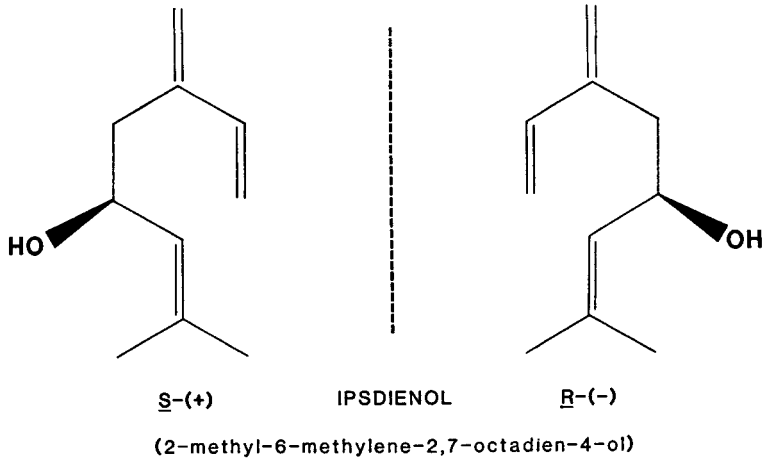

FIG. 1. Stereochemistry of the aggregation pheromone, ipsdienol, produced by male pine engravers, *Ips pini* (Say).

1985). To date, variation within populations of *I. pini* has been masked by the need for pooled samples of 300 or more beetles to obtain a sufficient quantity of ipsdienol for a single determination of chirality. It is now possible to determine the chirality of as little as 25 ng of ipsdienol by splitless gas chromatography following derivatization to acetyl lactate diastereomers (Slessor et al., 1985). By using this procedure we were able to elucidate the variation in quantity and chirality of ipsdienol within and between populations of *I. pini*.

METHODS AND MATERIALS

Collection of Pine Engravers. Populations of pine engravers were collected from four localities in North America. In 1984 we collected bolts of lodgepole pine infested with live broods of *I. pini* from Kimberley in southeastern British Columbia and just east of Manning Park in southwestern BC. Infested bolts were placed in rearing cages in the laboratory and adult beetles were collected after emergence as mature adults. In 1984 and 1985, newly emerged adults were transported by aircraft from Newcomb in New York, and Hat Creek in California. Red pine, *P. resinosa* Ait., was the brood host species for beetles from Newcomb; lodgepole pine was the brood host for beetles from the other three localities.

Procedure for Extracting and Analyzing Ipsdienol. 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 Man-

ning Park, BC. 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. These extracts were analyzed by splitless capillary gas chromatography (Hewlett Packard HP 5890 using a 30-m × 0.25-mm ID fused silica column), before and after derivatization to acetyl lactate diastereomers (Slessor et al., 1985). Retention times of ipsdienol and its derivatives were determined with racemic ipsdienol obtained from Borregaard A.S., Sarpsborg, Norway, and chiral 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 (Hewlett Packard HP 5985B).

Procedure for Statistical Analyses. Coefficients of variation (Sokal and Rohlf, 1981) were calculated for quantity and chirality of ipsdienol using transformed data to obtain normality in the data sets. In addition to the mean chiral ratio for individuals, a pooled chiral ratio was also determined for each population using the pooled quantities of each enantiomer. The pooled chiral ratio is comparable to the method used in previous studies (Stewart, 1975; Plummer et al., 1976; Birch et al., 1980; Lanier et al., 1980). For each pooled chiral ratio, a root-mean-squared error (RMSE) was calculated using the following expression:

$$\mathrm{RMSE} = (x_i - x_p)^2 + [\mathrm{SE}(x_i)]^2$$

where x_i stands for the mean chirality for population i, x_p is the chiral ratio using pooled data for population i and $\mathrm{SE}(x_i)$ is the standard error for the mean chiral ratio, x_i. Quantities were transformed by $\log(1 + X)$ while the data for chiralities were transformed by arcsin $\sqrt{X}$. Student-Newman-Keuls test at $P < 0.05$ was used to compare mean quantities of ipsdienol produced by males between the four localities. Coefficients of correlation between quantity and chirality of ipsdienol were determined for each locality and adjusted for degrees of freedom. The Minitab Statistical Package (Statistics Department, The Pennsylvania State University, University Park, Pennsylvania 16802) was used for Student-Newman-Keuls test and the calculations of coefficients of correlation.

RESULTS

Quantity of Ipsdienol. The mean quantities of ipsdienol per male varied between populations of *I. pini* (Table 1), probably due to environmental factors and differences in vigor. Males from southeastern BC were quick to bore into logs and produced copious amounts of frass, while beetles from New York were the least vigorous of all the populations with respect to rates of boring and

TABLE 1. QUANTITIES AND CHIRALITIES OF IPSDIENOL PRODUCED BY INDIVIDUAL MALE *Ips pini* (SAY) FROM 4 LOCALITIES IN NORTH AMERICA.

