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MUTUAL INHIBITION OF THE ATTRACTANT PHEROMONE RESPONSE BY TWO SPECIES OF *Ips* (COLEOPTERA: SCOLYTIDAE)[1]

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Abstract—The bark beetles, *Ips pini* and *I. paraconfusus*, are not cross-attractive in the field although they attack the same host material at the same time. Logs containing the pheromone-producing sex (males) of both species side by side attract significantly fewer beetles of each species than do males of either species alone. Ipsenol, a component of the male *I. paraconfusus* pheromone, duplicates the activity of male *I. paraconfusus* in inhibiting the response of *I. pini* to male *I. pini*. Linalool from male *I. pini* also reduces the catch of *I. paraconfusus* in response to male *I. paraconfusus*. Simultaneous production of a specific attractant pheromone and an interspecific chemical inhibitor favors exclusive use of the host substrate by the first arriving species.

Key Words—pheromone, inhibition, Scolytidae, *Ips*, *pini*, *paraconfusus*, ipsenol, linalool.

INTRODUCTION

The two bark beetle species, *Ips pini* (Say) and *I. paraconfusus* Lanier, are largely allopatric. They broadly overlap, however, in Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) over 5,000 feet elevation in the central Sierra Nevada mountains of California, and in ponderosa pine (*P. ponderosa* Laws.) in the southern Cascade mountain range. They occur in the same forest stands

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and infest the same portions of their common host, i.e., tops and limbs broken by wind or snow, logging slash, and large portions of the main bole. Both species attack this material at the same time of day and year. The two species are, however, seldom found in the same piece of host material and their galleries are not known to be intermixed.

It has been postulated that breeding isolation is maintained in sympatric species of *Ips* primarily by the specificity of their pheromones (Lanier, 1966; Wood, 1970; Lanier and Wood, 1975). The presence of only one species in any single piece of host material can similarly be attributed to the specificity of their pheromone systems. Earlier tests with these two species had shown that bolts containing either male *I. pini* or male *I. paraconfusus* do not attract the other species in the field (Lanier et al., 1972). In this paper we present experimental evidence suggesting that two mechanisms are involved in maintaining breeding isolation between *I. pini* and *I. paraconfusus* where they are sympatric: (1) specificity, in that attractant pheromones produced by one species are attractive only to that species, and (2) inhibition when the attraction response evoked by pheromones of one species is inhibited by volatile compounds produced by the other and vice versa.

METHODS AND MATERIALS

All field experiments but one were conducted during the summer and autumn of 1973 in the McCloud Flats area of the Shasta-Trinity National Forest, Siskiyou County, California. The area comprises approximately 50 square miles of ponderosa pine stands with abundant host material for *Ips*, originating from winter storm damage, logging activities, and chronic tree mortality caused by *Dendroctonus brevicomis* LeConte and *D. ponderosae* Hopkins. The one field test using linalool was conducted in the Sierra National Forest, Madera County, California, in a mixed conifer forest at 5,000 feet elevation where *I. paraconfusus* was known to be flying in the autumn of 1973.

Infested ponderosa pine was obtained from the McCloud Flats area and adult beetles were collected and sexed as they emerged from these logs in the laboratory (Browne, 1972).

Field evaluations followed procedures established over several years of work with species in this genus (Wood et al., 1968; Bedard and Browne, 1969; Lanier et al., 1972; Browne et al., 1973). Treatments, i.e., bolts containing males of either or both species, were placed into wire-mesh cylinders coated with Stikem Special® on pipe standards 4 feet above the ground. Each test consisted of several treatments set out at 50-meter intervals in a line. After each replication, i.e., one treatment in a given position for a 24-

hour period, the treatments were interchanged in a systematized way so that no treatment occupied the same site twice in any test. Beetles trapped during each replication were picked from the screens, placed in solvent, and later examined in the laboratory to check field identifications and to determine sex ratios.

Three separate field tests were conducted in which bolts of ponderosa pine containing both male *I. pini* and male *I. paraconfusus* side by side in the same bolt were compared with bolts containing each species separately and with bolts containing no beetles. Two densities of beetles were introduced into holes drilled in 25-cm bolts of ponderosa pine: 25 beetles of one species alone, or 25 plus 25 when the two species were combined; and 50 of one species alone, or 50 plus 50 when combined. Beetles were constrained in these holes by a fine metal screen, and each entire bolt was also wrapped with the same screen to prevent voluntary attacks by any of the wild population that may have evaded the sticky cylinder.

