Journal of Chemical Ecology, Vol. 24, No. 1, 1998

DISRUPTION OF SECONDARY ATTRACTION OF THE SPRUCE BEETLE, *Dendroctonus rufipennis*, BY PHEROMONES OF TWO SYMPATRIC SPECIES

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(Received February 28, 1997; accepted September 6, 1997)

Abstract—Capture of spruce beetles, *Dendroctonus rufipennis*, in multiple-funnel traps baited with frontalin and α-pinene was reduced by up to 42% in the presence of synthetic (+)-*exo*- and (+)-*endo*-brevicomin, aggregation pheromones of the sympatric species *Dryocoetes affaber*. (±)-*endo*-Brevicomin was inhibitory to spruce beetles in two experiments and (±)-*exo*-brevicomin was inhibitory in one experiment, reducing spruce beetle trap catches by up to 87% and 75%, respectively. Spruce beetle trap catches were also reduced by 85% by (±)- or (+)-ipsdienol, but not by (−)-ipsdienol. *Ips tridens*, a second sympatric species, produces both enantiomers of ipsdienol in its pheromone blend. Responses by *D. affaber* to its own pheromone were significantly enhanced by addition of the spruce beetle lure. Enantiospecific pheromones of secondary competing species, or less costly racemic substitutes, may be useful for managing spruce beetles using competitive displacement or exclusion. Baiting susceptible hosts with pheromones of secondary species may enhance attack by secondary species, while partially repelling spruce beetles.

Key Words—*Dendroctonus rufipennis*, *Ips tridens*, *Dryocoetes affaber*, bark beetle, pheromone, inhibition, frontalin, α-pinene, ipsdienol, *cis*-verbenol, *exo*-brevicomin, *endo*-brevicomin, enantiomers.

INTRODUCTION

The spruce beetle, *Dendroctonus rufipennis* Kirby, is a major pest of Engelmann spruce, *Picea engelmannii* Parry, white spruce, *Picea glauca* (Moench) Voss,

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and their hybrids in British Columbia (Safranyik, 1988). The beetles preferentially breed in freshly fallen or weakened trees; however, if breeding material is abundant and environmental conditions are favorable, populations can build up to epidemic levels and healthy standing trees may be attacked, resulting in extensive outbreaks (Furniss and Carolin, 1975).

The spruce beetle is frequently associated with several species of secondary bark beetles, including *Ips tridens* Mannerheim, *Ips perturbatus* Eichhoff, *Dryocoetes affaber* Mannerheim, and *Polygraphus rufipennis* Kirby (Werner and Holsten, 1984). The most common secondary species in southern British Columbia are *I. tridens* and *D. affaber*. The secondary species are not considered to be economically important in British Columbia because they are incapable of killing healthy trees; they generally attack downed material or trees already overcome and killed by the spruce beetle. However, in Alaska *I. tridens* has recently been reported killing young white spruce following heavy thinning and pruning treatments and selective logging aimed to minimize spruce beetle-caused tree mortality and reduce fire hazard in sensitive areas (Holsten et al., 1996). Interspecific competition for breeding material and food by secondary bark beetles including *Scierus annectans* LeConte, *P. rufipennis*, and *Ips* spp., primarily *Ips pilifrons* Swaine, was shown to be a major cause of larval mortality for the spruce beetle in Colorado (McCambridge and Knight, 1972).

Competitive interactions may be exploited as a management tool if secondary species can be induced by semiochemicals to preempt a resource and outcompete or exclude a primary pest species (Payne and Richerson, 1985; Borden, 1989). Such an effect has been demonstrated experimentally for the pine engraver, *Ips pini* (Say), a secondary bark beetle capable of outcompeting the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, a major pest of lodgepole pine, *Pinus contorta* var *latifolia* Engelmann (Rankin and Borden, 1991; Safranyik et al., 1996).

The efficacy of competitive displacement or exclusion might be enhanced if the semiochemicals used to induce attack by secondary species were repellent to the primary pest species. Interruption of pheromonal responses by competing sympatric species has been observed for several scolytids. For instance, in California *I. pini* and the California fivespined ips, *Ips paraconfusus* Lanier, compete for breeding material in weakened or fallen ponderosa pine, *Pinus ponderosa* Laws. Attraction of beetles in each species to their conspecifics was reduced in the presence of heterospecifics (Birch and Wood, 1975). The aggregation pheromones ipsenol (2-methyl-6-methylene-7-octen-4-ol) and (+)-ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol), produced by *I. paraconfusus*, disrupted attraction of *I. pini* to logs containing conspecific males (Birch and Light, 1977; Birch et al., 1980). In addition, (−)-ipsdienol produced by *I. pini* inhibited responses of *I. paraconfusus* to conspecifics (Birch et al., 1980). Similarly, attraction of western pine beetles, *Dendroctonus brevicomis* LeConte, and