	Quantity of ipsdienol (ng)			Chirality of ipsdienol (*S*)-(+):(*R*)-(−)						Correlations between quantity and chirality of ipsdienol[e]	
Locality	*N*	Mean ± SE[a]	*CV*[b]	*N*	Mean ratio	SE	*CV*[c]	Pooled ratio	RMSE[d]	*r*	*P* value
New York	110	162 ± 32a	80.5%	55	56.9:43.1	1.3	13.2%	63.8:36.2	7.0	+0.47	<0.001
California	73	203 ± 33b	36.0	62	8.9:91.1	2.1	19.0	1.9:98.1	7.3	−0.32	<0.01
Southwestern BC	457	312 ± 16b	40.0	344	65.7:34.3	1.0	33.2	65.3:34.7	1.0	0.00	NS
Southeastern BC	158	522 ± 41c	26.4	173	10.8:89.2	1.4	19.8	5.1:94.9	5.9	−0.41	<0.001

[a] Means followed by a different letter are significantly different, $P < 0.05$.
[b] Coefficients of variation (*CV*) for data transformed by log $(1 + X)$.
[c] Coefficients of variation (*CV*) for data transformed by arcsin $\sqrt{X}$.
[d] Root-mean-squared error (see text).
[e] Coefficients of correlation (*r*) were adjusted for degrees of freedom.

feeding. Geographic variation in brood host could have affected the ability of adult males to produce ipsdienol in lodgepole pine. New York beetles were bred in red pine, in contrast to beetles from the other three localities which were bred in lodgepole. Lodgepole used as a brood host could also vary significantly between localities. Beetles from southeastern BC were bred in logs of lodgepole pine with thicker phloem than logs used for beetles from southwestern BC.

Intrapopulation variation in the quantity of ipsdienol produced by individual males was found in all four populations (Figure 2A–D), with coefficients of variation ranging from 26.4 to 80.5% (Table 1). The high coefficient of variation for the New York population may be a consequence of the change from red pine, as a brood host, to lodgepole pine for pheromone production. Most males contained low quantities of pheromone and relatively few contained large amounts. The frequency distributions are similar to those for the production of *trans*-verbenol (*trans*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol) by female *Dendroctonus ponderosae* Hopk. (Borden et al., 1986) and *cis*-verbenol and 2-methyl-3-buten-2-ol by male *I. typographus* (L.) (Birgersson et al., 1984; Schlyter et al., 1985).

Chirality of Ipsdienol. Variation in the chirality of ipsdienol was very evident between populations (Figure 2E–H). Males from California and southeastern BC produced primarily (*R*)-(−)-ipsdienol with mean (*S*)-(+):(*R*)-(−) ratios of 9:91 and 11:89, respectively (Table 1). As expected, males from New York produced primarily (*S*)-(+)-ipsdienol with a mean (*S*)-(+):(*R*)-(−) ratio of 57:43. However, the mean chiralities for all three of the above populations differ significantly (*t* tests, $P < 0.001$) from the previously published (*S*)-(+):(*R*)-(−) ratios of 0:100 for California (Birch et al., 1980) and Idaho (similar to southwestern BC) (Plummer et al., 1976), and 65:35 for New York beetles (Lanier et al., 1980).

When the mean chiralities of ipsdienol in the same three populations were estimated from our pooled data (Table 1), the estimates did agree with the published estimates (*t* tests, $P > 0.05$). The bias in the estimator using pooled data is due to weak but significant correlations between the quantities and chiralities of ipsdienol in individual males (Table 1). However, the correlations are not consistent between the populations and change in magnitude and sign. Although ratio estimates on pooled samples are biased estimates of the true population means, they do reflect the overall chirality of ipsdienol produced by several hundred males on a single tree or log. The possibility exists that individuals attracted by the pooled pheromone from a large group of males may be favored differentially, by natural selection, over individuals attracted to the pheromone produced by an average male. Both methods of estimating chirality are valid but must be clearly stated and interpretation of the data related to the appropriate level of selection.

