

Competitive Exclusion of *Dendroctonus rufipennis* Induced by Pheromones of *Ips tridens* and *Dryocoetes affaber* (Coleoptera: Scolytidae)

THERESE M. POLAND¹ AND JOHN H. BORDEN

Centre for Pest Management, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6

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ABSTRACT We tested the feasibility of competitive exclusion as a potential management tactic for the spruce beetle, *Dendroctonus rufipennis* Kirby, using pre-attack baiting with pheromones of 2 secondary species, *Ips tridens* Mannerheim and *Dryocoetes affaber* Mannerheim. Spruce beetle attack densities, gallery lengths per square meter, and progeny densities were significantly reduced by up to 78% in individual felled trees baited with the *I. tridens* pheromones (\pm)-ipsdienol and ($-$)-*cis*-verbermol, and the *D. affaber* pheromones (\pm)-*exo*- and ($+$)-*endo*-brevicommin, or pheromones of both secondary species. A simplified *D. affaber* bait consisting of only (\pm)-*endo*-brevicommin also significantly reduced spruce beetle attacks, resource exploitation, and progeny production. Baiting with *I. tridens* pheromones also reduced spruce beetle attack and success in simulated patches of windthrown trees. Resource exploitation and indirect interference by synomonal inhibition of spruce beetle attack are the most likely competitive mechanisms invoked. Competitive exclusion of the spruce beetle may provide an alternative management tactic where traditional methods based on tree removal, widespread harvesting, and the use of insecticides are not feasible.

KEY WORDS *Dendroctonus rufipennis*, *Ips tridens*, *Dryocoetes affaber*, interspecific competition, competitive exclusion, pheromone

THE SPRUCE BEETLE, *Dendroctonus rufipennis* Kirby, is a serious pest of spruce trees, *Picea* spp., in western North America (Safranyik 1988). It attacks all native spruce species within its range. In British Columbia, the preferred hosts are Engelmann spruce, *Picea engelmannii* Parry; white spruce, *Picea glauca* (Moench.) Voss; and their hybrids. Interspecific competition by secondary bark beetles was a major source of mortality for the spruce beetle in Colorado (McCambridge and Knight 1972) and Alaska (Whitmore 1983, Gara et al. 1995). The 2 most common secondary species associated with the spruce beetle in southern and interior British Columbia are *Ips tridens* Mannerheim and *Dryocoetes affaber* Mannerheim.

The pheromones of *I. tridens*, (\pm)-ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) and *cis*-verbenol (*cis*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol) (Moeck et al. 1985), and of *D. affaber*, ($+$)-*exo*- and ($+$)-*endo*-brevicommin (7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane) (Camacho et al. 1994), disrupted attraction of the spruce beetle to traps baited with frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane) and α -pinene (2,6,6-trimethyl-bicyclo[3.1.1]hept-2-ene) (Poland and Borden 1998a). Pheromones of the secondary species applied to logs after attack by the spruce beetle also were effective in inducing competitive displacement of the

spruce beetle (Poland and Borden 1998b). The primary mechanisms of competition were resource exploitation by the primary-attacking spruce beetles and indirect interference by the secondary species through synomonal inhibition of subsequent spruce beetle attacks. However, the competitive effects were limited because the spruce beetle had already begun to use the scarce phloem resource. Therefore, in managing spruce beetle populations, the tactic of competitive exclusion to prevent spruce beetle establishment may be more promising than competitive displacement of already established populations. The competitive exclusion principle states that if there is no differentiation between the realized niches of 2 species, then one will exclude the other. Thus, competitive exclusion can influence the range and distribution of species (Begon and Mortimer 1986). This principle could be exploited by using semiochemicals to expand the realized niche of the secondary species and exclude attack by the spruce beetle. Competitive exclusion would be used to prevent population buildup in areas with suboutbreak populations and where abundant breeding material is available. This would be particularly effective if the pheromones of secondary species had a dual role in inhibiting spruce beetle attack while at the same time inducing secondary species to exploit available resources. Both interference and exploitation competition (Begon and Mortimer 1986) would be invoked.

The importance of interspecific competition in structuring communities has been widely investigated. Historically, observational studies of resource

¹ Current address: U.S. Forest Service, North Central Research Station, 1407 S. Harrison Rd., Rm. 220, Michigan State University, E. Lansing, MI 48823.

partitioning were conducted to provide evidence for interspecific competition. Experiments using phenological approaches were criticized and the role of interspecific competition was challenged. However, in a review of recent experimental field studies, the role of interspecific competition was reexamined. Interspecific competition occurred in 76% of interactions, was often asymmetric, and was most frequent among phytophagous insects that were closely related, introduced, sessile, aggregative, and fed on discrete resources such as internal feeding niches (Denno et al. 1995). Because these features are characteristic of bark beetles, interspecific competition may be maximized and greatly influence community structure. Therefore, competitive exclusion could have considerable potential for management of the spruce beetle.

The objective of this study was to determine the feasibility of competitive exclusion as a management tactic for the spruce beetle in felled trap trees that are baited with secondary species baits before spruce beetle flight. Our specific objectives were to test the hypotheses that spruce beetle attack and success is reduced as follows: (1) in individually felled trap trees baited with pheromones for *I. tridens*, *D. affaber*, or both; (2) in individually felled trap trees baited with an inexpensive single component or racemic substitutes for the complete pheromones of *D. affaber* and *I. tridens*; and (3) in groups of felled trap trees baited with *I. tridens* baits, *D. affaber* baits, or baits for both secondary species.

Materials and Methods

Four trap tree baiting experiments were conducted in forests of Engelmann and white spruce and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., near Mackenzie, BC. In experiments 1-3, trap trees (healthy, large-diameter spruces) were felled individually ≈ 30 m apart into the margins of the stand along rights-of-way. In experiment 4, groups of 4 healthy, large-diameter spruces within 5 m of each other were felled together to simulate patches of windthrown trees. Patches were separated by at least 50 m. Individual trees and all trees within a group were baited within 1 wk of felling at 3 positions—2 m from the severed butt, at the point where the bole measured 30 cm diameter, and midway between the 2. All baits were attached on the north or shaded side of the tree. Bait locations were selected to represent the range of locations along the bole of the tree where the spruce beetle and secondary scolytids are likely to interact. At midseason and again at the end of each experiment, bark sections (≈ 20 by 25 cm) were removed with a chisel and hammer and stored in plastic bags at -18°C . Bark samples were removed from the area immediately below each bait (or analogous positions on control trees). The 1st sample was taken ≈ 40 cm to one side of the bait position and the 2nd ≈ 40 cm to the other side. The bark samples were analyzed by measuring the area of the bark, counting the number of galleries, entrance holes, eggs, larvae, pupae, and callow adults of each species and measuring egg gallery

lengths. Densities of each of the measured variables were computed by dividing their values by the area of the bark sample. The identities of the attacking scolytid species were determined based on the characteristic shape and size of the galleries. In many instances, parental beetles in the egg galleries were used to confirm species identifications. A significant number of galleries formed by the scolytid *Polygraphus rufipennis* Kirby were present and it was not always possible to distinguish them from galleries formed by *D. affaber* unless adult beetles were present. Therefore, for *D. affaber*, only galleries with adults were tallied and measured, which would tend to slightly underestimate the measured *D. affaber* attack parameters. A few *I. perturbatus* Eichhoff also were found. They were distinguished from *I. tridens* by their larger body size, greater width/length ratio, and the conical and acutely shaped 3rd declivital spine (Bright 1976). Their egg galleries tended to be significantly wider than those of *I. tridens*. In addition, *I. tridens* egg galleries generally appeared as contiguous pairs with only a thin septum of phloem between them. Therefore, based on gallery pattern and the presence of adult beetles, galleries formed by *I. tridens* were reliably tallied and measured.

