

## Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine

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The pine engraver (PE), *Ips pini* (Say), often coexists with the mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopk., in lodgepole pine, *Pinus contorta* var. *latifolia* Engelm. The PE colonizes the upper bole, while the MPB infests the lower bole. We investigated the hypothesis that interspecific interactions between the PE and the MPB within trees can adversely affect MPB progeny production or survival. In lodgepole pine bark attacked by both species, PE and MPB emergence holes had a strong negative interrelationship, suggesting that high numbers of one species resulted in lower numbers of the other. In the laboratory, attacks by PEs on lodgepole pine logs resulted in significantly decreased numbers of MPB progeny, particularly when MPBs and PEs were allowed to attack logs simultaneously. Reductions in MPB progeny were 92.8 and 96.2% when the ratios of attacking beetles were 100 PE : 50 MPB per square metre and 200 PE : 50 MPB per square metre, respectively, compared with that in control logs with 50 MPB per square metre. In an August field experiment, pheromone-induced attack by the PE on trees just attacked by the MPB resulted in a 72.5% reduction in mean MPB progeny production compared with that in MPB-attacked control trees. Possible reasons for the reduced success of MPB when it and the PE coinhabit the same host may be exploitation competition, interference competition, or introduction of fungal competitors deleterious to the MPB. Induced infestation by PEs of MPB-infested trees may have the potential to reduce or control MPB populations.

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Le scolyte du pin (SP), *Ips pini* (Say), coexiste souvent avec le dendroctone du pin ponderosa (DPP), *Dendroctonus ponderosae* Hopk., dans le pin lodgepole, *Pinus contorta* var. *latifolia* Engelm. Le SP colonise la partie supérieure du tronc tandis que DPP se trouve dans la partie plus basse du tronc. Nous avons testé l'hypothèse selon laquelle les interactions interspécifiques entre le SP et le DPP nuisent à la production ou à la survie de la progéniture du DPP. Lorsque les deux espèces (SP, DPP) sont présentes dans l'écorce du pin lodgepole, on dénote une forte interrelation négative entre les trous d'émergence, suggérant ainsi que la présence accrue d'une espèce entraîne une quantité moindre de représentants de l'autre espèce. En laboratoire, les attaques de billes de pin lodgepole par le SP se traduisent par un nombre significativement inférieur de progéniture de DPP, ceci étant spécialement marqué lorsque les attaques par le SP et le DPP sont simultanées. Par rapport aux billes témoins, attaquées à raison de 50 DPP/m<sup>2</sup>, les réductions en nombre de progéniture furent de 92,8 et 96,2% lorsque les ratios d'attaques étaient respectivement de 100 SP : 50 DPP par mètre carré et de 200 SP : 50 DPP par mètre carré. Une expérience conduite sur le terrain au mois d'août a montré que les attaques par le SP, induites à l'aide de phéromone sur des arbres préalablement attaqués exclusivement par le DPP, se traduisaient par une réduction de 72,5% du nombre moyen de progénitures produites par DPP, comparativement aux arbres témoins uniquement attaqués par le DPP. Le succès réduit du DPP, lorsque celui-ci cohabite dans un même hôte avec le SP, pourrait hypothétiquement être relié, soit à des phénomènes de compétition au niveau de l'exploitation ou à de l'interférence, ou encore, à l'introduction de champignons nuisant au succès du DPP. L'induction d'attaque par le SP sur des arbres infestés par le DPP pourrait potentiellement réduire ou tenir en échec les populations de DPP.

[Traduit par la rédaction]

### Introduction

Trees are frequently attacked simultaneously by several species of bark beetles, creating potential competition for food and living space and the necessity for resource partitioning (Stark and Borden 1965; Berryman 1973; Birch and Wood 1975; Birch et al. 1980; Svihra et al. 1980; Paine et al. 1981; Dahlsten 1982; Wood 1982; Light et al. 1983). The mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopk., and the pine engraver (PE), *Ips pini* (Say), often coexist in the same tree. The PE colonizes the upper bole of pines already overcome by *Dendroctonus* spp. (Furniss and Carolin 1977). The MPB is the more aggressive tree killer, and galleries of the two species are seldom found intermixed.