I. paraconfusus to ponderosa pine bolts infested with conspecifics was mutually inhibited in the presence of nearby bolts infested with beetles of the other species (Byers and Wood, 1980). A blend of ipsenol, ipsdienol, and *cis*-verbenol (*cis*-4,6,6-trimethylicyclo[3.1.1]hept-3-en-2-ol), the aggregation pheromone for *I. paraconfusus*, inhibited the response of *D. brevicomis* to its pheromones *exo*-brevicomin (*exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane) and frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane) plus kairomonal myrcene (2-methyl-6-methylene-2,7-octadiene). Attraction of *I. paraconfusus* to its pheromones was unaffected by the aggregation pheromones of *D. brevicomis* but was reduced by the antiaggregation pheromone verbenone, 4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one (Byers and Wood, 1980). In British Columbia, *I. pini* coexists with the mountain pine beetle and *Ips latidens* LeConte. Attraction of *I. pini* to synthetic ipsdienol and attacks on felled lodgepole pine were reduced by ipsenol, an aggregation pheromone for *I. latidens*, and verbenone, an antiaggregation pheromone for the mountain pine beetle (Borden et al., 1992; Devlin and Borden, 1995). Blends of antiaggregation pheromones and repellent synomones produced by sympatric competitors may be even more effective. For instance, verbenone and ipsdienol acted synergistically in inhibiting attraction by the western pine beetle (Paine and Hanlon, 1991).

Semiochemical disruptants for primary pest species, which also induce attack by secondary species, may enhance management efforts through simultaneous disruption and competitive displacement. For instance, treating loblolly pines, *Pinus taeda* L., with a blend of *exo*- and *endo*-brevicomin for disruption of the southern pine beetle, *Dendroctonus frontalis* Zimmerman, also resulted in colonization and competitive displacement of *D. frontalis* by *Ips avulsus* Eichhoff (Payne and Richerson 1985).

While the fate of behaviorally disrupted beetles is unknown, prolonged dispersal in search of suitable hosts would likely result in greatly reduced survival due to predation, desiccation, and metabolic exhaustion. In field tests to evaluate the efficacy of verbenone for disruption of *D. frontalis*, growth of treated infestation spots was completely halted with few or no additional trees being attacked (Payne and Billings 1989). Therefore, disrupted or displaced beetles would be unlikely to establish new attacks or infestations successfully.

Secondary scolytids may outcompete the primary tree-killing species by rapid larval development and utilization of phloem tissue (McCambridge and Knight, 1972; Rankin and Borden, 1991). Successful colonization of healthy vigorous trees by primary attacking species is often dependent on the establishment of mutualistic blue stain fungi, which colonize the phloem tissue and sapwood medullary parenchyma, inhibiting water conduction by the tree and reducing host resistance (Reynolds, 1992). In weakened or dead trees, selective pressures favor opportunistic secondary species that can exploit the available resources rapidly. Therefore, secondary species may be able to attack in nature some days after initial attack by the primary species and still overcome their tree-killing rivals. It is possible that they exploit the pheromone of the primary species as an attractant alone or that the semiochemical blends of primary and secondary species interact in an additive or synergistic fashion in attracting the secondary species.

The commercial semiochemical lure for the spruce beetle consists of the pheromone frontalin (Gries et al., 1988) and the host kairomone α-pinene (2,6,6-trimethyl-bycyclo[3.1.1]hept-2-ene) (Furniss et al., 1976). The aggregation pheromone for *D. affaber* consists of a 1:2 mixture of (+)-*exo*- and (+)-*endo*-brevicomins (Camacho et al., 1994). *I. tridens* is attracted to a blend of (−)-*cis*-verbenol and (±)-ipsdienol (Moeck et al., 1985), two compounds that are produced, respectively, by males exposed to α-pinene vapors and by males boring into host logs (Poland, 1997). Enantiospecific pheromones are expensive, whereas racemic mixtures are cheaper and would be preferred for operational use if they were effective in eliciting appropriate beetle responses.

Our objectives were to test the hypotheses that: (1) known semiochemical attractants for *D. affaber* and *I. tridens* inhibit attraction of the spruce beetle to its pheromone; (2) racemic mixtures of *D. affaber* and *I. tridens* pheromones inhibit spruce beetle attraction to its pheromone as effectively as chirally pure blends; and (3) attraction of secondary species is enhanced when their pheromones are combined with that of the spruce beetle.

METHODS AND MATERIALS

Five field trapping experiments were conducted near Princeton, British Columbia, in mature stands composed of Engelmann spruce, lodgepole pine, and subalpine fir, *Abies lasiocarpa* (Hook) Nutt. All experiments utilized 12-unit funnel traps (Lindgren, 1983) set out in randomized complete blocks with at least 15 m between traps. Captured beetles were collected and stored in plastic bags at −18°C before they were sexed and counted. Ten replicates were set up initially for each experiment. For some experiments, all lures were collected after the first set of 10 replicates, and the experiments were repeated with an additional 10 replicates laid out in new randomized complete blocks, providing a total of 20 replicates in two time periods.