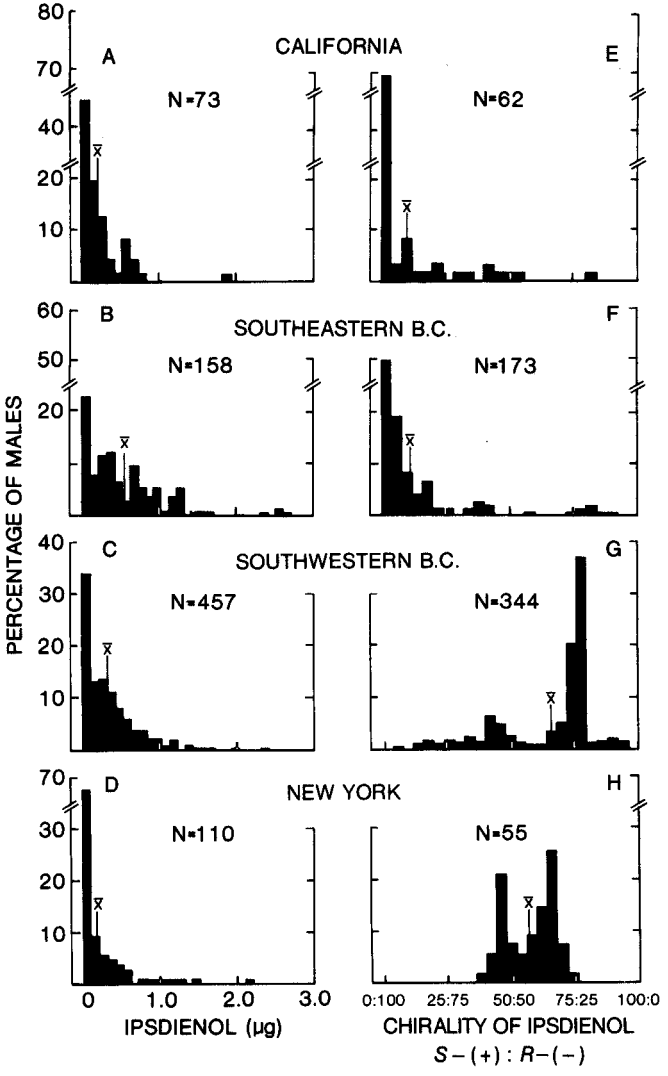

FIG. 2. Frequency distributions of the quantities (A–D) and the chiralities (E–H) of the aggregation pheromone, ipsdienol, produced by male pine engravers, *Ips pini* (Say). Means are denoted by $\bar{X}$.

The population from southwestern BC (Figure 2G) is remarkably different from the other two western populations (Figure 2E, F). Males in this population produced primarily (*S*)-(+)-ipsdienol with a mean (*S*)-(+):(*R*)-(−) ratio of 66:34 (Table 1). This population negates previous generalizations that western populations of *I. pini* are homogeneous with respect to the chirality of their aggregation pheromone. Of the four populations studied, this is the only population in which there is no correlation between quantities and chiralities of ipsdienol in individual males (Table 1). Both mean and pooled estimators of chirality yielded the same result.

Intrapopulation variation in the chirality of ipsdienol was found in all four populations (Figure 2E–H) with coefficients of variation ranging from 13.2% to 33.2% (Table 1). Variation in the modalities of the four distributions of the chirality of ipsdienol is also apparent. The distributions for the populations from California and southeastern BC have long tails but are strongly centered around an (*S*)-(+):(*R*)-(−) ratio between 5:95 and 15:85, with only one mode in each. Bimodality is evident in the New York population, with both modes almost equal in size. In the population from southwestern BC, the modes are distinctly different in size with the major mode between 75:25 and 80:20 (*S*)-(+):(*R*)-(−). Both New York and southwestern BC populations have modes between 40:60 and 45:55 (*S*)-(+):(*R*)-(−). The earlier estimates from pooled samples (Stewart, 1975; Plummer et al., 1976; Birch et al., 1980; Lanier et al., 1980) failed to disclose these striking differences between individuals in the same population as well as the bimodality in some populations.

DISCUSSION

In bark beetles, a pheromone message should be a reliable indicator of either host quality or the genetic quality of the sender. This message should not be subject to chance variation or noise. In *I. pini*, we found that there is substantial variation in both quantity and chirality of ipsdienol. Most of the variation in quantity can probably be attributed to variation in vigor and environmental factors, such as brood host and levels of precursors in the host tissue. Production of the pheromone, *cis*-verbenol, by male *I. paraconfusus* increased directly with the concentration of vapors of the precursor, (−)-α-pinene (Byers, 1981). In *I. typographus*, over 80% of the variation in quantities of *cis*-verbenol, *trans*-verbenol, and myrtenol were explained by the variation in the amounts of α-pinene in the host (Birgersson et al., 1984). In addition, the quantity of pheromone in the hindgut may vary over time in the same individual. The rates of ingestion and defecation may not be constant.

The major factors responsible for the variation in chirality of ipsdienol are not the same as those responsible for the variation in quantity. No more than

25% of the variation in chirality of ipsdienol in any population was explained by the variation in the quantity of ipsdienol (all $r^2 < 0.25$). In southwestern BC less than 1% of the variation in the chirality of ipsdienol was explained by the variation in quantity of ipsdienol ($r^2 < 0.01$). Since both enantiomers are produced from the same achiral precursor, myrcene (Hughes, 1974; Byers et al., 1979; Renwick and Dickens, 1979; Hendry et al., 1980; Byers, 1981; Fish et al., 1984), it seems unlikely that environmental factors should significantly affect the chirality of ipsdienol, certainly not to the extent seen in the quantity of ipsdienol. Variation in enzymatic composition due to genetic variation is the most probable source of the variation in chirality.