Materials assayed for biological activity were concentrates of volatiles from ponderosa pine logs infested with male beetles, synthetic ipsenol (2-methyl-6-methylene-7-octen-4-ol), and linalool (3,7-dimethyl-1,6-octadien-3-ol). Concentrates of volatile materials associated with male beetles boring in ponderosa pine were obtained by the method of Browne et al. (1973). In this procedure, a known number of males are inserted into holes drilled into the bark and phloem tissue of the host log, and the volatile attractants produced by these males boring for several days are condensed in a trap immersed in liquid nitrogen. The concentrate of condensed volatiles used for assay is obtained by ether extraction of the aqueous condensate followed by distillation of the ether. The concentrate can be diluted and eluted at a rate comparable to that of a stated number of males boring in a bolt per unit time, a rate expressed as beetle-minutes/minute (Browne et al., 1973).

Ipsenol was obtained from Chemical Samples Company, Cleveland, Ohio, at 95% purity and "research grade" linalool from Matheson Coleman and Bell. Both were further purified by gas-liquid chromatography in our laboratory to approximately 98% purity. Ipsenol is one of three synergistic terpene alcohols identified as the attractant pheromone produced by male *I. paraconfusus* (Silverstein et al., 1966), but apparently not by males of *I. pini* (Vité et al., 1972). Ipsenol was tested here following a preliminary field evaluation of potential attractant compounds for *I. pini* in 1972 (unpublished data). In that test, trap catches were reduced when ipsenol was eluted together with a bolt containing male *I. pini*, compared to catches on traps with male *I. pini* bolts alone. Linalool was tested following the concept of "differential diagnosis" (Vité and Renwick, 1970), since it is an isomer of ipsenol, does not occur in male *I. paraconfusus*, but is produced by male *I. pini* (Young et al., 1973*a*) and female *I. paraconfusus* (Young et al., 1973*a*), both of which

TABLE 1. EFFECT OF MALE *I. paraconfusus* AND MALE *I. pini* BORING SIDE BY SIDE IN THE SAME BOLT ON THE ATTRACTANT RESPONSE OF BOTH SPECIES: MCCLOUD FLATS, CALIFORNIA, 1973. MEAN NUMBER (RANGE IN PARENTHESES) AND SEX RATIO OF SPECIES TRAPPED ARE LISTED BY TREATMENT IN EACH TEST

	Treatment (males in bolt)	*I. pini*	♂:♀	*I. paraconfusus*	♂:♀	*E. lecontei*
Test 1[a]	25 ♂♂ *I. pini*	**21.0**[b1] (4–53)	1:2.0[c]	**0**	—	**0.5**[d] (0–1)
	25 ♂♂ *I. paraconfusus*	**0**	—	**2.8**[b4] (1–5)	1:0.9	**0.5** (0–2)
	25 ♂♂ *I. pini*+ 25 ♂♂ *I. paraconfusus*	**2.7**[b1] (0–10)	1:1.6	**0.2**[b4] (0–1)	—	**1.0** (0–4)
Test 2	25 ♂♂ *I. pini*	**27.8**[b2] (7–64)	1:1.2	**0**	—	**4.8** (0–12)
	25 ♂♂ *I. paraconfusus*	**0**	—	**4.0** (0–10)	1:1.4	**4.5** (1–9)
	25 ♂♂ *I. pini*+ 25 ♂♂ *I. paraconfusus*	**4.3**[b2] (1–8)	1:2.2	**0**	—	**6.0** (0–13)
Test 3	50 ♂♂ *I. pini*	**28.3**[b3] (5–64)	1:1.8	**0**	—	**5.6** (2–15)
	50 ♂♂ *I. paraconfusus*	**0**	—	**29.8**[b5] (5–51)	1:3.1	**4.5** (1–9)
	50 ♂♂ *I. pini*+ 50 ♂♂ *I. paraconfusus*	**11.3**[b3] (2–22)	1:1.7	**0.2**[b5] (0–1)	—	**6.6** (1–21)
Controls	Bolt containing no males (1 in each test)	**0**	—	**0**	—	**0.2** (0–1)

[a] Test 1: June 20–23, 1973. Tests 2 and 3: July 7–12, 1973. Six replicates of each treatment through time in each test.