Semiochemical attractants for the spruce beetle, *I. tridens*, and *D. affaber* are summarized in Table 1. Spruce beetle funnel lures (Phero Tech Inc., Delta, British Columbia) were used as the attractive semiochemical bait for the spruce beetle. The lures consisted of a 1.5-ml Eppendorf tube containing α-pinene released at 50–80 mg/24 hr and a 400-μl tube containing frontalin released at 2 mg/24 hr.

The attractive lure for *I. tridens* consisted of three bubble caps each releas-

TABLE 1. SUMMARY OF SEMIOCHEMICALS AND THEIR BIOLOGICAL ACTIVITIES FOR *Dendroctonus rufipennis*, *Ips tridens*, and *Dryocoetes affaber*

Species	Semiochemical	Biological Activity	Reference
D. rufipennis	α-pinene	attractive	Furniss et al. (1976)
	frontalin	attractive	Gries et al. (1988)
D. affaber	(+)-*exo*-brevicomin (+)-*endo*-brevicomin	optimal attraction to 1:2 ratio of (+) enantiomers of *exo*- and *endo*-brevicomin	Camacho et al. (1994)
	(−)-*exo*-brevicomin	no activity	
	(−)-*endo*-brevicomin	inhibits response to optimal blend	
I. tridens	(±)-ipsdienol	attractive	Moeck et al. (1985), Poland (1997)
	(−)-*cis*-verbenol	attractive	

ing (+)- and (−)-*cis*-verbenol in a 17:83 ratio at 0.6 mg/24 hr, and three bubble caps each releasing (±)-ipsdienol at 0.2 mg/24 hr. Chirally pure enantiomers of ipsdienol [97% pure (+)- or (−)-ipsdienol] were also released at 0.2 mg/24 hr from bubble caps. All release devices were obtained from Phero Tech.

Pheromone baits for *D. affaber* consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg/24 hr from glass capillary tubes (1.0 mm ID) sealed at one end and placed in perforated Eppendorf tubes (Stock et al., 1990). The presence of (−)-*exo*-brevicomin does not affect responses of *D. affaber*; however, (−)-*endo*-brevicomin is inhibitory. Therefore, (−)-*exo*-brevicomin and (+)-*endo*-brevicomin were used in a mixture that effectively delivered a 1:2 ratio of the (+) enantiomers (Camacho et al., 1994). Enantiomers of *exo*- and *endo*-brevicomin were released separately from devices prepared in the same manner as the *D. affaber* lures. Respective chemical and optical purities were: (+)-*exo*-brevicomin 98.1% and 94%; (−)-*exo*-brevicomin 97% and 95%; (+)-*endo*-brevicomin 98.8% and 90.15%; and (−)-*endo*-brevicomin 91% and 88%. Racemic *exo*- and *endo*-brevicomin (98% and 95.6% chemical purity, respectively) were obtained from Phero Tech. All chiral compounds were synthesized by B. D. Johnston (Department of Chemistry, Simon Fraser University) according to procedures developed by Johnston and Oehlschlager (1982).

Experiment 1 tested whether attraction of the spruce beetle to the spruce beetle lure is inhibited in the presence of the *D. affaber* pheromone. It comprised

10 replicates of four treatments: (1) unbaited control; (2) spruce beetle lure; (3) *D. affaber* lure; and (4) spruce beetle plus *D. affaber* lures.

Experiments 2 and 3 compared attraction of the spruce beetle to the different enantiomers of *exo*- and *endo*-brevicomin. Both comprised 20 replicates of five treatments. The treatments for experiment 2 were: (1) unbaited control; (2) spruce beetle lure; (3) spruce beetle lure plus (+)-*exo*-brevicomin; (4) spruce beetle lure plus (−)-*exo*-brevicomin; and (5) spruce beetle lure plus (±)-*exo*-brevicomin. Experiment 3 was identical to experiment 2 except that enantiomers of *endo*-brevicomin were used.

Experiment 4 compared (±)-*exo*- and (±)-*endo*-brevicomin alone and combined in 20 replicates of five treatments: (1) unbaited control; (2) spruce beetle lure; (3) spruce beetle lure plus (±)-*exo*-brevicomin; (4) spruce beetle lure plus (±)-*endo*-brevicomin; and (5) spruce beetle lure plus both (±)-*exo*- and (±)-*endo*-brevicomin.

Experiment 5 tested whether attraction of the spruce beetle to the spruce beetle lure is inhibited by the presence *I. tridens* pheromone. It was identical to experiment 1 except that *I. tridens* lures replaced *D. affaber* lures.

Experiment 6 tested whether the different enantiomers of ipsdienol disrupted attraction of the spruce beetle to the spruce beetle lure. It comprised 10 replicates of five treatments: (1) unbaited control; (2) spruce beetle lure; (3) spruce beetle lure plus (+)-ipsdienol; (4) spruce beetle lure plus (−)-ipsdienol; and (5) spruce beetle lure plus (±)-ipsdienol.