Interspecific competition occurs when a number of individuals utilize common resources that are in short supply, or when the individuals seeking the resource do harm to each other while utilizing the resource (Birch 1957). Interference competition (Brian 1956) is the capability of members of one species to damage those of another. This could occur indirectly by destroying or blocking access to a resource, or directly through aggressive attacks or cannibalism. Exploitation competition (Brian 1956) is the ability to detect, occupy, and retain vacant resources necessary for survival. These two forms of competition may occur together when bark beetles compete for phloem in the two-dimensional, subcortical world.

The MPB is the most lethal insect pest of lodgepole pine, *Pinus contorta* var. *latifolia* Engelm., in North America (Furniss and Carolin 1977). It is univoltine and monogamous. Females usually initiate attacks on standing trees in mid-

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summer (Reid 1962a), and beetles of both sexes produce aggregation pheromones that induce mass attack and eventually death of the tree (Borden et al. 1987). A threshold density of 40 galleries/m<sup>2</sup> is necessary for the beetles to overcome a tree's defences, and the optimal attack density is 62 attacks/m<sup>2</sup> (Raffa and Berryman 1983). Beyond this density a decline occurs in the number of progeny per female because of intraspecific competition (Raffa and Berryman 1983).

The PE occasionally kills pines of several species, but it usually attacks dead or dying trees or logs (Reid 1955; Thomas 1961; Kennedy 1969; Sartwell 1970, 1971; Sartwell et al. 1971). Throughout much of its range, it is sympatric with MPB, but is bi- or tri-voltine. Flight by the PE begins in April or May and persists through September (Thomas 1961; Sartwell et al. 1971). Males initiate the attack, construct a nuptial chamber in the phloem, and release an aggregation pheromone. Attack densities are usually between 120 and 190/m<sup>2</sup> (Anderson 1948; Light et al. 1983). PE males are usually joined by 2-4 females (Light et al. 1983; Thomas 1961; Schenk and Benjamin 1969; Schmitz 1972).

Interspecific competition can cause mortality in numerous subcortical species. Wood-borer larvae (Buprestidae, Cerambycidae) destroy bark beetle larvae and consume their food resource (Blackman 1931; Miller and Keen 1960; Schenk and Benjamin 1969; Coulson et al. 1976, 1980). The MPB and the western pine beetle, *Dendroctonus brevicomis* LeC., frequently attack at the same time, and their galleries intermingle (Miller and Keen 1960; Dahlsten 1982). *Pityokteines elegans* Swaine and *Pityophthorus pseudotsugae* Swaine can affect the abundance of the fir engraver, *Scolytus ventralis* LeC., when their galleries overlap (Stark and Borden 1965; Ashraf and Berryman 1969; Berryman 1973). Adult *Ips emarginatus* LeC. widen *D. brevicomis* galleries, destroying *D. brevicomis* brood (Miller and Keen 1960). The southern pine beetle, *Dendroctonus frontalis* Zimm., and four *Ips* species occupy less bark area per species than would be expected if there were no interspecific competition (Paine et al. 1981). When *Ips avulsus* (Eich.) and *D. frontalis* coinfect lightning-struck trees, the numbers of emerging *D. frontalis* decline significantly (Hodges and Pickard 1971). Interspecific competition by several secondary bark beetles caused significant mortality of the spruce beetle, *Dendroctonus rufipennis* (Kby.) (McCambridge and Knight 1972). Also, when trees recently infested by *D. frontalis* or *Dendroctonus mexicanus* Hopk. are cut and covered with brush, induced competition by secondary bark beetles is considered to be the principal factor in achieving control of the primary species (Islas 1974; Islas et al. 1981).

One species of bark beetle may build up large populations during an outbreak of another species of bark beetle, threatening the original species. Western pine beetle populations increase behind outbreaks of the California five-spined engraver, *Ips paraconfusus* Lanier, and eventually become the major constituent of the outbreak (Miller and Keen 1960; Furniss and Carolin 1977). There is some evidence to suggest that a similar relationship between the PE and the MPB exists. In British Columbia, extensive PE attack has been noted in trees attacked by the MPB, especially those attacked by the MPB during late summer or early fall, when the summer generation of PE is also attacking (Andrews 1987; Humphreys and Ferris 1987; Unger and Stewart 1987; L.J. Rankin and J.H. Borden, personal observation). Interspe-

cific competition could thus be one of the factors that cause the decline of a MPB outbreak, because the higher attack density of PE, and the more rapid development of PE than MPB larvae, would allow them to pre-empt the phloem resource.