[b] The probability (Student's *t* test) that means of trap catches assigned the same number would be obtained by chance is: (1) $P<0.05$; (2) $P<0.025$; (3) $P<0.2$ (NSD); (4) $P<0.005$; (5) $P<0.005$.

[c] Sex ratios of *I. pini* trapped within any test are not significantly different ($P>0.9$, χ^2 test).

[d] The probability (Student's *t* test) that means of trap catches of *E. lecontei* within each test would be obtained by chance is: Test 1, $P>0.5$; Test 2, $P>0.5$; Test 3, $P<0.4$.

reduce catches of *I. paraconfusus* on traps containing male *I. paraconfusus* bolts in the field (Table 1; Dahlsten, Wood and Bedard, unpublished).

Ipsenol and linalool were evaporated from 5-μl capillary tubes open at both ends (Drummond micro-caps®). The tubes were held in a vertical

position by taping them to the inside of a 35-mm film canister with holes drilled in its screw cap. The rate of evaporation of both ipsenol and linalool was approximately 1 mg over a 24-hour period, most of which probably evaporated during the daytime. This rate of evaporation was comparable to that used in earlier experiments with *I. paraconfusus* by Wood et al. (1968). The precise rate at which ipsenol is released by boring male *I. paraconfusus* is now being determined using the methods developed by Browne et al. (1973).

The response of beetles to the test materials in the laboratory was estimated by the number of beetles walking upwind to the source, in a multiple-choice, open-arena olfactometer (Wood et al., 1966). Beetles were assayed in groups of ten for a total of 50 to each stimulus. Those reaching the source after one or two attempts were scored as positive. Concentrates were eluted at a rate found to elicit a 70–80% response from females on the day of testing. Actual rates varied but were never above one beetle-minute/minute and were often much lower. The dosage level of ipsenol at 1×10^{-6} g/minute was used since this was the minimum level, at the time of testing, at which ipsenol alone elicited a measurable positive response from female *I. paraconfusus*.

RESULTS

Mutual Inhibition in the Field

In all three tests the bolts containing males of both species caught significantly fewer beetles of both species than did bolts containing males of either species alone (Table 1). Essentially no cross-attraction was found between the species as measured by trap catch on bolts infested with males of only one species.

Dissection of the bolts after Test 1 showed that there was no significant difference in the success of establishment of either species when alone, compared to both species when they were together in the same bolt. Only one or two individuals of either species failed to initiate boring activity in all cases. In addition, the activity of the males, as indicated by the extent of phloem excavation, did not differ noticeably between bolts containing both species together or separately. Thus it appeared that males of neither species were inhibiting the production of frass by the other species. This does not rule out the possibility, however, that production and/or composition of the pheromone present in the frass could be changed when males of both species are in close proximity.

The presence of male *I. pini* and male *I. paraconfusus* reduced the catch of *I. paraconfusus* over *I. paraconfusus* bolts alone by 97% on 25-male bolts

TABLE 2. INHIBITION OF THE ATTRACTANT RESPONSE OF FEMALE *I. paraconfusus* BY PHEROMONE CONCENTRATE FROM *I. pini* IN THE LABORATORY

Concentrate	Rate of delivery[a]	♀♀ *I. paraconfusus* (% response)
I. paraconfusus	0.1 bm/min	79[b]
I. paraconfusus+ *I. pini*	0.1 bm/min+ 0.5 bm/min	42
Controls (hexane only)	—	8

[a] Rates of delivery are expressed as beetle minutes/minute (bm/min).
[b] The probability (Student's *t* test) that these percent response figures would be obtained by chance is $P<0.001$.

and by 99% on 50-male bolts. In fact only two *I. paraconfusus* were caught on traps with bolts containing both species in all 18 replicates. At the same time, the presence of male *I. paraconfusus* in bolts containing 25 male *I. pini* reduced the catch of *I. pini* over traps containing only male *I. pini* bolts by 86%. This was a significant reduction in both tests. Although the catch was reduced on 50-male bolts by 60%, the difference was not significant. The sex ratios of *I. pini* caught on *I. pini* bolts alone and on the bolts containing both *I. pini* and *I. paraconfusus* were not significantly different, indicating that both sexes are equally affected by the treatment. Too few *I. paraconfusus* were caught by the bolts containing both species to make any comparison of sex ratios.

The predator *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae) was the only associate insect caught in appreciable numbers. As the results indicate (Tables 1 and 4) *E. lecontei* responded equally to both species of *Ips* alone and to bolts containing both species together, and thus was apparently unaffected by the treatment.