Our data are consistent with the hypothesis that the production of ipsdienol of a specific chirality by an individual male *I. pini* is a quantitative genetic trait. We are currently trying to quantify the variation in behavioral responses associated with ipsdienol. We plan to determine the heritability of both the production of and the responses to chiral ipsdienol in individual beetles. To date, heritability of pheromone quality has been clearly estimated only for the pink bollworm, *Pectinophora gossypiella* (Saunders). Collins and Cardé (1985) found that the heritability of the sex pheromone blend of the *Z,E* and *Z,Z* isomers of 7,11-hexadecadienyl acetate, produced by female *P. gossypiella* from a laboratory strain was 0.34. The variation of the chirality of ipsdienol in *I. pini* (Table 1) is more than that of the *E*:*Z* ratio of the sex pheromone in *P. gossypiella* (CV = 5.3%). Assuming that there is a large heritable component to the variation in ipsdienol chirality, then such high levels of variation should facilitate microevolutionary changes in relatively short periods of time, possibly giving rise to further geographic variation in *I. pini*.

In addition, bimodality in the populations from New York and southwestern BC suggests that distinct groups exist within populations and that disruptive selection may be occurring in these areas. The modes may separate further and possibly result in behavioral isolation and subsequent speciation. Alternatively, bimodality may be stable in these populations, representing mixed evolutionary stable strategies (Smith, 1982) in which individuals from both modes have equal fitness, on average.

Knowledge of the variation and heritability in the use of pheromones should help predict the consequences of artificial selection pressures such as mass trapping. Bark beetles are major economic pests of forestry (Furniss and Carolin, 1980), and pheromones are gaining acceptance as pest management tools. If pheromones are used to mass trap *I. pini*, would "resistance" to pheromone baits occur? Lanier et al. (1972) suggested that some populations of *I. pini* are already resistant to a single pheromone blend. Since the levels of variation of ipsdienol chirality were high in all four populations of *I. pini* (Table 1), we hypothesize that resistance to a pheromone blend could develop within a population as well. The development of resistance has been shown in laboratory

colonies of the khapra beetle, *Trogoderma granarium* Everts. After 18 generations of selection for nonresponse by males, there was a 74% reduction in mean response by males to the natural pheromone produced by female beetles (Rahalkar et al., 1985). The possibility exists that populations of bark beetles, such as *I. pini*, subjected to repeated use of pheromone-based trapping programs using a fixed pheromone blend, could develop resistance by shifting to another pheromone blend (Lanier et al., 1972; Lanier and Burkholder, 1974).

Competition for Pheromone Channels of Communication. An understanding of the mechanisms of any behavior must go along with an understanding of the functional value of that behavior. With respect to any insect using pheromones, we need to ask why a pheromone blend exists as well as how. Selection should favor individuals that use a communication system, such as pheromones, that minimizes the expenditure of energy and time (Matthews and Matthews, 1978). The pheromone blends used by different insect species can be called pheromone channels of communication (Cardé and Baker, 1984). Each channel is comprised of a cluster of points in an *n*-dimensional space. Each axis, in this space, is an array of quantities of a single and unique semiochemical. The coordinates of each point represent one possible pheromone blend that has a probability, greater than zero, of successfully communicating the pheromone message. The density of points varies within the cluster. The highest density is located centrally and represents the optimal pheromone blend for communication. In tortricid moths, the dimensions of the pheromone channels consist of a variety of 12- and 14-carbon-chain-length acetates, aldehydes, and alcohols, and their isomers when double bonds are present along the carbon chain (Cardé and Baker, 1984).

Bark beetles use pheromones to transmit information about location to conspecifics, usually to facilitate mating or feeding. In British Columbia, 82 scolytid species have been found either on or in lodgepole pine; at least 56 species breed in lodgepole pine (Bright, 1976; S.L. Wood, 1982; Evans, 1983). Although most of these species have not been investigated for the use of pheromones, the ubiquitousness of pheromone communication in the Scolytidae (Klassen et al., 1982) suggests that such communication should oceur in many of the 56 species breeding in lodgepole pine. The number of potential competitors for pheromone channels of communication just among bark beetles is very high. In addition, there are insects in 10 other orders that are known to use pheromone communication (Klassen et al., 1982), many of which have representatives in stands of lodgepole pine (Furniss and Carolin, 1980). If the number of channels, particularly those with the best physiochemical traits for communication, is limited, then competition for pheromone channels should occur, particularly if the channels also differ in quality as a communication system.

If competition does occur, then three major predictions can be made.