The numbers of beetles of each species captured were transformed by $\log_{10}(x + 1)$ to satisfy assumptions of normality and homogeneity of variances (Zar, 1984), and then analyzed by ANOVA for randomized complete block design treating replicates as blocks (SAS, 1990). An additional blocking factor for collection time was included for experiments with 20 replicates over two collection periods. The Ryan-Einot-Gabriel-Welsh (REGW) stepwise multiple comparison procedure was used to compare means because of its power and control of the experimentwise type I error rate (Day and Quinn, 1989). Captures of male beetles were similar to those of female beetles in all experiments. In experiments 1 and 5 data for the two sexes were pooled to compensate for low power due to relatively few replicates and low trap catches. In all cases $\alpha = 0.05$.

RESULTS

In experiment 1, spruce beetles were significantly more attracted to spruce beetle lures than to unbaited controls or traps baited with the pheromone of *D. affaber* (Figure 1). Attraction of spruce beetles to spruce beetle lures plus the pheromone of *D. affaber* was intermediate between that to unbaited controls

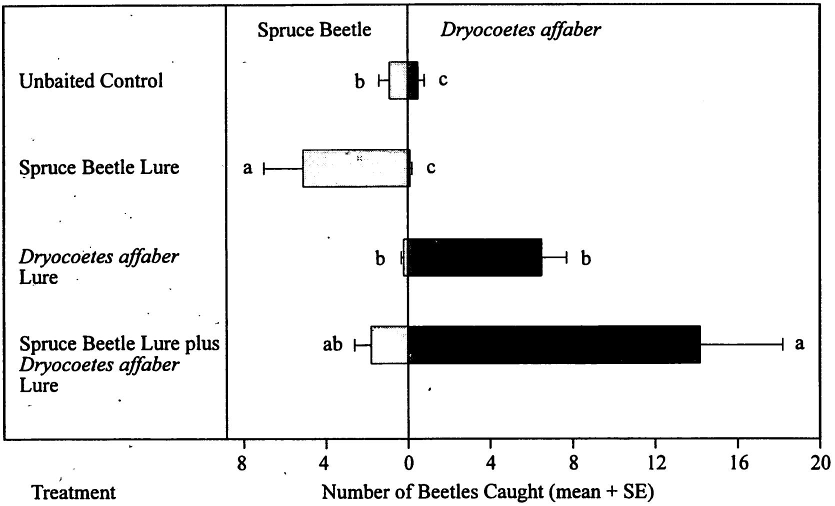

FIG. 1. Numbers of spruce beetles and *Dryocoetes affaber* captured in multiple funnel traps in experiment 1 (May 28–July 7, 1993) Slate Creek, Princeton, British Columbia. Spruce beetle lures consisted of frontalin released at 2 mg/24 hr and α-pinene released at 50–80 mg/24 hr. *Dryocoetes affaber* pheromone consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg/24 hr. $N = 10$. Bars for each species with the same letter are not significantly different, REGW test $P < 0.05$.

and spruce beetle lures alone. *Dryocoetes affaber* was significantly attracted to its own pheromone but not to spruce beetle lures (Figure 1). Attraction to its own pheromone was significantly enhanced in the presence of the spruce beetle lure.

In experiments 2–4 the numbers of spruce beetles captured were significantly different between the two collection periods. Because high numbers of beetles were caught early in the flight period and low numbers later on at the time of the second collection, the overall means were intermediate with large overall variances. Nevertheless, differences in responses to different treatments were similar between the two time periods and were significant when blocking factors for time and replicate were included.

In experiment 2 spruce beetles of both sexes were attracted in significant numbers to traps baited with spruce beetle lures alone or combined with (−)- or (±)-*exo*-brevicomin (Figure 2). The presence of (+)-*exo*-brevicomin reduced catches slightly, but significantly to a level not different from that to unbaited control traps (Figure 2). Catches of *D. affaber* were very low and were not significantly different between treatments.

Attraction of spruce beetles in experiment 3 was similarly reduced by 42%

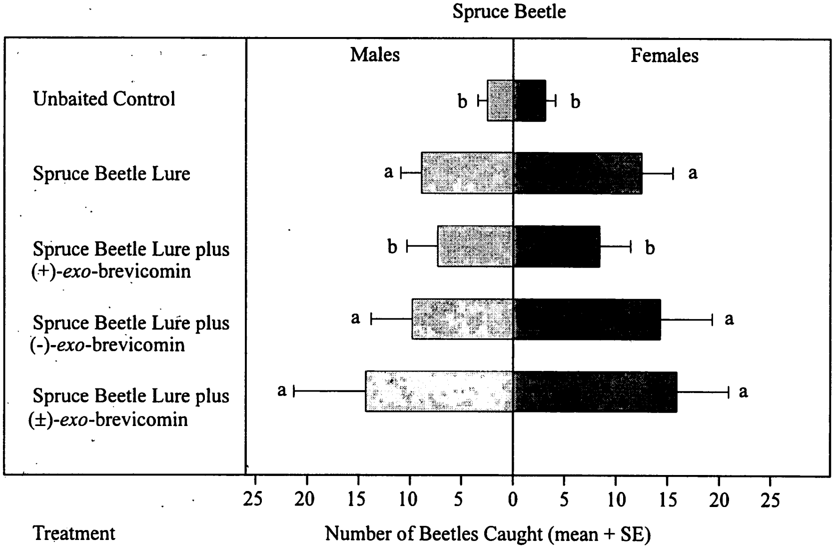

FIG. 2. Numbers of male and female spruce beetles captured in multiple funnel traps in experiment 2 (April 26–June 29, 1994) in Arastra Creek, Princeton, British Columbia. Spruce beetle lures consisted of frontalin released at 2 mg/24 hr and α-pinene released at 50–80 mg/24 hr. Enantiomers of *exo*-brevicomin were released at 0.2 mg/24 hr. $N = 20$. Bars for each sex with the same letter are not significantly different, REGW test, $P < 0.05$.