Mutual Inhibition in the Laboratory

In the laboratory studies, concentrates from each species were effective in significantly reducing the response of females of the other species (and also males of *I. pini*) to volatiles produced by males of their own species (Tables 2 and 3). This response parallels that in the field although the reduction is not as great. The use of concentrates rather than active male beetles in the laboratory assay eliminates the possibility of visual and sound stimuli

TABLE 3. INHIBITION OF THE ATTRACTANT RESPONSE OF *I. pini* BY PHEROMONE CONCENTRATES OF *I. paraconfusus* AND BY IPSENOL IN THE LABORATORY

Concentrate	Rate of delivery[a]	*I. pini* (% response)	
		♀♀	♂♂
I. pini	0.5 bm/min	81[b1,3]	76[b2]
I. pini+ *I. paraconfusus*	0.5 bm/min+ 1.0 bm/min	28[b1,4]	20[b2]
I. pini+ ipsenol	0.5 bm/min 1×10^{-6} g/min	16[b3,4]	—
ipsenol	1×10^{-6} g/min	0	—
I. paraconfusus	1.0 bm/min	8	—
Controls (hexane only)	—	8	—

[a] Rates of delivery are expressed as beetle minutes/minute (bm/min) and as grams/minute (g/min).

[b] The probability (Student's *t* test) that percent response figures assigned the same number would be obtained by chance is: (1) $P<0.001$; (2) $P<0.001$; (3) $P<0.001$; (4) $P<0.2$ (NSD).

being involved from the males. However, further field tests are required in order to verify that the inhibition of attractant response observed in the field is a result of chemical stimuli.

Source of Inhibition—Effect of Ipsenol on I. pini

In four field tests, ipsenol significantly reduced the catch of *I. pini* on traps containing male *I. pini* (Table 4). The first of these tests demonstrated that ipsenol at the concentration used was as effective as actively boring male *I. paraconfusus* in inhibiting the attractant response of *I. pini*. The sex ratios of beetles caught on all three treatments were virtually identical, indicating a similar effect on both sexes.

Although beetle catch during the second test was low due to adverse weather conditions, the results still indicate a significant effect by ipsenol. Results of the third and fourth tests show that ipsenol will reduce trap catches of *I. pini* even at high population densities. When all tests are taken together, ipsenol reduced the catch of *I. pini* on traps containing bolts infested with 25 males of *I. pini* by 78% and with 50 males of *I. pini* by 71%.

In the laboratory, ipsenol delivered in place of *I. paraconfusus* concentrate also significantly reduced the response level of female *I. pini* to *I. pini* concentrate (Table 3). There was no significant response by female *I. pini* to

TABLE 4. EFFECT OF IPSENOL ON ATTRACTANT RESPONSE OF *I. pini* TO BOLTS INFESTED WITH MALE *I. pini*: MCCLOUD FLATS, CALIFORNIA, 1973. MEAN NUMBER (RANGE IN PARENTHESES) AND SEX RATIO OF SPECIES TRAPPED ARE LISTED BY TREATMENT IN EACH TEST

	Treatment (males in bolt)	*I. pini*	♂:♀	Replications	*E. lecontei*
Test 1[a]	50 ♂♂ *I. pini*	**4.50**[b1,2] (15–90)	1 : 1.8[c]	7	**5.7**[b7] (1–19)
	50 ♂♂ *I. pini*+ 50 ♂♂ *I. paraconfusus*	**2.8**[b1,3] (0–8)	1 : 1.8	6	**10.6**[b7] (3–41)
	50 ♂♂ *I. pini*+ ipsenol[d]	**4.0**[b2,3] (0–15)	1 : 1.9	5	**4.2**[b7] (0–10)
Test 2	25 ♂♂ *I. pini*	**3.3**[b4] (1–10)	—	12	—
	25 ♂♂ *I. pini*+ ipsenol	**0.75**[b4] (0–3)	—	12	
Test 3	50 ♂♂ *I. pini*	**192.6**[b5] (53–361)	—	8	—
	50 ♂♂ *I. pini*+ ipsenol	**54.6**[b5] (24–114)	—	8	—
Test 4	25 ♂♂ *I. pini*	**14.6**[b6] (2–48)	—	8	—
	25 ♂♂ *I. pini*+ ipsenol	**3.25**[b6]	—	8	—
Controls	Bolt with no beetles (1 in each test line)	**0**	—	—	—