Firstly, sympatric species of bark beetles should use separate and distinct pheromone channels in order to minimize competition for a resource or to maintain species specificity in mating (D.L. Wood, 1970; Lanier and Burkholder, 1974; Cardé and Baker, 1984; West-Eberhard, 1984). In California, the pheromone channel for *I. pini* is comprised primarily of (*R*)-(−)-ipsdienol (Birch et al., 1980; Plummer et al., 1976) (Figure 2E). The channel for the sympatric species, *I. paraconfusus*, is a blend of (*S*)-(+)-ipsdienol, (*S*)-*cis*-verbenol and (*S*)-(−)-ipsenol (Silverstein et al., 1966a,b; D.L. Wood et al., 1967, 1968).

Secondly, if competition is structuring the use of pheromones, then the channels should not only be distinct, they should also be widely separated (Matthews and Matthews, 1978; Cardé and Baker, 1984). Widely separated signals (i.e., signals with high signal-to-noise ratios) minimize the possibility of making a costly mistake. The cost may involve loss of time or energy or may be a higher risk of predation because of greater exposure time before finding a host or mate.

In California *I. pini* and *I. paraconfusus* seem to have separated their channels almost maximally with respect to the chirality of ipsdienol and with respect to the presence of ipsenol (Light and Birch, 1977). *I. pini* produces primarily (*R*)-(−)-ipsdienol (Plummer et al., 1976) (Figure 2E) and response is inhibited by ipsdienol when the percentage of the (*S*)-(+) enantiomer is greater than 5% (Birch et al., 1980). Most male *I. paraconfusus* produce ipsdienol with a chiral ratio probably between 90:10 (Silverstein and Young, 1976) and 95:5 (*S*)-(+):(*R*)-(−) (Stewart, 1975). Response of *I. paraconfusus* to ipsdienol is inhibited when the chirality is predominantly (*R*)-(−) (Light and Birch, 1977; Birch et al., 1980). *I. paraconfusus* also uses (*S*)-(−)-ipsenol as part of its pheromone channel (Silverstein et al., 1966a,b; D.L. Wood et al., 1967, 1968). (*S*)-(−)-Ipsenol inhibits response of *I. pini* to (*R*)-(−)-ipsdienol (Birch and Wood, 1975; Birch and Light, 1977; Birch et al., 1977).

Lastly, one should expect geographic variation in the specificity and separation of pheromone channels due to geographic differences in competition pressures (Cardé and Baker, 1984). Competition pressure should increase with either an increase in the absolute number of scolytid species or an increase in the number of superior competitors. In areas where the pressure is lower, the channels should be either different or broader. In California *I. pini* is sympatric with *I. paraconfusus* and uses primarily (*R*)-(−)-ipsdienol (Birch et al., 1980) (Figure 2E). In New York where *I. paraconfusus* is absent (S.L. Wood, 1982), *I. pini* produces ipsdienol with (*S*)-(+):(*R*)-(−) ratios close to 50:50 (Figure 2H). Furthermore, the variation in chiral ratios is greater in the New York population than in the population from California (Table 1).

These three predictions are fairly straightforward; however, not all of our evidence appears to support them. For example, separation of all channels does not seem maximal. In 15 species of *Ips* studied to date, males in 14 species

produce ipsdienol and males in 10 produce ipsenol (Vité et al., 1972; Lanier and Burkholder, 1974; Francke et al., 1980; Borden, 1982; D.L. Wood, 1982). Three species of *Pityokteines* use ipsenol and two use ipsdienol (Harring, 1978). Ipsdienol is produced by males in four species of *Dendroctonus* following exposure to myrcene vapors (Hughes, 1973; Renwick et al., 1976; Byers, 1982; Hunt et al., 1986). One possibility is that physiochemical constraints limit the dimensions of pheromone channels to very few compounds, such as ipsenol and ipsdienol (Silverstein, 1977; Cardé and Baker, 1984). Another possibility is that parsimony of semiochemicals is beneficial (Blum, 1970, 1977). One compound may serve as a pheromone in various ways, or as an allomone or a kairomone, depending on the context in which it is used. The advantage may be a saving in production or receptor hardware without giving up the potential for a diversity of messages (Matthews and Matthews, 1978).

Another area of uncertainty regarding our predictions is that existing geographic differences are not all easily explained, nor do differences necessarily exist when they should, according to our predictions. *I. pini* is sympatric with *D. brevicomis* and *D. ponderosae* in both southwestern and southeastern BC (S.L. Wood, 1982), yet populations of *I. pini* from these two regions produce ipsdienol with different chiral ratios (Figure 2F, G). *I. paraconfusus* is not found in Canada (Bright, 1976), but the distribution of chiral ratios for *I. pini* is not much different between southeastern BC and California (Figure 2E, F). It is possible that some of the geographic variation may be a product of colonization of *I. pini* from different refugia following the last Ice Age.