Experiment 1, conducted from 10 May to 4 August 1994, examined competitive interactions between the spruce beetle, *I. tridens*, and *D. affaber* and tested whether spruce beetle attack and success is reduced in logs that are baited with secondary species pheromones before spruce beetle flight. The experiment comprised 8 replicates of 4 treatments as follows: (1) unbaited control, (2) *I. tridens* pheromone, (3) *D. affaber* pheromone, and (4) *I. tridens* pheromone plus *D. affaber* pheromone. Thirty-two trap trees were felled in 5 locations within 30 km of each other. All replicates were laid out within 1 location. The tree diameter 2 m from the severed butt was $43.4 \pm .82$ cm (mean \pm SE). The distance between the baits at the butt and crown positions was $13.6 \pm .6$ m. *I. tridens* baits consisted of 3 bubble caps each releasing (\pm)-ipsdienol at 0.2 mg/24 h and 3 bubble caps each releasing *cis*-verbenol in a 83:17 ratio of the (-) and (+) enantiomers at 0.6 mg/24 h (Phero Tech, Delta, BC). *D. affaber* baits consisted of a 1:1 mixture of (\pm)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg/24 h from glass capillary tubes (1.0 mm inside diameter) which were sealed at one end and placed in perforated 400- μl Eppendorf tubes. The tubes were enclosed in open-sided waxed carton containers to protect from exposure to rain and ultraviolet light and to enable the baits to be fastened to the trees. (\pm)-*exo*-Brevicomin (96.1 % pure) was obtained from Phero Tech. (+)-*endo*-Brevicomin (98.8 % chemical and 90.2% optical purity) was synthesized by B. D. Johnston (Department of Chemistry, Simon Fraser University) according to procedures developed by Johnston and Oehlschlager (1982).

Experiments 2 and 3, conducted from 16 May to 6 August 1995, tested whether simplified or racemic pheromone components were as effective as the enantiospecific complete pheromones of *I. tridens* and

D. affaber in reducing spruce beetle attack and success on felled spruce trees. Twenty-one and 28 trap trees were felled for experiments 2 and 3, respectively. The diameters of trap trees 2 m from the severed butt were $45.2 \pm .58$ cm (mean \pm SE) and $40.2 \pm .57$ cm in experiments 2 and 3, respectively. The average distances between baits at the butt and crown positions were $14.6 \pm .38$ m and $12.7 \pm .30$ for experiments 2 and 3, respectively. Experiment 2 comprised 7 replicates of 3 treatments—(1) unbaited control, (2) *D. affaber* bait, and (3) (\pm)-endo-brevicomin. Experiment 3 comprised 7 replicates of 4 treatments—(1) unbaited control, (2) *I. tridens* bait, (3) (\pm)-ipsdienol, and 4) (\pm)-ipsdienol plus amitinol. Amitinol (*trans*-2-methyl-6-methylene-3,7-octadien-2-ol) is a candidate pheromone for *I. tridens* (Poland 1997). *D. affaber* baits were identical to those used in experiment 1 except that the Eppendorf tubes were placed in polyethylene bags instead of waxed carton containers. (\pm)-endo-brevicomin baits were prepared in the same way as the *D. affaber* baits but contained only (\pm)-endo-brevicomin (95.6% pure, Phero Tech) released at 0.2 mg/24 h rather than the 1:1 mixture of (\pm)-exo- and (+)-endo-brevicomin. *I. tridens* baits were identical to those used in experiment 1. (\pm)-Ipsdienol baits consisted of 3 bubble caps each releasing (\pm)-ipsdienol at 0.2 mg/24 h (Phero Tech). Amitinol was synthesized by H. D. Pierce, Jr., (Department of Biological Sciences, Simon Fraser University) by the method of Francke et al. (1980) from (\pm) ipsdienol (BRI, Danbury, CT) and purified to 98% by flash chromatography on silica gel using pentane-ether (2:1) (vol.:vol.) as eluent. It was released from bubble caps at 0.02 mg/24 h (Phero Tech). All semiochemical release rates were determined at 20–24°C in the laboratory.

Experiment 4, designed to simulate patches of windthrown trees, was conducted from 26 May to 10 August 1995 in the McGregor Model Forest (Northwood Pulp and Timber Tree Farm License Number 30) near Prince George, BC. The experiment comprised 6 replicates of 4 treatments laid out in randomized complete blocks. Ninety-six trap trees were felled in 24 patches of 4 trees. The diameter 2 m from the severed butt was 54.7 ± 1.68 cm (mean \pm SE). The distance between baits at the butt and crown positions was 17.5 ± 0.61 m. Each patch of 4 trees was assigned a single treatment as follows: (1) unbaited control, (2) all 4 trees baited with *I. tridens* bait, (3) all 4 trees baited with *D. affaber* bait, or (4) 2 trees baited with *I. tridens* bait and 2 trees baited with *D. affaber* bait. *D. affaber* and *I. tridens* baits were placed on separate trees to minimize any interference effects caused by combining pheromones of the 2 species. *I. tridens* baits were identical to those used in experiment 1. *D. affaber* baits were similar to those used in experiment 1 except that a 1:2 mixture of (\pm)-exo- and (\pm)-endo-brevicomin was used instead of a 1:1 mixture of (\pm)-exo- and (\pm)-endo-brevicomin. (+)-endo-brevicomin was used because insufficient quantities of (+)-endo-brevicomin were available. The (–) enantiomer in (+)-endo-brevicomin partially inhibited the response by *D. affaber* in trapping experiments (Camacho et al.

1994) but (+)-endo-brevicomin has the offsetting advantage of inhibiting spruce beetle attraction (Poland and Borden 1998a).

On 7 July and 4 August 1994, 3 bark samples, 1 from each bait position, were collected from each tree in experiment 1. In experiments 2–4, 2 bark samples were collected during the 1st sampling period (11–14 July 1995) and 4 in the 2nd (7–10 August 1995). The 1st bark samples were taken from the bait position at the butt of the tree and the position equidistant between the baits at the butt and the midpoint of the bole. The 2nd set of 4 samples included additional samples from the bait positions at the midpoint of the bole and near the crown (or analogous positions on control trees). The initial samples provided an indication of early attack levels. The full set of 4 samples at the end of the experiment yielded rich information about gallery establishment and progeny production for all species. Samples from between-bait locations were included to determine the range of efficacy of the baits on the large-diameter section of the bole where spruce beetles prefer to attack.