[a] Test 1: July 7–12, 1973. Test 2: August 15–19, 1973. Tests 3 and 4: August 28–31, 1973.
[b] The probability (Student's *t* test) that means of trap catches assigned the same number would be obtained by chance is: (1) $P<0.005$; (2) $P<0.01$; (3) $P<0.2$ (NSD); (4) $P<0.025$; (5) $P<0.005$; (6) $P<0.05$; (7) $P>0.4$ (NSD).
[c] Sex ratios of beetles caught by the three treatments in test 1 are not significantly different ($P>0.9$, χ^2 test).
[d] Ipsenol evaporated at 1 mg/24 hr.

ipsenol delivered alone, or to *I. paraconfusus* concentrate. Thus, at these dosage levels in the olfactometer, ipsenol can duplicate the inhibitory effect of male *I. paraconfusus* concentrate toward *I. pini*.

TABLE 5. EFFECT OF LINALOOL ON ATTRACTANT RESPONSE OF *I. paraconfusus* TO BOLTS INFESTED WITH MALE *I. paraconfusus*: SIERRA NATIONAL FOREST, CALIFORNIA, 1973[a]. MEAN NUMBER (RANGE IN PARENTHESES) AND SEX RATIO (*I. paraconfusus*) OF SPECIES TRAPPED ARE LISTED BY TREATMENT

Treatment (males in bolt)	*I. paraconfusus*	♂:♀	*I. pini*
25 ♂♂ *I. paraconfusus*	**39.2**[b1,2] (0–183)	1:2.1[c]	**0.2**[b5] (0–2)
25 ♂♂ *I. paraconfusus* + 25 ♂♂ *I. pini*	**7.4**[b1,3] (0–15)	1:2.6	**0**
25 ♂♂ *I. paraconfusus* + linalool[d]	**10.5**[b2,3] (0–36)	1:2.1	**0**
25 ♂♂ *I. pini*	**0.25**[b4] (0–3)	—	**1.3**[b5,6] (0–7)
25 ♂♂ *I. pini* + linalool	**0.25**[b4] (0–3)	—	**0.4**[b6] (0–3)
Control (bolt containing no males)	**0.1**[b4] (0–1)	—	**0**

[a] Test run: August 7–16, 1973 with 12 replicates of each treatment.
[b] The probability (Student's *t* test) that means of trap catches would be obtained by chance is: (1) $P<0.05$; (2) $P<0.10$; (3) $P<0.20$ (NSD); (4) $P>0.50$ (NSD); (5) $P<0.10$; (6) $P<0.20$ (NSD).
[c] Sex ratios of *I. paraconfusus* trapped by the three treatments are not significantly different ($P>0.90$, χ^2 test).
[d] Linalool evaporated at 1 mg/24 hr.

Source of Inhibition—Effect of Linalool on I. paraconfusus

Bolts infested with males of both species reduced the catch of *I. paraconfusus* by 81% over the number caught on traps containing bolts infested with male *I. paraconfusus* alone (Table 5). However, the effect of linalool on the catch of *I. paraconfusus* was more variable and could only be demonstrated at a level of significance lower than that recorded for male *I. pini*. There was no significant difference between the number of *I. paraconfusus* responding to traps containing either male *I. pini* together with male *I. paraconfusus*, or linalool with male *I. paraconfusus*. However, the lack of any significant catch of *I. paraconfusus* on traps containing male *I. pini* bolts alone indicates that linalool is not the sole contributor from male *I. pini* that accounts for reduced catches of *I. paraconfusus* on traps containing male *I. pini*.

DISCUSSION

Inhibition of response to the sex pheromone of one species by another species, usually closely related, is a well established phenomenon in the Lepidoptera. When females of two species are confined together in a trap, catches are reduced over those when both are exposed separately (Ganyard and Brady, 1971; Haile et al., 1973). Berisford and Brady (1973) have also shown that combined extracts of two species of Olethreutidae catch fewer moths than do the individual extracts. In addition there are several examples showing that differences in the presence or concentration of one or more geometric isomers of the female sex pheromone can effect reproductive isolation between two species (Roelofs and Comeau, 1969, 1971; Roelofs et al., 1972; Kaae et al., 1973; Klun et al., 1973). The phenomenon of inhibition of attractant response by pheromone compounds has been demonstrated in two species of Coleoptera. Werner (1972) showed that pheromones from beetles of the genus *Dendroctonus* inhibit the response of *Ips grandicollis* Eichh. to host tree terpenes. Wood et al. (1967) demonstrated that the response of *I. latidens* LeC. to two of the three components of the pheromone of *I. paraconfusus* was inhibited by addition of the third component. The present study appears to be the first, however, which demonstrates *mutual* inhibition of attractant response to pheromones between closely related species of Coleoptera.