Clearly, there is a need for more baseline information on the use of semiochemicals by all competing species in a given habitat before the selection pressures can be elucidated. An understanding of the population genetics in the use of pheromones should facilitate the testing of quantitative predictions about the various selection pressures affecting pheromone production and response and elucidate the importance of competition in structuring communities of bark and ambrosia beetles (Sturgeon and Mitton, 1982). Our data on the variation of pheromone production in *I. pini* constitute only one step towards understanding the mechanism structuring pheromone channels of communication. The hypothesis that competition is the major driving force in the structuring of pheromone channels in communities of bark beetles is still the most supportable, but the effects of competition may be dampened by benefits of parsimony of semiochemicals, in which many species share certain semicochemicals for differing reasons (Blum, 1970, 1977).

Acknowledgments—We thank G.N. Lanier and D.L. Wood for their continual support and encouragement. G.N. Lanier and S. Seybold kindly supplied beetles from New York and California, respectively. E.K. Czyzewska resolved both enantiomers of ipsdienol, and G.G.S. King provided assistance with gas chromatography. The research was supported by an H.R. MacMillan Family Fund Fellowship to the senior author and by the Natural Sciences and Engineering Research Council, Canada, Operating Grants A3881, A3785, and A0851; and Strategic Grant G1039.

REFERENCES

ANDERSON, R.F. 1948. Host selection by the pine engraver. *J. Econ. Entomol.* 41:596–602.

BIRCH, M.C. 1984. Aggregation in bark beetles, pp. 331–353, *in* W.J. Bell and R.T. Cardé (eds.). Chemical Ecology of Insects. Chapman and Hall, London.

BIRCH, M.C., and LIGHT, D.M. 1977. Inhibition of the attractant pheromone response in *Ips pini* and *I. paraconfusus* (Coleoptera: Scolytidae): field attraction of ipsenol and linalool. *J. Chem. Ecol.* 3:257–267.

BIRCH, M.C., and WOOD, D.L. 1975. Mutual inhibition of the attractant pheromone response by two species of *I ps* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 1:101–113.

BIRCH, M.C., LIGHT, D.M., and MORI, K. 1977. Selective inhibition of response of *Ips pini* to its pheromone by the (*S*)-(−)-enantiomer of ipsenol. *Nature* 270:738–739.

BIRCH, M.C., LIGHT, D.M., WOOD, D.L., BROWNE, L.E., SILVERSTEIN, R.M., BERGOT, B.J., OHLOFF, G., WEST, J.R., and YOUNG, J.C. 1980. Pheromonal attraction and allomonal interruption of *Ips pini* in California by the two enantiomers of ipsdienol. *J. Chem. Ecol.* 6:703–717.

BIRGERSSON, G., SCHLYTER, F., LÖFQVIST, J., and BERGSTRÖM, G. 1984. Quantitative variation of pheromone components in the spruce bark beetle *Ips typographus* from different attack phases. *J. Chem. Ecol.* 10:1029–1055.

BLUM, M.S. 1970. The chemical basis of insect sociality, pp. 61–94, *in* M. Beroza (ed.). Chemicals Controlling Insect Behavior. Academic Press, New York.

BLUM, M.S. 1977. Behavioral responses of Hymenoptera to pheromones and allomones, pp. 149–167, *in* H.H. Shorey and J.J. McKelvey, Jr. (eds.). Chemical Control of Insect Behavior. John Wiley & Sons, New York.

BORDEN, J.H. 1967. Factors influencing the response of *Ips confusus* (Coleoptera: Scolytidae) to male attractant. *Can. Entomol.* 99:1164–1193.

BORDEN, J.H. 1982. Aggregation pheromones, pp. 74–139, *in* J.B. Mitton and K.B. Sturgeon (eds.). Bark Beetles in North American Conifers. University of Texas Press, Austin, Texas.

BORDEN, J.H., HUNT, D.W.A., MILLER, D.R., and SLESSOR, K.N. 1986. Orientation in forest Coleoptera: An uncertain outcome of responses by individual beetles to variable stimuli, pp. 97–109, *in* T.L. Payne and M.C. Birch (eds.). Mechanisms in Insect Olfaction. Oxford University Press, New York.

BRIGHT, D.E., JR. 1976. The bark beetles of Canada and Alaska (Coleoptera: Scolytidae). Agriculture Canada Publ. 1576.

BRIGHT, D.E., JR., and STARK, R.W. 1973. The bark and ambrosia beetles of California: Scolytidae and Platypodidae. *Bulletin of the California Insect Survey* 16. University of California Press, Berkeley, California.

BYERS, J.A. 1981. Pheromone biosynthesis in the bark beetle, *Ips paraconfusus*, during feeding or exposure to vapours of host plant precursors. *Insect Biochem.* 11:563–569.

BYERS, J.A. 1982. Male-specific conversion of the host plant compound myrcene to the pheromone (+)-ipsdienol, in the bark beetle, *Dendroctonus brevicomis*. *J. Chem. Ecol.* 8:363–371.