Two replicates were eliminated from experiment 1 because baits had been removed and destroyed by animals (probably bears) before sample collection. A 3rd replicate was removed from the analysis because no spruce beetle galleries were observed in any sample from any treatment including control trees. Therefore, the final analysis included 5 of the original 8 replicates.

An analysis of the effect of low, medium, and high attack densities of the 3 species on gallery construction and progeny production by each species also was conducted for experiment 1 to test for direct interactions between the spruce beetle and the secondary species. For the 3 species, the ranges of attack densities for each class were as follows: (1) *D. rufipennis* low, $<15/\text{m}^2$; medium, $15\text{--}30/\text{m}^2$; and high, $>30/\text{m}^2$; (2) *I. tridens* low, $<20/\text{m}^2$; medium, $20\text{--}70/\text{m}^2$; and high, $>70/\text{m}^2$; (3) *D. affaber* low, $<10/\text{m}^2$; medium, $10\text{--}20/\text{m}^2$; and high, $>20/\text{m}^2$. For each species transformed data, $\log_{10}(x + 1)$ to satisfy assumptions of normality and homoscedasticity (Zar 1989), for gallery length per m^2 , progeny density per square meter, length per gallery, and number of progeny per gallery were analyzed by a split-plot analysis of variance (ANOVA) with model factors for spruce beetle attack density class, *I. tridens* attack density class, and the interaction between them. A separate split-plot ANOVA was performed with model factors for spruce beetle attack density class, *D. affaber* attack density class, and the interaction between them.

For all 4 experiments, the transformed data, $\log_{10}(x + 1)$, for the density of each of the measured variables were analyzed for each sample collection period by a univariate split-plot 3-factor ANOVA. The main effects in the model were treatment, replicate and the split-plot variable bark sample position. The model also tested for interactions between treatment and replicate and between treatment and position. Means for treatment and for position were compared by a least squares means multiple comparison procedure

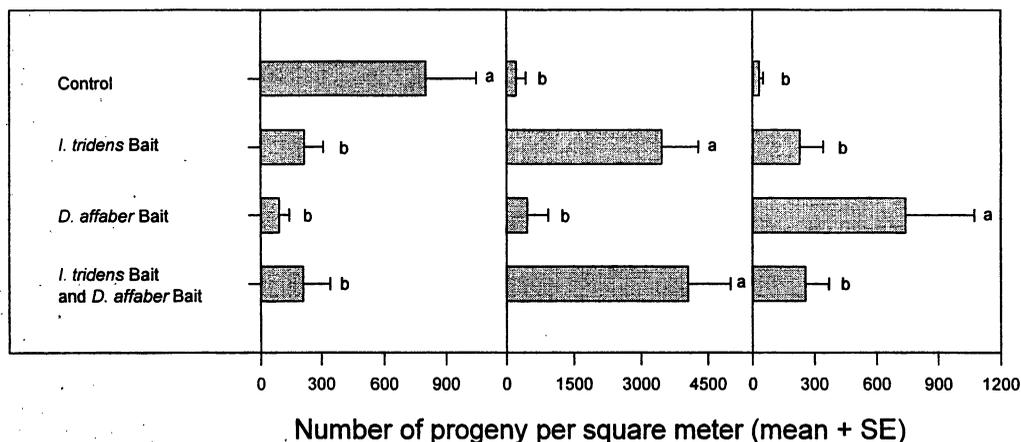
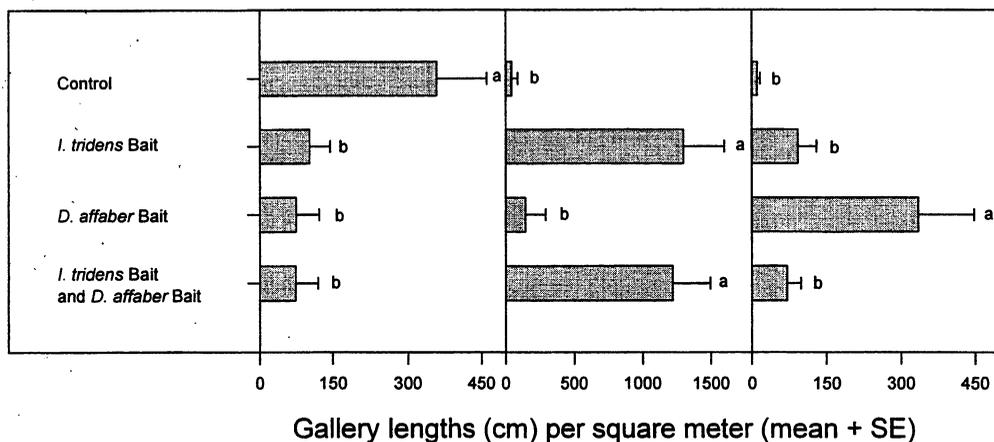
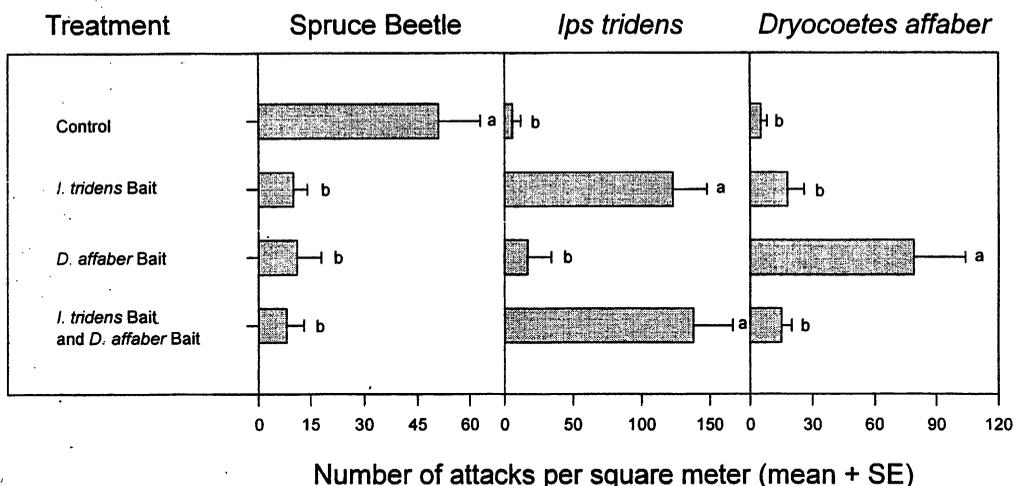


Fig. 1. Spruce beetle, *I. tridens*, and *D. affaber* attack densities, gallery lengths per square meter, and progeny densities in experiment 1 (10 May–4 August 1994), Mackenzie, BC. Control trees were unbaited. *I. tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg/24 h, respectively. *D. affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicommin released at 0.2 mg/24 h. N = 5. Bars topped by the same letter are not significantly different, Ryan–Einot–Gabriel–Welsch test, P < 0.05.