when spruce beetle lures were combined with (+)- or (±)-*endo*-brevicomin (Figure 3). *Dryocoetes affaber* was attracted to spruce beetle lures combined with either (+)- or (±)-*endo*-brevicomin.

In experiment 4 spruce beetles were attracted at significant levels only to traps baited with spruce beetle lures (Figure 4). Addition of (±)-*exo*-brevicomin, (±)-*endo*-brevicomin, or both to spruce beetle lures reduced the numbers of spruce beetles captured by 75%, 87%, and 77% respectively, levels not significantly different from that to unbaited control traps (Figure 4). *Dryocoetes affaber* was significantly attracted to spruce beetle lures plus (±)-*endo*-brevicomin alone or combined with (±)-*exo*-brevicomin but not to spruce beetle lures plus (±)-*exo*-brevicomin alone.

The results of experiment 5 were very similar to those of experiment 1. The attraction of spruce beetles to the combination of spruce beetle and *I. tridens* attractants was reduced to a level intermediate between that to unbaited controls and spruce beetle lures (Figure 5). *Ips tridens* was significantly attracted to its

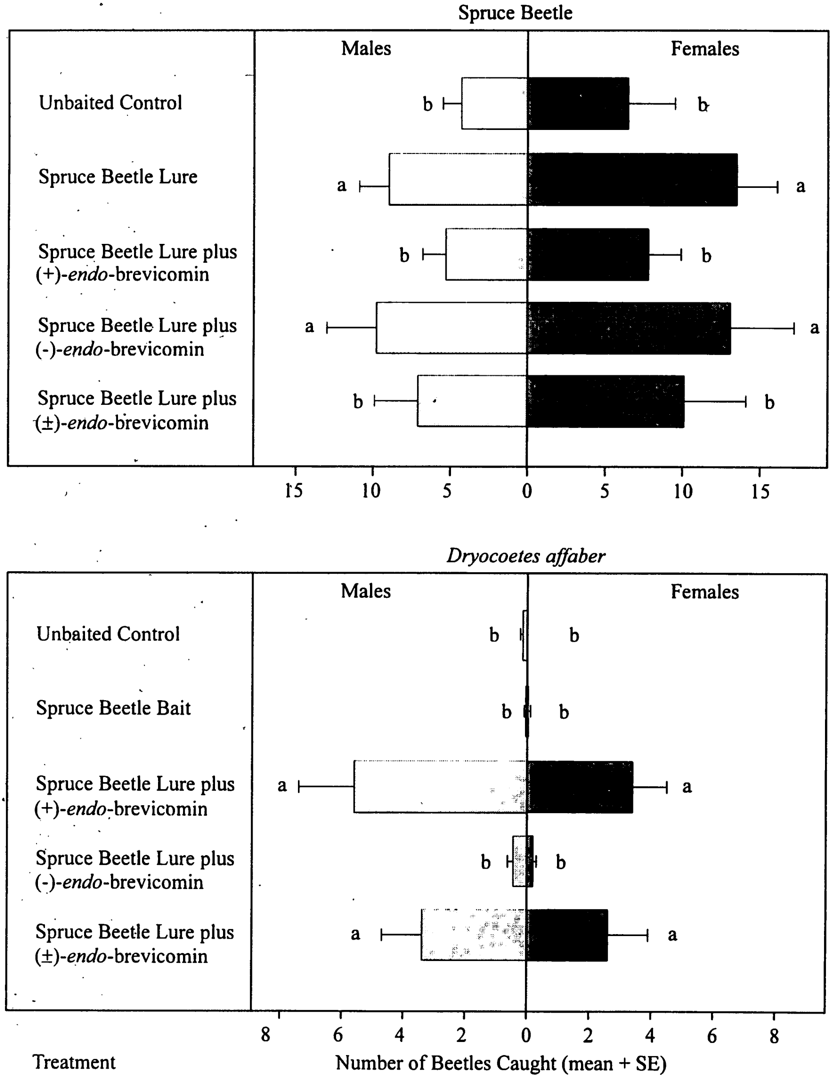

FIG. 3. Numbers of male and female spruce beetles and *Dryocoetes affaber* captured in multiple funnel traps in experiment 3 (April 26–June 29, 1994) in Arastra Creek, Princeton, BC. Spruce beetle lures consisted of frontalin released at 2 mg/24 hr and α-pinene released at 50–80 mg/24 hr. Enantiomers of *endo*-brevicomin were released at 0.2 mg/24 hr. $N = 20$. Bars with the same letter within each species and sex are not significantly different, REGW test, $P < 0.05$.