BYERS, J.A., WOOD, D.L., BROWNE, L.E., FISH, R.H., PIATEK, B., and HENDRY, L.B. 1979. Relationship between a host plant compound myrcene, and pheromone production in the bark beetle, *Ips paraconfusus*. *J. Insect Physiol.* 25:477–482.

CARDÉ, R.T., and BAKER, T.C. 1984. Sexual communication with pheromones, pp. 355–383, *in* W.J. Bell and R.T. Cardé (eds.), Chemical Ecology of Insects. Chapman and Hall, New York.

CHAMBERLIN, W.J. 1958. The Scolytoidea of the Northwest—Oregon, Washington, Idaho and British Columbia. Oregon State Monographs. Studies in Entomology, No. 2. Oregon State University Press, Corvallis, Oregon.

COLLINS, R.D., and CARDÉ, R.T. 1985. Variation in and heritability of aspects of pheromone

production in the pink bollworm moth, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). *Ann. Entomol. Soc. Am.* 78:229–234.

EVANS, D. 1983. Annotated checklist of insects associated with native pines in British Columbia. Canadian Forest Service Information Report BC-X-244.

FISH, R.H., BROWNE, L.E., and BERGOT, B.J. 1984. Pheromone biosynthetic pathways: Conversion of ipsdienone to (−)-ipsdienol, a mechanism for enantioselective reduction in the male bark beetle, *Ips paraconfusus*. *J. Chem. Ecol.* 10:1057–1064.

FRANCKE, W., SAUERWEIN, P., VITÉ, J.P., and KLIMETZEK, D. 1980. The pheromone bouquet of *Ips amitinus*. *Naturwissenschaften* 67:147–148.

FURNISS, R.L., and CAROLIN, V.M. 1980. Western Forest Insects. *USDA Forest Service Miscellaneous Publication* No. 1339.

HARRING, C.M. 1978. Aggregation pheromones of the European fir engraver beetles *Pityokteines curvidens*, *P. spinidens* and *P. vorontzovi* and the role of juvenile hormone in pheromone biosynthesis. *Z. Angew. Entomol.* 85:281–317.

HENDRY, L.B., PIATEK, B., BROWNE, L.E., WOOD, D.L., BYERS, J.A., FISH, R.H., and HICKS, R.A. 1980. *In vivo* conversion of a labelled host plant chemical to pheromones of the bark beetle *Ips paraconfusus*. *Nature* 284:485.

HUGHES, P.R. 1973. *Dendroctonus*: Production of pheromones and related compounds in response to host monoterpenes. *Z. Angew. Entomol.* 73:294–312.

HUGHES, P.R. 1974. Myrcene: A precursor of pheromones in *Ips* beetles. *J. Insect Physiol.* 20:1271–1275.

HUNT, D.W.A., BORDEN, J.H., PIERCE, H.D., JR., SLESSOR, K.N., KING, G.G.S., and CZYZEWSKA, E.K. 1986. Sex-specific production of ipsdienol and myrcenol by *Dendroctonus ponderosae* (Coleoptera: Scolytidae) exposed to myrcene vapors. *J. Chem. Ecol.* 12:1579–1586.

KLASSEN, W., RIDGWAY, R.L., and INSCOE, M. 1982. Chemical attractants in integrated pest management programs, pp. 13–130, *in* A.F. Kydonieus and M. Beroza (eds.). Insect Suppression with Controlled Release Pheromone Systems. CRC Press, Boca Raton, Florida.

LANIER, G.N. 1972. Biosystematics of the genus *Ips* (Coleoptera: Scolytidae) in North America. Hopping's groups IV and X. *Can. Entomol.* 104:361–388.

LANIER, G.N., and BURKHOLDER, W.E. 1974. Pheromones in speciation of Coleoptera, pp. 161–189, *in* M.C. Birch (ed.). Pheromones. North-Holland, London.

LANIER, G.N., BIRCH, M.C., SCHMITZ, R.F., and FURNISS, M.M. 1972. Pheromones of *Ips pini* (Coleoptera: Scolytidae): Variation in response among three populations. *Can. Entomol.* 104:1917–1923.

LANIER, G.N., CLASSON, A., STEWART, T., PISTON, J.J., and SILVERSTEIN, R.M. 1980. *Ips pini:* The basis for interpopulational differences in pheromone biology. *J. Chem. Ecol.* 6:677–687.

LIGHT, D.M., and BIRCH, M.C. 1977. Inhibition of the attractive pheromone response of *Ips paraconfusus* by (*R*)-(−)-ipsdienol. *Naturwissenschaften* 66:159–160.

MATTHEWS, R.W., and MATTHEWS, J.R. 1978. Chemical communication, pp. 176–233, *in* R.W. Matthews and J.R. Matthews (eds.). Insect Behavior. John Wiley & Sons, New York.

PLUMMER, E.L., STEWART, T.E., BYRNE, K., PEARCE, G.T., and SILVERSTEIN, R.M. 1976. Determination of the enantiomeric composition of several insect pheromone alcohols. *J. Chem. Ecol.* 2:307–331.