Table 1. Spruce beetle, *I. tridens*, and *D. affaber* gallery lengths per square meter, and progeny densities by spruce beetle (SBclass) and *I. tridens* (ITclass) attack density classes in felled trap trees and results of ANOVA in experiment 1

SBclass	ITclass	N	Spruce Beetle		<i>I. tridens</i>		<i>D. affaber</i>	
			Gallery length/m ²	Progeny density	Gallery length/m ²	Progeny density	Gallery length/m ²	Progeny density
Low	Low	18	0 ± 0	0 ± 0	0 ± 0	0 ± 0	244 ± 84	530 ± 250
Low	Medium	4	0 ± 0	0 ± 0	1,152 ± 754	1,236 ± 348	170 ± 118	603 ± 400
Low	High	17	0 ± 0	0 ± 0	2,060 ± 179	6,649 ± 561	59 ± 24	266 ± 107
Medium	Low	7	218 ± 71	443 ± 154	43 ± 43	137 ± 137	25 ± 20	43 ± 43
Medium	Medium	2	193 ± 13	415 ± 112	896 ± 307	1,988 ± 173	145 ± 145	94 ± 94
High	Low	12	529 ± 83	1,193 ± 259	0 ± 0	0 ± 0	83 ± 56	83 ± 35
High	Medium	2	825 ± 450	1,703 ± 723	651 ± 109	3,180 ± 479	0 ± 0	0 ± 0
SBclass								
F			141.78	36.86	0.60	0.61	1.13	1.05
df			2	2	2	2	2	2
P			0.0001	0.0001	0.570	0.566	0.371	0.393
ITclass								
F			0.01	0.06	346.10	346.41	0.89	0.52
df			2	2	2	2	2	2
P			0.985	0.940	0.0001	0.0001	0.417	0.600

Spruce beetle attack density classes were low, <15/m²; medium, 15–30/m²; and high, >30/m². *I. tridens* attack density classes were low, <20/m²; medium, 10–70/m²; and high, >70/m².

using the Ryan-Einot-Gabriel-Welsh multiple range test (SAS Institute 1990). In all cases $\alpha = 0.05$.

Results

In all 4 experiments the results for the 2 sampling periods were similar, but by the August sampling period differences between treatments had increased markedly. Therefore, only results from the 2nd bark sample collection are reported.

For experiment 1, ANOVA revealed a significant effect for treatment on spruce beetle attack density ($F = 3.75$, $df = 3$, $P = 0.036$), gallery length per square meter ($F = 4.83$, $df = 3$, $P = 0.016$), and progeny density ($F = 4.70$, $df = 3$, $P = 0.018$), *I. tridens* attack density ($F = 8.89$, $df = 3$, $P = 0.002$), gallery length per square meter ($F = 9.44$, $df = 3$, $P = 0.001$), and progeny density ($F = 9.78$, $df = 3$, $P = 0.001$), and *D. affaber* attack density ($F = 3.80$, $df = 3$, $P = 0.019$), gallery length per square meter ($F = 3.31$, $df = 3$, $P = 0.033$), and progeny density ($F = 2.93$, $df = 3$, $P = 0.049$). Spruce beetle attack densities were significantly reduced in trees that were baited with *I. tridens* baits, *D. affaber* baits, or baits for both secondary species compared to unbaited control trees (Fig. 1). On the other hand, *I. tridens* attack density was significantly increased on trap trees baited with *I. tridens* baits alone or combined with *D. affaber* baits. Attacks by *D. affaber* were significantly increased on trees baited with *D. affaber* baits alone. Similar patterns of responses were seen for gallery length per square meter and progeny density per square milliliter (Fig 1).

Mean gallery lengths did not differ between treatments for the spruce beetle (range, 5.7–10.4 cm; $F = 0.62$, $df = 3$, $P = 0.636$), *I. tridens* (range, 8.8–10.5 cm; $F = 0.26$, $df = 3$, $P = 0.854$), or *D. affaber* (range 2.4–5.4 cm; $F = 2.36$, $df = 3$, $P = 0.170$). Similarly, the mean number of progeny per gallery did not differ between treatments for the spruce beetle (range, 8.2–29.1; $F = 0.36$, $df = 3$, $P = 0.786$), *I. tridens* (range, 26.2–28.5; $F =$

0.19, $df = 3$, $P = 0.896$), or *D. affaber* (range, 8.0–19.0; $F = 3.07$, $df = 3$, $P = 0.1126$). By August, all spruce beetle, *I. tridens*, and *D. affaber* progeny were still larvae. There were significant conspecific effects of attack density class but no heterospecific effects (Tables 1 and 2). Therefore, high attack densities per square meter for 1 species were not associated with low values for gallery length per square meter or progeny density per square meter for any other species.

In experiment 2, ANOVA showed a significant effect for treatment on spruce beetle attack density ($F = 4.23$, $df = 2$, $P = 0.021$), gallery length per square meter ($F = 4.27$, $df = 2$, $P = 0.039$), and progeny density per square meter ($F = 5.99$, $df = 2$, $P = 0.005$), *I. tridens* attack density ($F = 5.98$, $df = 2$, $P = 0.016$), gallery length per square meter ($F = 7.06$, $df = 2$, $P = 0.002$), and progeny density per square meter ($F = 8.00$, $df = 2$, $P = 0.001$), and *D. affaber* attack density ($F = 4.54$, $df = 2$, $P = 0.034$), and gallery length per square meter ($F = 5.28$, $df = 2$, $P = 0.023$). In experiment 3, ANOVA showed a significant effect for treatment on spruce beetle attack density ($F = 6.20$, $df = 3$, $P = .004$), gallery length per square meter ($F = 4.61$, $df = 3$, $P = 0.015$), and progeny density per square meter ($F = 5.75$, $df = 3$, $P = 0.006$), and *I. tridens* attack density ($F = 4.17$, $df = 3$, $P = 0.021$), gallery length per square meter ($F = 8.90$, $df = 3$, $P = 0.0001$), and progeny density per square meter ($F = 8.55$, $df = 3$, $P = 0.0001$). The lack of significant effect for position in both experiments indicates that the baits were as effective at inducing attack between baits as they were at each bait position.

In experiment 2, spruce beetle attack densities were significantly reduced in trees that were baited with (\pm)-*endo*-brevicomin, but in contrast to experiment 1 (Fig. 1), not in trees that were baited with *D. affaber* baits (Fig. 2). Both *I. tridens* and *D. affaber* attack densities were significantly increased in trees baited with (\pm)-*endo*-brevicomin compared with densities in unbaited control

Table 2. Spruce beetle, *I. tridens*, and *D. affaber* gallery lengths per square meter, and progeny densities by spruce beetle (SBclass) and *D. affaber* (DAclass) attack density classes in felled trap trees and results of ANOVA in experiment 1