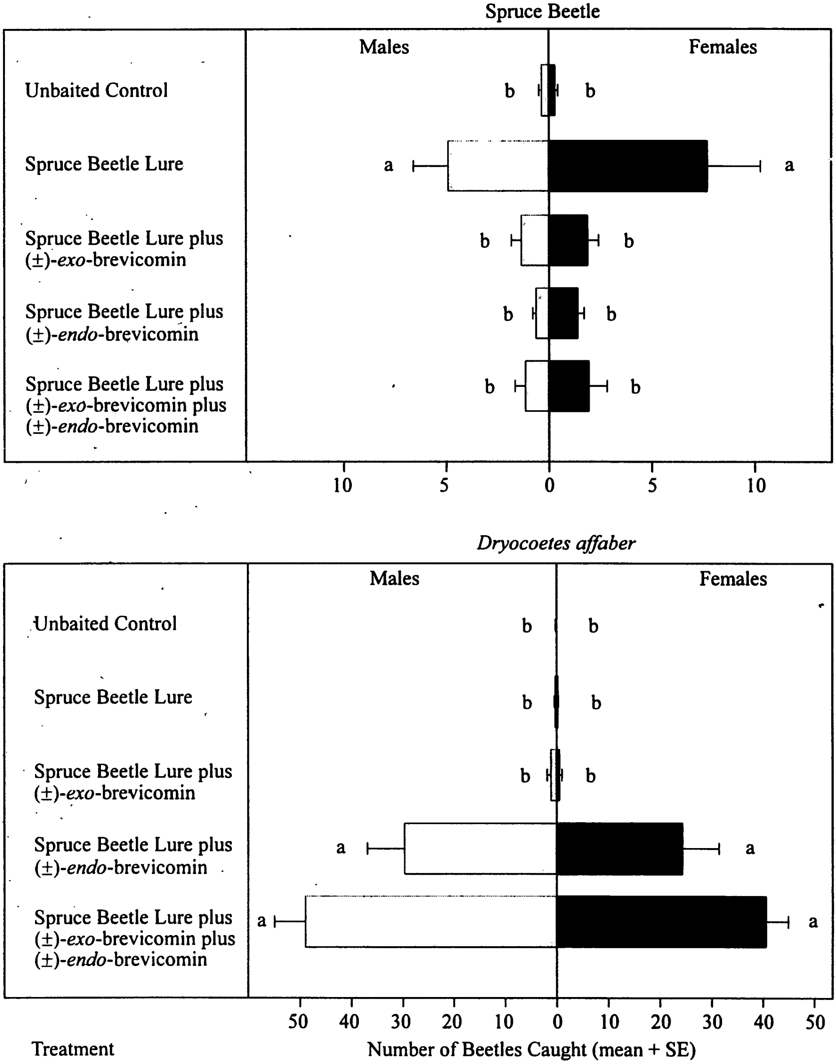

FIG. 4. Numbers of male and female spruce beetles and *Dryocoetes affaber* captured in multiple funnel traps in experiment 4 (June 29–August 17, 1994) in Arastra Creek, Princeton, British Columbia. Spruce beetle lures consisted of frontalin released at 2 mg/24 hr and α-pinene released at 50–80 mg/24 hr. The (±)-*exo*- and (±)-*endo*-brevicomin were released at 0.2 mg/24 hr. $N = 20$. Bars with the same letter within each species and sex are not significantly different, REGW test, $P < 0.05$.

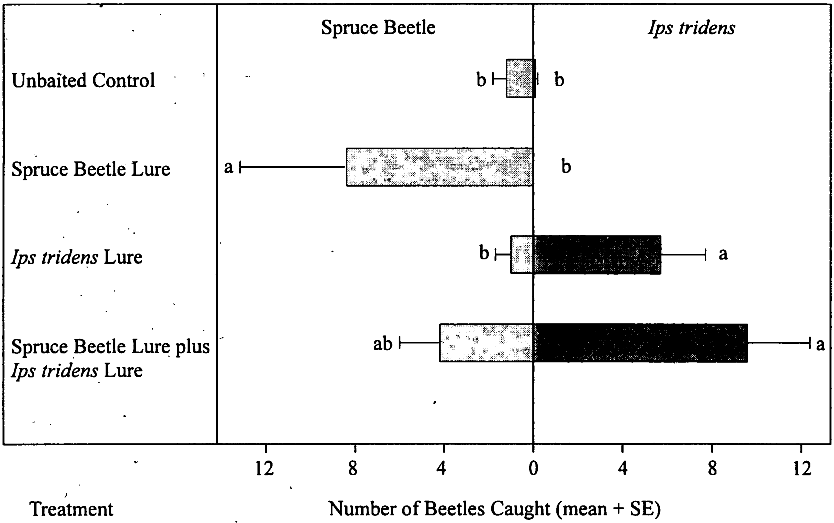

FIG. 5. Numbers of spruce beetles and *Ips tridens* captured in multiple funnel traps in experiment 5 (May 28–July 7, 1993) Slate Creek, Princeton, British Columbia. Spruce beetle lures consisted of frontalin released at 2 mg/24 hr and α-pinene released at 50–80 mg/24 hr. *Ips tridens* lures consisted of (±)-ipsdienol and (−)-*cis*-verbenol released at 0.6 and 1.8 mg/24 hr, respectively. $N = 10$. Bars for each species with the same letter are not significantly different, REGW test $P < 0.05$.

putative pheromone alone or in combination with spruce beetle lures, but unlike *D. affaber* its attraction was not significantly enhanced in the presence of the spruce beetle lure (Figure 5).