Our objectives were to test the hypothesis of interspecific competition by (i) investigating differential emergence rates from trees attacked by both species, (ii) evaluating progeny production from logs attacked by both species or either species alone in the laboratory, and (iii) evaluating progeny production from MPB-attacked trees in which coattack by the PE was induced in the field.

## Materials and methods

### *Emergence of MPB and PE from infested pines*

Lodgepole pines ca. 30 km east of Princeton, British Columbia, in a stand that had been initially infested by MPB over 1 year previously, as indicated by pitch tubes on the bark surface, were assessed for the number of MPB and PE emergence holes. *Ips* emergence holes were small (max. diam. 1.9 mm,  $\bar{x}$  = 1.57 mm, personal observation), similar to the 1.5 mm diameter recorded by Clemens (1916). A cylindrical wire (1.9 mm diam.) was used to distinguish PE emergence holes from those caused by MPB (> 1.9 mm diam.) (Safranyik and Linton 1985). Exit holes in a rectangular area 40 × 20 cm at breast height (1.3 m) on the east side of the bole were tallied. The bark was removed to ensure that the initial MPB attack had been successful and to verify that no beetles remained under the bark. To measure the extent of MPB-PE interaction throughout a stand, previously attacked trees were counted and classified by whether they had been attacked by either or both species.

### *Attack by MPB and PE alone or together in the laboratory*

Infested pine logs containing MPB or PE were collected from early April through May 1987 near Princeton, British Columbia. The logs were waxed at both ends and held at 4°C. When necessary the logs were placed in screened cages and maintained at 27°C and approximately 40% RH. Emergent beetles were collected daily and held from 0 to 7 days at 4-5°C in jars containing slightly moistened tissues (Watson 1971).

Fresh uninfested pine trees, approximately 28 cm in diameter at breast height, were felled in the same locations as infested logs. They were cut into bolts so that the phloem surface of each was approximately 0.5 m<sup>2</sup>. The bolts were waxed at both ends and stored in shade until used in experiments.

The sex of PE adults was determined by the male's large knob on the third dorsal spine on the elytral declivity (Bright 1976). MPB were roughly sorted by size (Amman and Cole 1983) and then separated accurately by sexual dimorphism of the seventh abdominal tergite (Lyon 1958). To simulate densities found in the field, two attack densities were employed for male PE: 100 and 200 attacks/m<sup>2</sup>. A ratio of three female PE for every male was used. For MPB, an attack density of 50 females/m<sup>2</sup> was employed, corresponding to a moderate attack density in nature; one male was paired with each female.

A separate pine bolt was used for each treatment. MPB females were placed on the log and permitted to select attack sites. After 24 h, an equal number of males were placed on the log and allowed to join females. When treatments involved both species, an additional day was allowed for MPB gallery establishment; introductions of PE were begun on the 3rd day.

PEs were added to uninfested and MPB-infested logs in an identical manner. Males were placed on the log and permitted to select attack sites and to bore into the bark for 24 h. At this time the nuptial chambers are approximately 6.3 mm in diameter and the male will accept a mate (Schmitz 1972). An equal number of females were placed on the logs and allowed to join males. Two more additions of females were made on subsequent days. During

the introduction period, dead beetles were replaced by healthy beetles of the same sex. The preceding procedure was designated as a simultaneous attack by both species. In other treatments, PE introductions were made 2 and 4 weeks after attack by MPB.

Two experiments were conducted. A three-replicate preliminary experiment, using bolts from a single pine tree, tested only simultaneous introductions. In the second experiment, nine bolts from one tree were used to complete each of five replicates. Treatments for each experiment are given in Table 1.

The experiments were evaluated by comparing the numbers of progeny of each species that were produced from each bolt. In the case of single species controls and simultaneous introductions of both species, the bolts were kept in rearing cages for 6 weeks and all emergent adults were collected. The logs were then peeled and adults, pupae, and larvae were counted. If PE attack was delayed, the duration that bolts were kept in the rearing cage was extended by the amount of the delay period. Parental beetles were distinguished from new adults based on abraded setae and color. All emergent PEs were weighed and sexed. Most MPBs had not reached maturity by the time the logs were debarked, and none were weighed.