SBclass	DAclass	N	Spruce Beetle		<i>I. tridens</i>		<i>D. affaber</i>	
			Gallery length/m ²	Progeny density	Gallery length/m ²	Progeny density	Gallery length/m ²	Progeny density
Low	Low	24	0 ± 0	0 ± 0	1,225 ± 95	3,607 ± 815	0 ± 0	0 ± 0
Low	Medium	10	0 ± 0	0 ± 0	990 ± 299	3,024 ± 902	201 ± 31	608 ± 126
Low	High	5	0 ± 0	0 ± 0	63 ± 63	234 ± 234	743 ± 127	2,078 ± 508
Medium	Low	6	243 ± 78	424 ± 172	251 ± 196	520 ± 363	0 ± 0	0 ± 0
Medium	Medium	3	157 ± 44	465 ± 147	196 ± 196	604 ± 604	155 ± 76	170 ± 89
High	Low	8	591 ± 133	1,296 ± 279	162 ± 108	795 ± 528	0 ± 0	0 ± 0
High	Medium	5	554 ± 154	1,380 ± 514	0 ± 0	0 ± 0	59 ± 6	160 ± 63
High	High	1	501	458	0	0	701	206
SBclass								
F			74.41	26.43	1.56	1.51	0.22	1.39
df			2	2	2	2	2	2
P			0.0001	0.0003	0.222	0.232	0.805	0.304
DAclass								
F			1.97	1.21	1.60	1.68	2,437.8	111.07
df			2	2	2	2	2	2
P			0.1531	0.310	0.215	0.199	0.0001	0.0001

Spruce beetle attack density classes were low, <15/m²; medium, 15–30/m²; and high, >30/m². *D. affaber* attack density classes were low, <10/m²; medium, 10–20/m²; and high, >20/m².

trees. Nearly identical patterns (statistically) occurred for gallery length per square meter and progeny density per square meter for all 3 species.

In experiment 3, spruce beetle attack density was significantly reduced only in trees that were baited with the *I. tridens* bait which consisted of (±)-ipsdienol plus *cis*-verbenol (Fig. 3). Attack densities were not reduced in trees that were baited with (±)-ipsdienol alone or (±)-ipsdienol plus amitinol. Conversely, *I. tridens* attack densities were significantly increased in trees baited with *I. tridens* baits. There were no significant differences in *D. affaber* attack densities between the different treatments. The conspecific patterns for gallery length per square meter and progeny density per square meter were similar to those for attack density.

In experiment 4, ANOVA again showed a significant effect for treatment on spruce beetle attack density ($F = 5.28$, $df = 4$, $P = 0.005$), gallery length per square meter ($F = 4.30$, $df = 4$, $P = 0.011$), and progeny density per square meter ($F = 4.35$, $df = 4$, $P = 0.010$), *I. tridens* attack density ($F = 8.78$, $df = 4$, $P = 0.0003$), gallery length per square meter ($F = 8.45$, $df = 4$, $P = 0.0004$), and progeny density per square meter ($F = 8.48$, $df = 4$, $P = 0.0004$), and *D. affaber* attack density ($F = 3.10$, $df = 4$, $P = 0.039$), gallery length per square meter ($F = 4.35$, $df = 4$, $P = 0.011$), and progeny density ($F = 4.30$, $df = 4$, $P = 0.011$). Spruce beetle attack densities and gallery lengths per square meter were significantly reduced by all treatments but *D. affaber* baits alone (Fig. 4). Progeny density was reduced only in trees baited with *I. tridens* baits either in patches baited with *I. tridens* pheromones or the pheromones of both secondary species. *I. tridens* attack densities, gallery lengths per square meter, and progeny densities were lowest in trees from patches in which all trees were baited with *D. affaber* baits and highest in patches baited with *I. tridens* baits, or in trees baited with its own pheromone in co-baited

patches. *D. affaber* attack densities, gallery lengths per square meter, and progeny densities were low in patches baited with *I. tridens* baits, and high in patches baited with *D. affaber* baits or trees baited with its own pheromone in co-baited patches.

Discussion

The results of these experiments uphold all 3 hypotheses. Spruce beetle attack and success was reduced in individually felled trap trees baited before spruce beetle flight with pheromones of either or both secondary species (Fig. 1), with the single component (±)-*endo*-brevicomin (Fig. 2), and in simulated patches of windthrown trees baited with *I. tridens* pheromones (Fig. 4). In all 4 experiments when trees were baited with secondary species baits before spruce beetle flight, spruce beetle attack was inhibited and the secondary species were able to attack successfully and exploit the resource.

For experiment 1, spruce beetles exploited the resource in unbaited control trees at the expense of the secondary species (Fig. 1). Success of the secondary species was enhanced on trees baited with their respective pheromones, allowing them to exploit the resource at the expense of spruce beetles (Fig. 1). These results indicate that resource exploitation and indirect interference in accessing the resource are important mechanisms of competitive interactions between the spruce beetle, *I. tridens*, and *D. affaber*. This conclusion provides further support for the role of interspecific competition in the community structure of phytophagous insects. Our results also agree with the finding that interference competition was more prevalent among internal feeders and closely related, aggregative insects (Denno et al. 1995). Differences in host preference by spruce beetles, *I. tridens*, and *D. affaber* are unlikely to account for differential degrees of success, because all trees in the study were similar in diameter, vigor, and placement in