In experiment 6 spruce beetles of both sexes were significantly more attracted to traps baited with spruce beetle lures than to unbaited controls. The presence of (+)- or (±)-ipsdienol significantly reduced spruce beetle attraction by 85% to a level that did not differ from that to unbaited control traps (Figure 6).

DISCUSSION

The experimental results uphold all three hypotheses, at least in part. Attraction of spruce beetles to traps baited with the aggregation pheromone frontalin plus the host kairomone α-pinene was reduced by up to 87% by both pheromones of *D. affaber* (Figures 1 and 4). Spruce beetle attraction was reduced by the naturally produced (+) enantiomers of both *exo*- and *endo*-brevicomin

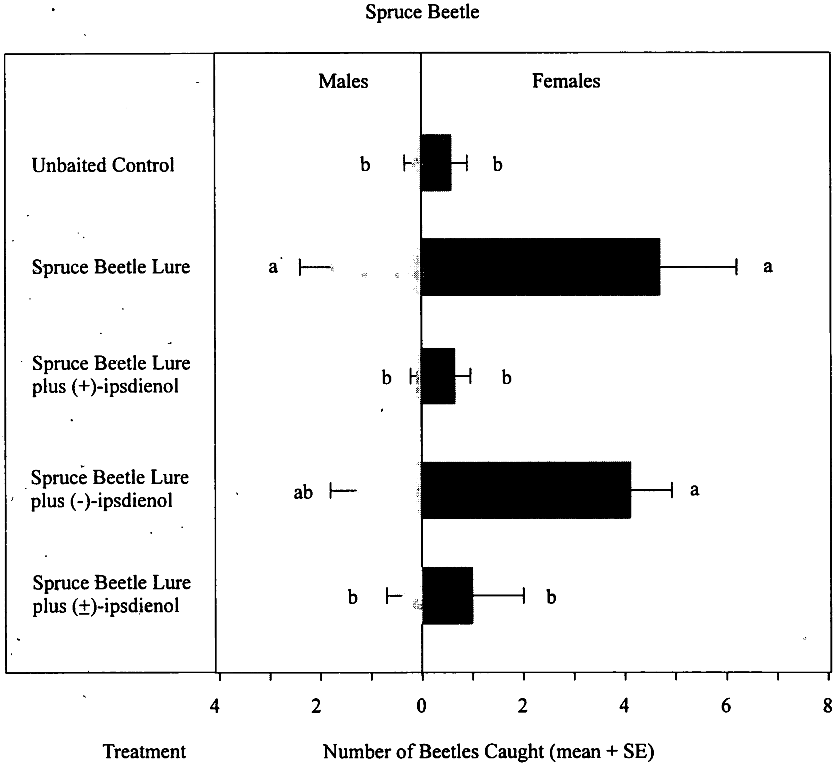

FIG. 6. Mean numbers of male and female spruce beetles captured in multiple funnel traps in experiment 6 (July 14–August 17, 1994) in Arastra Creek, Princeton, British Columbia. Spruce beetle lures consisted of frontalin released at 24 mg/24 hr and α-pinene released at 50–80 mg/24 hr. Enantiomers of ipsdienol were released at 0.2 mg/24 hr. $N = 20$. Bars for each sex with the same letter are not significantly different, REGW test, $P < 0.05$.

(Figures 2 and 3). (±)-*endo*-Brevicomin also reduced attractiveness of the spruce beetle lure in experiments 3 and 4 (Figures 3 and 4) and (±)-*exo*-brevicomin in experiment 4 (Figure 4). (±)-Ipsdienol as well as its (+) enantiomer reduced attraction of the spruce beetle to the spruce beetle lure (Figure 6). On the other hand, spruce beetle lures enhanced attraction of *D. affaber* to its pheromone (Figure 1), but no such effect was observed for *I. tridens* (Figure 5).