#### Induced attack in the field by PE on MPB-infested trees

Two approaches were taken to simulate natural interactions of the PE and MPB. In the first field experiment, five trees east of Princeton, British Columbia, that had been attacked naturally the previous summer by the MPB were baited in May and June 1987 with polypropylene microcentrifuge tubes (1.5 mL) containing ten 2  $\mu$ L Microcap disposable pipettes filled with ( $\pm$ )-ipsdienol (Phero Tech Inc., Delta, B.C., chemical purity 97%). Each treated tree had six baits stapled along the north side of the bole at 0.33-m intervals from 0.5 to 2.5 m in height. These baits released ipsdienol at approximately 100 mg per day. They were effective for 1 week and were replaced once. After attack by PE, the trees were felled and one sample bolt was removed from each. Single bolts from 13 control trees, attacked only by MPB, were also collected. In addition, six trees attacked naturally by both species of beetle (three from east of Penticton) were felled and one bolt was collected from each. The bolts were placed in rearing cages, and the emergent beetles of both species were counted and sexed.

In a second experiment, healthy pines east of Princeton, British Columbia, were baited with MPB tree baits (Phero Tech Inc., Delta, B.C.) in August 1987. Within 10–20 days after attack by the MPB, the baits were removed and replaced by six ipsdienol baits that released ipsdienol from C-Flex tubing at a rate of approximately 600 mg per day. Attacked trees were felled 8 days after ipsdienol baiting; bolts were collected from the region of overlapping baits and treated as in the first experiment.

#### Statistical analysis

The data on emergence were evaluated using linear regression analysis of PE on MPB emergence holes. Since the data were not normally distributed, they were transformed by  $y' = \sqrt{(y + 0.5)}$  (Zar 1984).

To analyze for interaction between attack density and time effects for the second laboratory experiment, a two-dimensional regression model (PE attack density and time effects) was employed for MPB progeny, while a three-dimensional model (PE attack density, MPB attack density, and time effects) was used for PE progeny (models developed by S. Ng, Statistical Consulting, Department of Mathematics, Simon Fraser University). Each regression model mimics an analysis of variance, separates interaction effects, and indicates whether time and attack density effects function independently.

Other data were analyzed according to Zar (1984). The data on progeny production from both laboratory experiments and the first field experiment were evaluated using the Kruskal–Wallis test followed by a multiple comparison test for equal and unequal sample sizes. Data from the second field experiment in August were analyzed using a Mann–Whitney test. A one-way analysis of

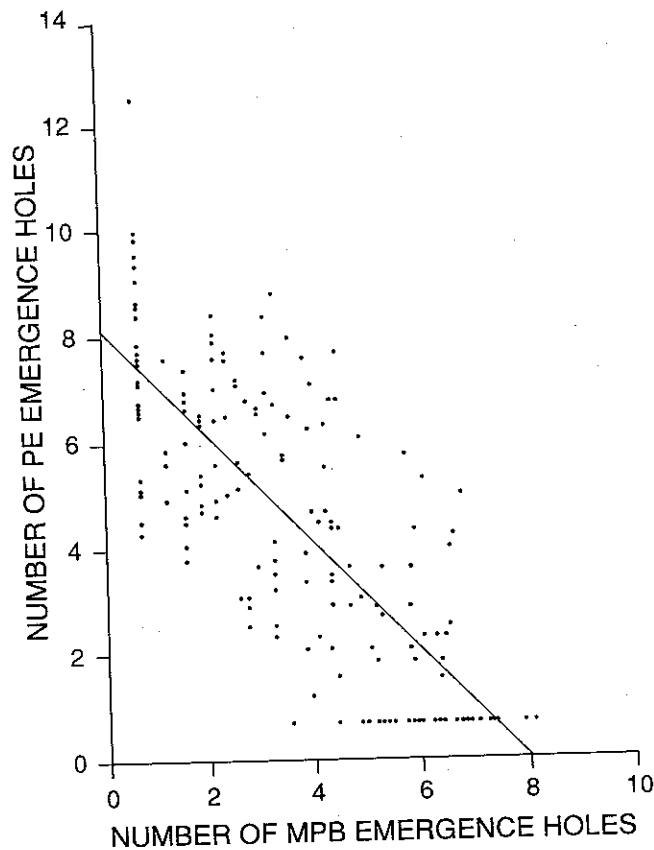


FIG. 1. Relationship between emergence holes per 800 cm<sup>2</sup> of MPBs and PEs in a sample of 191 naturally attacked trees near Princeton, British Columbia, 1987. Regression equation:  $y = 8.10 - 1.01x$ ,  $r^2 = 0.634$ ,  $P < 0.0005$ . Zero values were adjusted to  $y + 0.5$  prior to square-root transformation. All data are shown in square-root form.

variance and the Newman–Keuls test were used to analyze PE weights. The sex ratio of PE progeny from various treatments was analyzed using a one-way analysis of variance after transformation by  $p' = \arcsin \sqrt{p}$ .