It has been hypothesized that the specificity of pheromones among sympatric species of bark beetles is probably an important mechanism in preventing interspecific mating and in minimizing competition for space and food (Wood, 1970; Lanier and Wood, 1975; Lanier and Burkholder, 1974). This would be especially true for sympatric species which breed in the same host tree species, such as *I. paraconfusus*, *I. latidens*, and *I. pini* in California, or *I. grandicollis*, *I. calligraphus* Germ., and *I. avulsus* Eichh. in the Southern United States. In each area of the country these sympatric species are in different species groups (Hopping, 1963) and are more distantly related than those species within species groups. Specificity has been demonstrated for several species which occur together in California (Vité and Gara, 1962; Wood, 1970; Lanier et al., 1972; Lanier and Wood, 1975) and other areas (summarized by Lanier and Wood, 1975). Within species groups, cross-attraction occurs between species and their distributions are generally allopatric (Lanier and Burkholder, 1974; Lanier and Wood, 1975).

The present study demonstrates, however, a mechanism other than the production of different attractant compounds or mixtures of compounds to account for and maintain species isolation: i.e., *I. paraconfusus* and *I. pini* boring in the same host log chemically inhibit the attractant response of one another. This mechanism is strongly supported by the field data. Pre-

liminary data also suggest that the source of this inhibition originates from the attractant pheromone system of the other species. Thus, active inhibition of the response of *I. pini* to boring males of *I. pini* can be mimicked by ipsenol, one component of the attractant pheromone system of *I. paraconfusus*. With *I. paraconfusus* inhibition, linalool, one component of the complex of volatiles produced by boring *I. pini* males, appears to mimic some of the inhibitory effect of *I. pini* males. To discuss the chemical mechanisms involved, however, we must know much more about the attractant pheromone systems of both species, especially *I. pini*, in which linalool has not otherwise been shown to have any biological activity. In addition, the more variable results recorded for inhibition caused by linalool might be clarified by testing different concentrations and by investigating the involvement of other compounds.

Studies in a number of *Ips* species (Renwick and Vité, 1972; Vité et al., 1972; Young et al., 1973*a*, *b*) have revealed no additional pheromone compounds to the three terpene alcohols identified by Silverstein et al. (1966) from *I. paraconfusus*. Several species utilize one or more of these compounds as attractants and one species, *I. calligraphus*, apparently requires host odors to increase activity (Renwick and Vité, 1972). A sequential isolation program (Silverstein et al., 1967) is clearly required to identify the compounds that elicit the inhibition of response demonstrated here.

In earlier work with *I. paraconfusus* (Silverstein et al., 1966), ipsenol was not attractive in the laboratory assay at a dosage level of 1×10^{-4} g. This is in contrast to the present study, where females responded to ipsenol at 1×10^{-6} g/minute. The apparent difference may be attributable to many factors, including varying response levels in different batches of the test insects, undetected trace amounts of active substances, and/or different methods used for evaporation of compounds.

Mutual pheromone inhibition imparts a clear adaptive advantage to the pioneer species by excluding a potential competitor for the supply of host substrate. For example, suitable host material, such as snow or wind breakage, occurs only periodically (although logging operations now ensure a more plentiful supply), and in many years this supply is undoubtedly scarce. In addition, the lack of cross-attraction between species helps to assure that the competitor will not arrive on the host at the same time. Thus, simultaneous production of a specific attractant pheromone and an interspecific inhibitor of the attractant response favors exclusive use of the host substrate by the first arrival.

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REFERENCES

BEDARD, W.D., and BROWNE, L.E. 1969. A delivery-trapping system for evaluating insect chemical attractants in nature. *J. Econ. Entomol.* 62:1202–1203.

BERISFORD, C.W., and BRADY, U.E. 1973. Specificity and inhibition of attraction of male *Rhyacionia frustrana* and *R. rigidana* to their female sex pheromone. *Nature* 241:68–69.

BROWNE, L.E. 1972. An emergence cage and refrigerated collector for wood-boring insects and their associates. *J. Econ. Entomol.* 65:1499–1501.