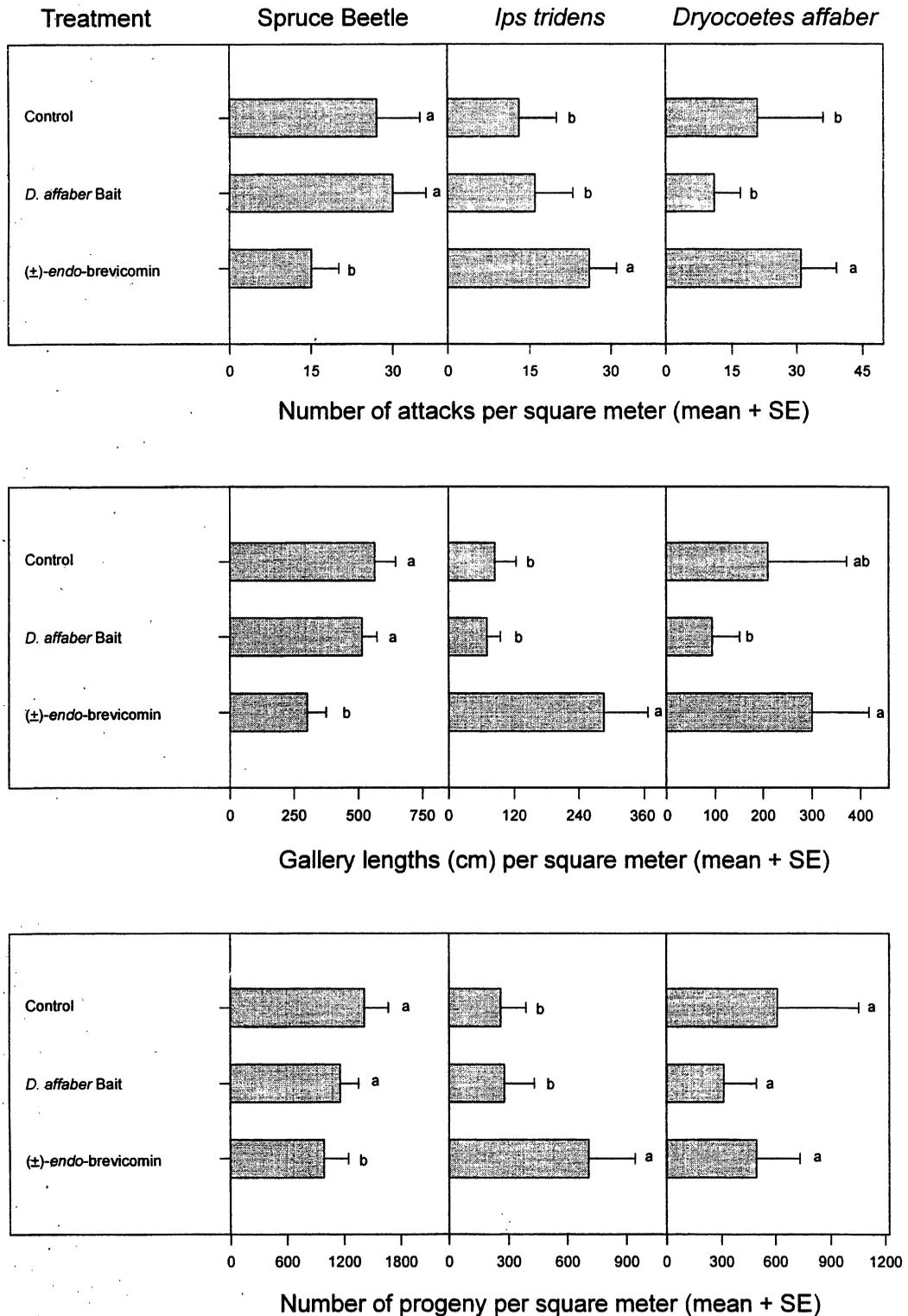


Fig. 2. Spruce beetle, *I. tridens*, and *D. affaber* attack densities, gallery lengths per square meter, and progeny densities in experiment 2 (16 May–6 August 1994), Mackenzie, BC. Control trees were unbaited. *D. affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg/24 h. (±)-*endo*-Brevicomin was released at 0.2 mg/24 h. $N = 7$. Bars topped by the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch test, $P < 0.05$.

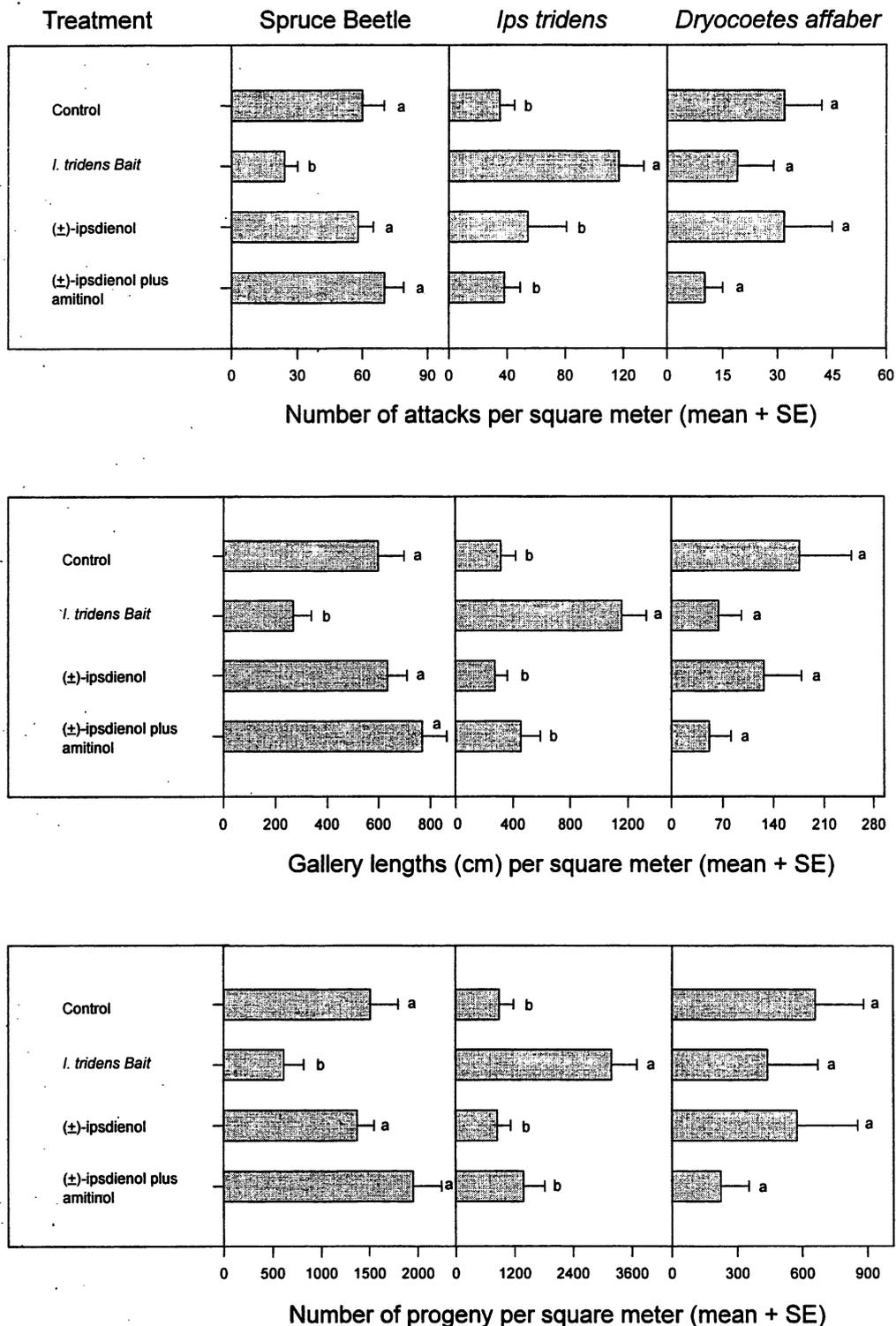


Fig. 3 Spruce beetle, *I. tridens*, and *D. affaber* attack densities, gallery lengths per square meter, and progeny densities in experiment 3 (16 May-6 August 1994), Mackenzie, BC. Control trees were unbaited. *I. tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg/24 h, respectively. (±)-Ipsdienol and amitinol were released at 0.6 and 0.02 mg/24 h, respectively. N = 7. Bars topped by the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch test, P < 0.05.