#### Results

There was a strong negative relationship between PE and MPB emergence holes (Fig. 1), suggesting that high numbers of one species predicted low numbers of the other. A survey of additional previously attacked trees in the same pine stand indicated that 69.6% of the trees were attacked only by MPB, 5.2% were infested by PE alone, and 25.2% had attacks by both species.

The first laboratory experiment suggested a tendency for PE infestation to reduce the numbers of MPB progeny (Table 1). There was no significant difference in progeny production between treatments for either species, probably because of the small number of replicates and because of the contamination of one of the two MPB control logs with PE, which appeared to have reduced the numbers of MPB progeny.

Regression analysis indicated that in the second laboratory experiment all time effects (no delay, 2-week delay, and 4-week delay) and both PE attack densities exerted change on numbers of MPB progeny. Numbers of PE progeny were influenced by all three time effects and by the MPB attack density, but not by PE attack density. There was no inter-

TABLE 1. Comparison of progeny production in experiments in lodgepole pine logs infested in the laboratory by MPBs or PEs alone or together

Expt. No.	Species	Treatment	Attack density		No. of progeny*
			(no./m <sup>2</sup> )	(MPB:PE)	
1	MPB	Control	50:0	2	110.0 ± 53.0a
		Simultaneous	50:100	3	40.0 ± 12.5a
		MPB-PE attack	50:200	3	27.3 ± 7.5a
	PE	Control	0:100	3	1628.0 ± 153.0a
			0:200	3	1839.0 ± 199.0a
		Simultaneous	50:100	3	1369.7 ± 45.4a
		MPB-PE attack	50:200	3	791.0 ± 124.0a
2	MPB	Control	50:0	5	448.0 ± 62.6a
		Simultaneous	50:100	5	32.4 ± 10.3d
		MPB-PE attack	50:200	5	17.0 ± 5.9d
		2-week delay for PE	50:100	5	71.8 ± 26.6c
			50:200	5	64.6 ± 20.3c
		4-week delay for PE	50:100	5	98.2 ± 21.5c
			50:200	5	135.4 ± 15.7b
	PE	Control	0:100	5	1452.0 ± 230.0a
			0:200	5	1649.0 ± 258.0a
		Simultaneous	50:100	5	1163.8 ± 92.2ab
		MPB-PE attack	50:200	5	1130.0 ± 168.0ab
		2-week delay for PE	50:100	5	813.0 ± 52.5bc
			50:200	5	621.4 ± 85.3c
		4-week delay for PE	50:100	5	219.4 ± 51.4c
			50:200	5	199.6 ± 30.5c

\*Data are presented as  $\bar{x} \pm SE$ . Means for each species within an experiment followed by the same letter are not significantly different according to the multiple comparison test for even and uneven sample sizes;  $P < 0.05$ .

action between MPB and PE attack density and time effects. The greatest reductions in MPB progeny occurred when MPB and PE attacks were simultaneous (Table 1), resulting in only 7.2 and 3.8% production for PE attack densities of 100 and 200/m<sup>2</sup>, respectively, of that achieved by the MPB alone (Fig. 2). Conversely, numbers of PE progeny were significantly reduced when attack was delayed by 2 or 4 weeks (Table 1), with only 12.1% of the maximal production occurring when PE attacks at 200/m<sup>2</sup> had 4-week delays (Fig. 2).

When the logs attacked simultaneously by the MPB and the PE were peeled and visually inspected, almost all of the phloem resource was observed to be occupied by PE galleries. With delayed PE attacks, phloem utilization was not as thorough and many logs had underutilization of phloem, but PE galleries still predominated.