Several species of bark beetles are known to produce and respond to enantiospecific pheromones (Birch, 1984; Borden, 1985; Byers, 1989). Specificity in the enantiomeric composition of pheromones may be an important mechanism in maintaining breeding isolation between sympatric congeners. The western balsam bark beetle, *Dryocoetes confusus* Swaine, is sympatric with *D. affaber* and shares the aggregation pheromones (+)-*exo*- and (+)-*endo*-brevicomin. Optimal attraction of *D. affaber* is elicited by a 1:2 ratio of the two compounds, whereas a 9:1 ratio results in optimal attraction of *D. confusus* (Camacho et al., 1993). Attraction of *D. affabar* was reduced when (+)-*exo*-brevicomin was released with (+)-*endo*-brevicomin at the 9:1 ratio and (−)-*endo*-brevicomin was also found to be inhibitory (Camacho et al., 1994). (+)-*endo*-Brevicomin was inhibitory to *D. confusus* when released with (+)-*exo*-brevicomin at a 1:1 ratio (Camacho et al., 1993; Stock et al., 1994) and (−)-*exo*-brevicomin disrupted attaction to the optimal blend (Camacho et al., 1993).

Olfactory receptor cells specific to enantiomers of aggregation pheromones are present in *I. pini* and *I. paraconfusus* (Mustaparta et al., 1980, 1984), *I. typographus* (Tømmeros et al., 1984); and *Scolytus scolytus* (F.) (Wadhams et al., 1982). Perception of the species-specific enantiomeric blends of (+)-*exo*- and (+)-*endo*-brevicomin by *D. affaber* and *D. confusus* is likely similarly achieved by specific olfactory receptor cells. Because attraction of spruce beetles is reduced by naturally produced (+) enantiomers of *exo*- and *endo*-brevicomin (Figures 3 and 4), they may also possess enantiospecific receptor cells. This suggests that spruce beetles and *D. affaber* coevolved since it would be adaptive for spruce beetles to recognize the enantiospecific pheromones of competing secondary species.

Spruce beetle attraction was also reduced by (±)- and (+)-ipsdienol. We have found that *I. tridens* produces ipsdienol in a 1:4 ratio of (+)- and (−)-enantiomers (unpublished). Ipsdienol is produced and utilized by many scolytid species (Borden, 1982). The (+) enantiomer may be a major pheromone component for other secondary species associated with the spruce beetle. Production of some (+)-ipsdienol by *I. tridens* would be adaptive since it reduces spruce beetle attraction and would minimize competitive interactions.

Combinations of pheromones of several associated secondary species may further reduce spruce beetle attraction. Additional research is needed to test the effect of combining the pheromones of *I. tridens*, *D. affaber*, *I. perturbatus*, *P. rufipennis*, and other secondary scolytids on spruce beetle attraction.

Recognition of the pheromones of sympatric species and avoidance of already colonized resources would be adaptive whenever interspecific encounters could result in reduced fitness (Borden, 1996). Weakened or dead host trees colonized by secondary species would generally be unsuitable for primary bark beetles that attack freshly fallen or living trees. Therefore, it would be adaptive for primary bark beetles to recognize and avoid secondary species. On the other hand, secondary species attack only downed trees or those already weakened or killed by primary bark beetles. Therefore, secondary species may exploit the pheromones of tree killing bark beetles to aid in host location.

Interspecific pheromonal inhibition is also common among lepidopterans.

For instance, the bollworm, *Heliothis zea* Boddie, and the tobacco budworm, *Heliothis virescens* F., share four pheromone components, (Z)-11-, (Z)-9-, and (Z)-7-hexadecenal and hexadecanal. Three additional components, (Z)-9-tetradecenal, tetradecanal, and (Z)-11-hexadecen-1-ol, in *H. virescens* are responsible for pheromone specificity and reproductive isolation of the two species (Stadelbacher et al., 1983).

Our results indicate that spruce beetles recognize the pheromones of secondary species and thereby probably are able to avoid direct competitive interactions. They suggest that this phenomenon could be exploited by using the pheromones of secondary species, or less expensive substitutes to induce competitive displacement or exclusion of the spruce beetle by secondary species. Such treatments could reduce or replace the use of arsenical-treated lethal trap trees (Hodgkinson, 1985). Baiting susceptible hosts for secondary species would have two positive effects: (1) inducing attack by the secondary species, and (2) partially repelling spruce beetles. The efficacy of competitive exclusion in reducing spruce beetle attack density, gallery lengths per square meter, and progeny density has been experimentally demonstrated in felled trap trees baited with semiochemical attractants for either or both of the secondary species (Poland, 1997). These tactics may provide a technique for spruce beetle management, especially in remote or environmentally sensitive areas.

Acknowledgments—We thank L. J. Chong, C. Kikegawa, P. Kohen, R. D. Poland, and R. R. Setter for assistance, and L. Safranyik, G. Gries, and B. S. Lindgren for helpful suggestions on the manuscript. The research was supported by the Natural Sciences and Engineering Council of Canada, the Canadian Forest Service, the British Columbia Ministry of Forests, the Science Council of British Columbia, The Coast Forest and Lumber Association, the Interior Lumber Manufacturers' Association, the Cariboo Lumber Manufacturers' Association, Phero Tech Inc., Canadian Forest Products Ltd., International Forest Products Ltd., Finlay Forest Products Ltd., Northwood Pulp and Timber Ltd., TimberWest Ltd., Tolko Industries Ltd., Western Forest Products Ltd., and Weyerhaeuser Canada Ltd.

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