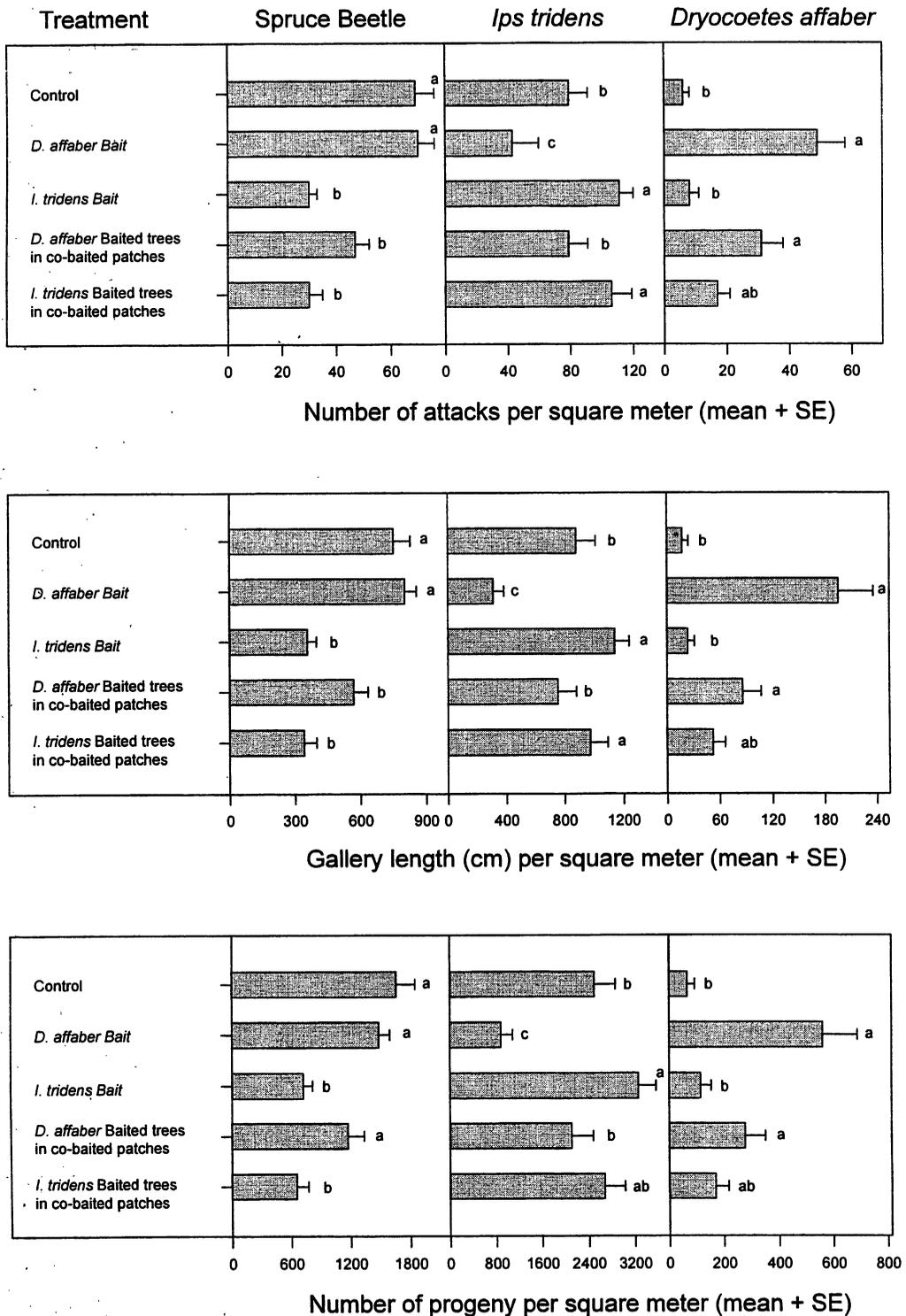


Fig. 4 Spruce beetle, *I. tridens*, and *D. affaber* attack densities, gallery lengths per square meter, and progeny densities in experiment 4 (26 May–10 August 1994), Prince George, BC. Control trees were unbaited. *I. tridens* baits consisted of (\pm)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg/24 h, respectively. *D. affaber* baits consisted of a 1:2 mixture of (\pm)-*exo*- and (\pm)-*endo*-brevicomin released at 0.2 mg/24 h. $N = 6$. Bars topped by the same letter are not significantly different, Ryan-Einot-Gabriel-Welsch test, $P < 0.05$.

the stand. In addition, randomization and replication of treatments would have removed any potential bias from host differences.

The lack of significant differences in mean gallery lengths and mean numbers of progeny per gallery for the 3 species between treatments and the lack of effect of attack density class of any species on total gallery length or progeny densities of any other species (Tables 1 and 2) suggests that direct interference is unlikely to be an important mechanism of competitive interaction.

The lack of significant differences in mean gallery lengths and numbers of progeny per gallery for the spruce beetle between treatments may be a result of combined intra- and interspecific effects. Because trees with low secondary species attack densities tended to have high spruce beetle attack densities (Fig. 1), reductions in interspecific encounters would be offset by increased intraspecific encounters. The reverse situation would exist in trees with low spruce beetle attack densities and high secondary species attack densities. Safranyik and Linton (1985) found that increased intraspecific competition resulted in reduced gallery lengths and numbers of progeny per female. The mean gallery lengths and numbers of progeny per gallery in experiment 1 were similar to those found in the highest spruce beetle density treatments tested by Safranyik and Linton (1985). Therefore, intra- and interspecific effects may offset each other in reducing gallery lengths and progeny production in the different treatments.

Attack densities, gallery lengths per square meter, and progeny densities for both secondary species were significantly increased in trees baited with their respective pheromones (Fig. 1). This result contrasts with low attack densities by *D. affaber* and *I. tridens* when trees were baited with pheromones for the secondary species to induce competitive displacement of the spruce beetle following its establishment (Poland and Borden 1998b). In further contrast to the results for inducing competitive displacement (Poland and Borden 1998b), attack densities by the spruce beetle were much lower and were significantly reduced in trees baited with secondary species pheromones before spruce beetle attack (Fig. 1). These differences may be due in part to a somewhat lower spruce beetle population level in the area of this study than in the area studied for competitive displacement (Poland and Borden 1998b). However the main effect undoubtedly stems from placement of the secondary species pheromones on the trees before spruce beetle flight, thus interfering with spruce beetle attack from the outset.

The reduction in spruce beetle attack densities, gallery lengths per square meter and progeny densities in trees baited with secondary species pheromones (Fig. 1) suggests that competitive exclusion may have considerable potential for use in spruce beetle management. Less expensive single-component or racemic mixtures would be preferable to enantiospecific pheromones for operational implementation of such a management tactic.

The results of experiment 2 (Fig. 2) show that (\pm)-*endo*-brevicomin was effective in reducing spruce

beetle attack density and in increasing attack densities by both *I. tridens* and *D. affaber*, whereas in contrast to experiment 1 (Fig. 1), the *D. affaber* bait was not. This suggests that (\pm)-*endo*-brevicomin could be a cost-effective substitute for the expensive *D. affaber* bait. On the other hand, in experiment 3 only the *I. tridens* bait was effective in reducing spruce beetle attack density and in increasing *I. tridens* attack density (Fig. 3). Therefore, (\pm)-*ipsdienol* in combination with *cis*-*verbenol* appears to be the only effective *I. tridens* bait available at present for managing spruce beetle populations through competitive exclusion.