RAHALKAR, G.W., TAMHANHAR, A.J., and GOTHI, K.K. 1985. Selective breeding for reduced male response to female sex pheromone in *Trogoderma granarium* Everts (Coleoptera: Dermestidae). *J. Stored Prod. Res.* 21:123–126.

RENWICK, J.A.A., and DICKENS, J.C. 1979. Control of pheromone production in the bark beetle, *Ips cembrae*. *Physiol Entomol.* 4:377–381.

RENWICK, J.A.A., HUGHES, P.R., PITMAN, G.B., and VITÉ, J.P. 1976. Oxidation products of terpenes identified from *Dendroctonus* and *Ips* bark beetles. *J. Insect Physiol.* 22:725–727.

ROELOFS, W.L., and CARDÉ, R.T. 1974. Sex pheromones in the reproductive isolation of lepidopterous species, pp. 96–114, *in* M.C. Birch (ed.). Pheromones. North-Holland, London.

SCHLYTER, F., BIRGERSSON, G., BERGSTRÖM, G., and LÖFQVIST, J. 1985. Field response of the spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates, pp. 135–157, *in* F. Schlyter, Fil. kand. Ld dissertation. University of Lund, Lund, Sweden.

SILVERSTEIN, R.M. 1977. Complexity, diversity, and specificity of behavior-modifying chemicals: Examples mainly from Coleoptera and Hymenoptera, pp. 231–251, *in* H.H. Shorey and J.J. McKelvey, Jr. (eds). Chemical Control of Insect Behavior. John Wiley & Sons, New York.

SILVERSTEIN, R.M., and YOUNG, J.C. 1976. Insects generally use multicomponent pheromones, pp. 1–29, *in* M. Beroza (ed.). Pest Management with Insect Sex Attractants. ACS Symposium Series 23.

SILVERSTEIN, R.M., RODIN, J.O., and WOOD, D.L. 1966a. Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. *Science* 154:509–510.

SILVERSTEIN, R.M., RODIN, J.O., WOOD, D.L., and BROWNE, L.E. 1966b. Identification of two new terpene alcohols from frass produced by *Ips confusus* in ponderosa pine. *Tetrahedron* 22:1929–1936.

SLESSOR, K.N., KING, G.G.S., MILLER, D.R., WINSTON, M.L., and CUTFORTH, T.L. 1985. Determination of chirality of alcohol or latent alcohol semiochemicals in individual insects. *J. Chem. Ecol.* 11:1659–1667.

SMITH, J.M. 1982. Evolution and the Theory of Games. Cambridge University Press, New York.

SOKAL, R.R., and ROHLF, F.J. 1981. Biometry, 2nd ed. W.H. Freeman, San Francisco, California.

STEWART, T.E. 1975. Volatiles isolated from *Ips pini*: Isolation, identification, enantiometric composition, biological activity. MSc thesis. College of Environmental Science and Forestry, SUNY, Syracuse, New York.

STURGEON, K.B., and MITTON, J.B. 1982. Evolution of bark beetle communities, pp. 350–393, *in* J.B. Mitton and K.B. Sturgeon (eds.). Bark Beetles in North American Conifers. University of Texas Press, Austin, Texas.

SVIHRA, P., BIRCH, M.C., and PAINE, T.D. 1980. Interspecific olfactory communications in southern pine beetles. *Naturwissenschaften* 67:518–520.

VITÉ, J.P., BAKKE, A., and RENWICK, J.A.A. 1972. Pheromone in *Ips* (Coleoptera: Scolytidae): Occurrence and production. *Can. Entomol.* 104:1967–1975.

WEST-EBERHARD, M.J. 1984. Sexual selection, competitive communication and species-specific signals in insects, pp. 283–324, *in* T. Lewis (ed.). Insect Communication. Academic Press, New York.

WOOD, D.L. 1970. Pheromones of bark beetles, pp. 301–316, *in* D.L. Wood, R.M. Silverstein, and M. Naajima (eds.). Control of Insect Behavior by Natural Products. Academic Press, New York.

WOOD, D.L. 1982. The role of pheromones, kairomones and allomones in the host selection and colonization behavior of bark beetles. *Annu. Rev. Entomol.* 27:411–426.

WOOD, D.L., STARK, R.W., SILVERSTEIN, R.M., and RODIN, J.O. 1967. Unique synergistic effects produced by the principal sex attractant compounds of *Ips confusus* (LeConte) (Coleoptera: Scolytidae). *Nature* 215: 206.

WOOD, D.L., BROWNE, L.E., BEDARD, W.D., TILDEN, P.E., SILVERSTEIN, R.M., and RODIN, J.O. 1968. Response of *Ips confusus* to synthetic sex pheromones in nature. *Science* 159:1373–1374.

WOOD, S.L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs* 6.