The sex ratios of PE progeny did not differ between treatments and did not vary substantially from the normal 1:1 ratio (Thomas 1961; Schenk and Benjamin 1969). However, weights for both males and females decreased when MPBs were present, as PE density increased, and when PE introduction was delayed (Table 2). Male weights were significantly greater than female weights in all but the 4-week delay treatments (Table 2).

In the spring field experiment, only three of the five ipsdienol-baited trees were attacked by PE. There was no indication of interspecific competition between MPB and PE as a result of natural and induced PE infestation approx-

imately 9–10 months after MPB attack (Table 3). Production of PE progeny from natural and induced attacks was not significantly different. In the second field experiment in August 1987, seven of the eight trees baited with ipsdienol were heavily attacked by PE. Progeny production by MPB in these trees was only 27.6% of that in trees attacked by MPB alone (Table 3).

### Discussion

The negative relationship between PE and MPB emergence holes (Fig. 1) suggests that PE and MPB in the field are interacting competitively. On the basis of data from 215 infested lodgepole pines, Berryman (1976) concluded that interspecific competition had little impact on MPB populations and suggested that competitors only attack smaller hosts or areas of the tree where MPB is not established. Our data (Fig. 1, Table 3) refute this hypothesis, at least in part. If second-generation PEs attack in the summer before the MPB establishes extensive gallery systems, the PEs appear to be able to exert a major negative effect on MPB progeny. In addition, if the PEs were to attack in the spring before the MPB became active, the PEs might also be very competitive, especially if the MPB had attacked in late summer and the gallery systems were not well established.

In the absence of the MPB, the PE often invades the entire bole of lodgepole pine (Reid 1955). Unless it is very thin, the thickness of the phloem is not a barrier for the breeding of most scolytids, and the size of an attacking beetle is not

TABLE 2. Weights of female and male PE progeny from lodgepole pine logs infested in the laboratory with PEs alone or MPBs and PEs together

Treatment	Attack density (no./m <sup>2</sup> ) (MPB:PE)	Females		Males		P for t-test female vs. male
		N	Weight (mg)*	N	Weight (mg)*	
PE control	0:100	507	4.51 ± 0.03a	454	4.88 ± 0.04a	<0.0001
	0:200	539	4.43 ± 0.03ab	470	4.77 ± 0.04b	<0.0001
Simultaneous MPB-PE attack	50:100	454	4.39 ± 0.03b	388	4.77 ± 0.04b	<0.0001
	50:200	452	4.28 ± 0.03c	380	4.64 ± 0.04c	<0.0001
2-week delay for PE	50:100	538	4.19 ± 0.03d	419	4.61 ± 0.04c	<0.0001
	50:200	351	3.97 ± 0.04e	300	4.27 ± 0.04d	<0.0001
4-week delay for PE	50:100	90	3.83 ± 0.08e	83	3.97 ± 0.10e	>0.05
	50:200	158	3.87 ± 0.06e	133	3.94 ± 0.07e	>0.05

\*Data are presented as  $\bar{x} \pm SE$ . Means within a column and experiment followed by the same letter are not significantly different according to the Newman-Keuls test;  $P < 0.05$ .

correlated with the thickness of the phloem it inhabits (Birch 1978; Svihra et al. 1980; Paine et al. 1981). Thus, PE appears to have the same fundamental habitat in standing trees as the MPB. The competitive exclusion principle concludes that "if there is no differentiation between realized niches of two competing species, or if such differentiation is precluded by the limitations of the habitat, then one species will eliminate or exclude the other" (Begon and Mortimer 1982). Under normal circumstances, the PE and the MPB apparently coexist within trees by partitioning the phloem resource. The most likely mechanism by which mutual exclusion is initially achieved is through semiochemicals. The MPB produces verbenone, which repels PEs, while the PE produces ipsdienol, which repels MPBs (Hunt and Borden 1987). Numerous other bark beetles apparently segregate colonies within specific portions of a tree or between trees through synomonal inhibition (Byers and Wood 1980; Blight et al. 1978, 1979; Birch et al. 1980; Paine et al. 1981).

We hypothesize that exploitation competition (Brian 1956) is the principal means by which the PE interacts with the MPB under the bark. Since PEs have a rapid 31- to 48-day life cycle with 2-3 generations per year (Prebble 1933; Reid 1955; Schenk and Benjamin 1969), they are capable of utilizing an unexploited phloem resource before the MPB has access to it. Moreover, at an attack density of 100/m<sup>2</sup>, the PE can utilize 80-90% of the phloem in a log during one generation (Light et al. 1983).