Interactions between the 2 secondary species must be considered in the implementation of competitive exclusion of the spruce beetle as a management tactic. Attack by *I. tridens* was not inhibited by the pheromone for *D. affaber* in experiment 1 (Fig. 1) and was enhanced by baits consisting only of (\pm)-*endo*-brevicomin in experiment 2 (Fig. 2). The bait for *D. affaber* contained (\pm)-*exo*-brevicomin, a compound identified in volatiles produced by *I. tridens* males boring in Engelmann spruce logs (Poland 1997) and which elicited antennal responses by *I. tridens* females. *D. affaber* attack density was significantly enhanced only on trees baited with *D. affaber* baits alone, and was strongly inhibited when baits for both secondary species were combined in experiment 1 (Fig. 1). Similarly, in experiment 3, *I. tridens* baits were not attractive to *D. affaber*. Attacks by *D. affaber* were not increased by the presence of (\pm)-*ipsdienol*, (\pm)-*ipsdienol* plus *amitinol*, or (\pm)-*ipsdienol* plus *cis*-*verbenol* (Fig. 3). This relationship suggests that *I. tridens* with a shorter life cycle is adapted to outcompete *D. affaber* in exploiting the phloem tissue resource. It may be adaptive for weak competitors to avoid colonizing hosts that are already occupied, whereas strong competitors or species that are able to co-exist successfully in the same host (e.g., *I. pini* and *Pityogenes knechteli* Swaine) (Poland and Borden 1994) need not avoid each other. Even though *I. tridens* may be the superior competitor, it might be desirable to maintain or enhance *D. affaber* populations in an operational implementation of competitive exclusion of the spruce beetle by baiting some of the trees with *D. affaber* baits alone.

The results of experiment 4 show that baiting patches of felled trees with *I. tridens* baits, regardless of whether the trees were all baited with *I. tridens* baits or were adjacent to trees baited with *D. affaber* baits, was effective in reducing spruce beetle attack density, resource exploitation, and progeny production. In turn, *I. tridens* attack density, gallery length per square meter, and progeny density were increased (Fig. 4). Although *D. affaber* attack density and success was significantly increased in trees baited with *D. affaber* baits, regardless of patch treatment, spruce beetle attack density and success was not correspondingly reduced. These results lead to a tentative conclusion that competitive exclusion of the spruce beetle would be feasible in patches of trees, but they illustrate the complexity of implementing it as a management tactic. Although the results suggest that *I. tridens* may be a

stronger competitor than *D. affaber*, a similar result could have been obtained if *I. tridens* were more abundant than *D. affaber*. *D. affaber* attack densities were not as high as they were on trees baited with *D. affaber* pheromones in experiment 1 (Fig. 1) in which inhibition of spruce beetle attack by *D. affaber* baits was effective, and were only slightly higher than those in experiment 2 in which inhibition of spruce beetle attack was ineffective (Fig. 2). The fact that (\pm)-*endo*-brevicommin was substituted for (+)-*endo*-brevicommin in experiment 4 was probably not significant because in experiment 2 spruce beetle attack density was significantly reduced in trees baited with (\pm)-*endo*-brevicommin (Fig. 2).

Another possible explanation for the lack of competitive exclusion of the spruce beetle by *D. affaber* in experiment 4 is that environmental conditions can influence the outcome of competitive interactions (Begon and Mortimer 1986). Therefore, while *D. affaber* may be a strong competitor under some conditions (McCambridge and Knight 1972), its competitive ability may be reduced under other conditions. Its peak flight period occurs ≈ 1 mo later than that for the spruce beetle and *I. tridens* (Bright 1976, Camacho-Vera 1993). If early-season environmental conditions are favorable for spruce beetle development in the absence of *I. tridens*, it may gain a competitive advantage over *D. affaber* through rapid exploitation of the phloem resource.

Ips tridens attack densities were significantly higher on trees baited with *I. tridens* baits than on trees baited with *D. affaber* baits regardless of patch treatment (Fig. 4). Therefore, *I. tridens* was not cross-attracted to the *D. affaber* bait on its own. *I. tridens* attack densities were actually significantly reduced when all trees in a patch were baited with *D. affaber* baits. However, it is not possible to conclude from this experiment that *D. affaber* baits would disrupt the attraction of *I. tridens* because no disruptive effect occurred in experiment 1 when trees were co-baited for both secondary species (Fig. 1).

Dryocoetes affaber attack densities were significantly increased only in trees that were baited with *D. affaber* baits regardless of patch treatment (Fig. 4). This result agrees with the results from experiment 1, which showed that *D. affaber* was not cross-attracted to trees baited with *I. tridens* baits (Fig. 1).

Overall, experiment 4 shows that baiting patches of felled trees with *I. tridens* baits before spruce beetle flight was effective in reducing spruce beetle colonization and increasing colonization by *I. tridens*. These data coupled with the results of experiments 1–3 indicate that baiting trees with secondary species baits before spruce beetle flight consistently results in reduced spruce beetle attack density, gallery length per square meter, and progeny density. If implemented operationally, baiting of susceptible hosts for secondary species would have 2 positive effects—inducing attack by the secondary species, and partially repelling spruce beetles. Thus spruce beetle attack could be reduced and the probability of population buildup to outbreak levels would be minimized. Inducing attack by the

secondary scolytids would increase their populations which may remain high if windthrow and slash are abundant. However, the secondary species are unable to colonize healthy standing trees and, therefore, would not pose an economic threat. Secondary scolytid populations may subsequently decline in the absence of fallen trees or suitable hosts killed or weakened by the aggressive, primary-attacking spruce beetle.

The operational success of pheromone-induced competitive exclusion in preventing spruce beetle population buildup would be dependent on interactions between populations of the spruce beetle and the secondary species, the distribution and availability of suitable hosts, environmental conditions, and other pest management tactics with which it might be integrated. It is most likely to succeed where endemic beetle populations are at suboutbreak levels, populations of secondary species are abundant, host resources such as fresh windthrown trees are available, the stand is relatively healthy, and climatic conditions are relatively cool and moist. These conditions typically are found in riparian zones which often are protected from intrusions such as harvesting but which can be sources of outbreaks if spruce beetle populations build up in the blowdown in these areas. Therefore, competitive exclusion could be of great value in managing the spruce beetle in these sensitive sites where conventional management approaches are not desired.

More complete resource exploitation might be achieved if the entire guild of competitor species were present. These might include *Polygraphus rufipennis* Kirby, *Scierus annectans* LeConte, and *I. perturbatus* Eichhoff (Werner and Holsten 1984). It is probable that their pheromones also disrupt spruce beetle attraction and could be judiciously included in a cost-effective treatment. It also is possible that different inhibitory semiochemicals may enhance the competitive exclusion effect depending on how they might affect the secondary species. Other inhibitors may include the antiaggregation pheromone for the spruce beetle, methylcyclohexenone (MCH) (Kline et al. 1974, Furniss et al. 1976), resistant host compounds (Hayes et al. 1994, Werner 1995), and nonhost or green leaf volatiles (Dickens et al. 1992, Wilson et al. 1996).

Other pheromone-based management tactics such as containment and concentration with aggregation pheromones could be used with and complement competitive exclusion. Shore et al. (1990) found that grid-baiting with α -pinene plus frontalin was effective in containing and concentrating a spruce beetle infestation in a grid-baited stand before sanitation harvesting. The use of attractive felled trap trees where their removal is possible, and grid-baiting infested areas that subsequently can be harvested could be used as the *pull* component in a *push-pull* management strategy (Lindgren and Borden 1993), in which the *push* component involved competitive exclusion in adjacent riparian or sensitive leave areas, as well as the use of antiaggregation pheromones and nonhost volatiles in reserve stands of commercial timber. In such an integrated management program, competitive exclu-

sion could reduce or replace the use of arsenical-treated lethal trap trees (Hodgkinson 1985).

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