BROWNE, L.E., BIRCH, M.C., and WOOD, D.L. 1973. Novel trapping and delivery systems for airborne insect pheromones. *J. Insect Physiol.* 20:183–193.

GANYARD, M.C. JR., and BRADY, U.E. 1971. Inhibition of attraction and cross-attraction by interspecific sex pheromone communication in Lepidoptera. *Nature* 234:415–416.

HAILE, D.G., SNOW, J.W., and GOODENOUGH, J.L. 1973. Reduced capture of tobacco budworm and corn earworm males in electric grid traps baited simultaneously with virgin females of both species. *J. Econ. Entomol.* 66:739–740.

HOPPING, G.R. 1963. The natural groups of species in the genus *Ips* DeGeer (Coleoptera: Scolytidae) in North America. *Can. Entomol.* 95:508–516.

KAAE, R.S., SHOREY, H.H., and GASTON, L.K. 1973. Pheromone concentration as a mechanism for reproductive isolation between two Lepidopterous species. *Science* 179:487–488.

KLUN, J.A., CHAPMAN, O.L., MATTES, K.C., WOJTKOWSKI, P.W., BEROZA, M., and SONNET, P.E. 1973. Insect sex pheromones: minor amount of opposite geometrical isomer critical to attraction. *Science* 181:661–663.

LANIER, G.N. 1966. Interspecific mating and cytological studies of closely related species of *Ips* DeGeer and *Orthotomicus* Ferrari (Coleoptera: Scolytidae). *Can. Entomol.* 98:175–188.

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

LANIER, G.N., WOOD, D.L. 1975. Specificity of response to pheromones in the genus *Ips* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 1:9–23.

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.

RENWICK, J.A.A., and VITÉ, J.P. 1972. Pheromones and host volatiles that govern aggregation of the six-spined engraver beetle, *Ips calligraphus*. *J. Insect Physiol.* 18:1215–1219.

ROELOFS, W.L., and COMEAU, A. 1969. Sex pheromone specificity: taxonomic and evolutionary aspects in Lepidoptera. *Science* 165:398–400.

ROELOFS, W.L., and COMEAU, A. 1971. Sex pheromone perception: synergists and inhibitors for the red-banded leaf roller attractant. *J. Insect Physiol.* 17:435–448.

ROELOFS, W.L., CARDÉ, R.T., BARTELL, R.J., and TIERNEY, P.G. 1972. Sex attractant trapping of the European corn borer in New York. *Environ. Entomol.* 1:606–608.

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

SILVERSTEIN, R.M., RODIN, J.O., and WOOD, D.L. 1967. Methodology for isolation and identification of insect pheromones with reference to studies on California five-spined *Ips*. *J. Econ. Entomol.* 60:944–949.

VITÉ, J.P., and GARA, R.I. 1962. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera: Scolytidae). *Contrib. Boyce Thompson Inst.* 21:251–273.

VITÉ, J.P., and RENWICK, J.A.A. 1970. Differential diagnosis and isolation of population attractants. *Contrib. Boyce Thompson Inst.* 24:323–328.

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

WERNER, R.A. 1972. Response of the beetle *Ips grandicollis*, to combinations of host and insect produced attractants. *J. Insect Physiol.* 18:1403–1412.

WOOD, D.L. 1970. Pheromones of bark beetles, pp. 301–316, *in* D. L. Wood, R. M. Silverstein, and M. Nakajima (eds.), Control of insect behavior by natural products. Academic Press, New York.

WOOD, D.L., BROWNE, L.E., SILVERSTEIN, R.M., and RODIN, J.O. 1966. Sex pheromones of bark beetles. I. Mass production, bio-assay, source and isolation of the sex pheromone of *Ips confusus* (LeC.). *J. Insect Physiol.* 12:523–536.

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, 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.

YOUNG, J.C., BROWNLEE, R.G., RODIN, J.O., HILDEBRAND, D.N., SILVERSTEIN, R.M., WOOD, D.L., BIRCH, M.C., and BROWNE, L.E. 1973*a*. Identification of linalool produced by two *Ips* species bark beetles. *J. Insect Physiol.* 19:1615–1622.

YOUNG, J.C., SILVERSTEIN, R.M., and BIRCH, M.C. 1973*b*. Aggregation pheromone of the beetle *Ips confusus*: isolation and identification. *J. Insect Physiol.* 19:2273–2277.