The numbers of MPB progeny possibly could also be reduced through interference competition, i.e., direct aggression or cannibalism, or blocking access to a resource (Brian 1956). However, MPB larvae grow much larger than PE larvae, and only with a head start would PE larvae have an advantage in aggressive encounters. Although cannibalism occurs intraspecifically between MPB larvae (Cole 1973), there is no evidence that PE larvae attack MPB larvae, and no crossing of larval galleries was observed on debarked logs. Interference competition could be evaluated using Plexiglas or glass phloem "sandwiches" (Reid 1958).

Introduction of fungi into the host log may have had a reciprocal negative impact on both species (Table 1; Fig. 2), providing a third possible mechanism for interspecific competitive exclusion. Fungi can inhibit the colonization of one beetle species into a habitat previously invaded by another species (Yearian et al. 1972). Inhibition of larval develop-

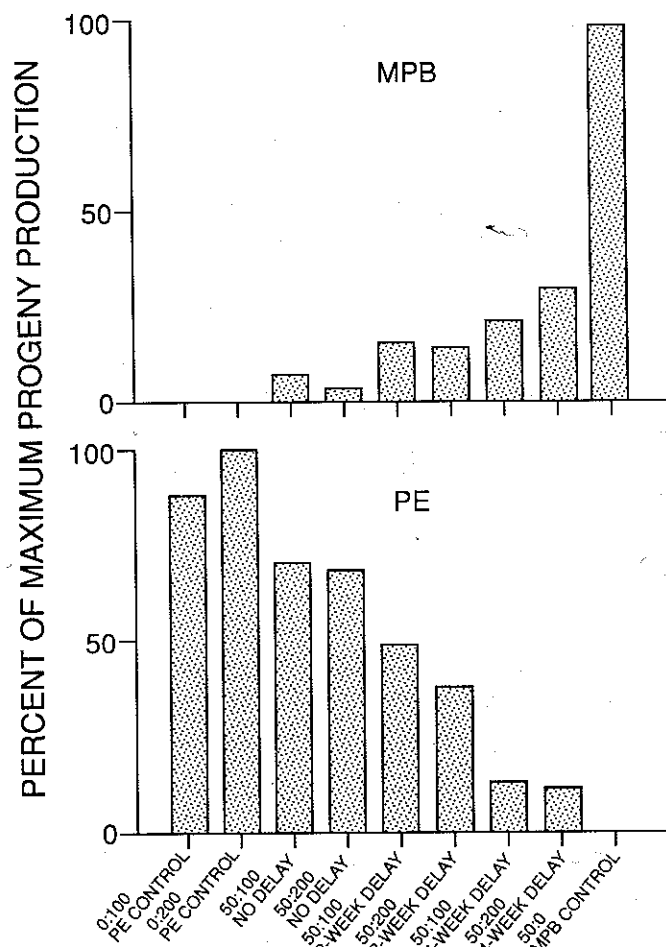


FIG. 2. Percent of maximum progeny production by MPB and PE alone and in coinfaested logs at different attack densities and time delays before PE attack.

ment and oviposition in *D. frontalis* (Barras 1970) and *Ips* species (Yearian 1967; Yearian et al. 1972; Bridges et al. 1985) occurs when the phloem is colonized by *Ceratocystis minor* (Hedgecock) prior to beetle introduction, even though these beetles are often closely associated with *C. minor* (Mathre 1964). Free amino acids, reducing sugars, and total sugars were decreased in the phloem tissue of *Pinus taeda*

TABLE 3. Numbers of MPBs and PEs reared from lodgepole pine trees attacked naturally by the MPB in summer 1986 and by PEs induced to attack in May 1987 (experiment 1), or after a simultaneous MPB-PE pheromone-induced attack in August 1987 (experiment 2)

Expt. No.	Treatment	N	Density (no./m <sup>2</sup> )*	
			MPB	PE
1	MPB control	13	515.8 ± 84.3a	14.5 ± 6.9a
	MPB-PE (natural)	6	378.0 ± 115.0a	865.0 ± 214.0b
	MPB-PE (PE induced)	3	678.0 ± 357.0a	1102.0 ± 550.0b
2	MPB control (induced)	5	212.4 ± 38.4a	0.0 ± 0.0a
	MPB-PE (both induced)	7	59.3 ± 19.0b	708.0 ± 140.0b

\*Data are presented as  $\bar{x} \pm SE$ . Means within a column followed by the same letter are not significantly different according to the multiple comparisons test ( $P < 0.05$  (experiment 1)) and the Mann-Whitney test ( $P < 0.05$  (experiment 2)).

L. by *C. minor* and associated fungi (Hodges et al. 1968; Barras and Hodges 1969; Hodges and Pickard 1971; Cook and Hain 1985). Blue-stain fungi also reduce the nutritional value of Scots pine, *Pinus sylvestris* L., phloem as food for the larvae of the house longhorn beetle, *Hylotrupes bajulus* L. (White 1962). Thus, fungal colonization could also be the mechanism by which the oviposition rate for female PEs at high densities and the weights of PE brood (Table 2) are reduced.

We further hypothesize that the ability by PEs to exploit a phloem resource competitively has selected against MPBs that orient to moribund and windthrown trees, wherein they would be outcompeted by PEs. Thus MPBs are restricted primarily to vigorous, living trees, which require an expenditure of much more energy to attack than windthrown trees. They have compensated for this hardship by coevolving with aggressive fungi that are lethal to newly attacked trees (Safranyik et al. 1975).

Intraspecific competition by the PE for the phloem resource probably caused reduced weights of PE brood at the higher attack density (Table 2). The number of brood per attack was also significantly reduced by approximately 50% for PE progeny at the higher attack density (multiple comparison test,  $p < 0.05$ , Zar 1984). However, in no case was there a significant difference in the number of PE progeny produced per log. Light et al. (1983) determined that low PE attack density (100/m<sup>2</sup>, 2.6 females per male) did not affect PE larval survival, while at a high attack density (200/m<sup>2</sup>, 3.6 females per male) larval survival was only slightly reduced. Oviposition, however, was reduced by >50% at the high attack density, resulting in reduced intraspecific competition for the phloem resource and a normal rate (>50%) of brood survival. Light et al. (1983) suggested that at high attack density there may be a negative-feedback mechanism that regulates the numbers of eggs laid per female. Such a phenomenon may have occurred in both laboratory experiments (Table 1).

There was decreasing weight of PE progeny from logs where PEs competed with MPBs in all three time effects (simultaneous attack, 2-week delay, and 4-week delay) and with themselves in the high-density treatment. One can

hypothesize that there was a corresponding decrease in fitness, the ability of an individual to leave offspring (Smith 1980). Interspecific competition between two species for a limited supply of a resource (phloem) may cause reductions in the fitness of each species owing to some combination of lowered fecundity and survivorship (Begon and Mortimer 1982). There is considerable evidence to support the reduced fitness hypothesis. The size and weight of scolytids have important implications for their survival, fecundity, and population quality (Safranyik 1976; Sahota and Thompson 1979). Larger MPBs survive cold storage longer (Safranyik 1976) than smaller MPBs, and larger females lay more eggs than smaller females (Reid 1962b; 1963; McGheley 1971; Amman 1972, 1973; Amman and Cole 1983). Small Douglas-fir beetles, *Dendroctonus pseudotsugae* Hopk., contain proportionately less fat than large beetles and consequently have a poor ability to disperse via flight (Atkins 1967). Adult MPB that survived the most crowded larval conditions were the smallest (Amman and Pace 1976), constructed the least amount of gallery per day (Amman and Cole 1983), and produced the fewest eggs (Cole 1973). The live weights of *Tomicus piniperda* (L.), *Scolytus scolytus* (F.), and *Scolytus multistriatus* (Marsh.) were reduced by density effects owing to intraspecific competition (Beaver 1974; Saarenmaa 1983).

Because our laboratory and field experiments indicate that interspecific interactions between the PE and the MPB could occur in the field to the detriment of the MPB, induced PE infestation on MPB-infested trees may potentially be used, as suggested by Moeck and Safranyik (1984), to reduce MPB population densities. Where high PE populations have developed within a MPB outbreak, semiochemical baiting could be utilized to draw both species of beetle into interspecific competition. This inexpensive and simple treatment could impede the development or spread of an outbreak, especially in inaccessible stands where other control methods are not feasible.

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