Semiochemical Interactions between *Scolytus ventralis* LeConte and *Pityokteines elegans* (Swaine) (Coleoptera: Scolytidae)[1]

Jorge E. Macías-Sámano and John H. Borden[2]

El Colegio de la Frontera Sur, ECOSUR, 30700 Tapachula, Chiapas, México.

J. Entomol. Sci. 36(3): 251-258 (July 2001)

Abstract Two experiments evaluated the effect of baiting uninfested grand fir logs and trees undergoing initial attack by *Scolytus ventralis* LeConte with *Pityokteines elegans* (Swaine) pheromone, on the subsequent attack by both species. Two more experiments assessed the effect of synthetic bark oil, *exo*-brevicomin, and *P. elegans* pheromone on the response by each species to multiple-funnel traps baited with attractants for the other species. The pheromone of *P. elegans* on unattacked logs did not have an inhibitory effect on the attack by *S. ventralis*. However, trees attacked by *S. ventralis* that were baited with *P. elegans* pheromone just after attack, yielded significantly fewer *S. ventralis* progeny than the unbaited controls. Neither synthetic bark oil nor *exo*-brevicomin caused a significant change in the catch of *P. elegans* in traps baited with its pheromone, but the predator *Thanasimus undatulus* Say was caught in traps baited with (±)-ipsenol, (±)-ipsdienol and synthetic bark oil, and another predator, *Enoclerus sphegeus* F., was caught in traps baited with *exo*-brevicomin alone or in combination with ipsenol and ipsdienol. The results do not support the hypothesis that interference competition based on semiochemical communication occurs between the two species.

Key Words Semiochemicals, *Scolytus ventralis, Pityokteines elegans, Thanasimus undatulus, Enoclerus sphegeus, Abies grandis,* ipsenol, ipsdienol, *exo*-brevicomin, bark oil

The fir engraver, *Scolytus ventralis* LeConte, is widely recognized as a tree-killing bark beetle (Struble 1957, Ashraf and Berryman 1969). Like other primary species its galleries may intermingle in part with those of less aggressive (secondary) species of bark beetles, particularly *Pityokteines elegans* (Swaine), but also *Pityophthorus pseudotsugae* Swaine, *Pseudohylesinus grandis* Swaine, *P. granulatus* LeConte, *Scolytus opacus* Blackman, *S. praeceps* LeConte, and *S. subscaber* LeConte (Struble 1957, Stark and Borden 1965, Ashraf and Berryman 1969). Hertert et al. (1975) always found *P. elegans* in the presence of *S. ventralis* and never in sound fir or in the absence of other bark beetles. This reinforces the hypothesis that it is a secondary colonizer.

In general, the fir engraver inhabits the major part of the bole, while the other species establish themselves mostly in the lower bole or in the thin-diameter crown of the tree (Struble 1957, Berryman 1968). As for guilds of pine-infesting bark beetles

---

[1] Received 21 December 1999; accepted for publication 12 November 2000.

[2] Centre for Environmental Biology, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., V5A 1S6, Canada; To whom offprint requests are to be made.

(Dixon and Payne 1979, Birch et al. 1980, Paine et al. 1981, Rankin and Borden 1991, Poland and Borden 1994), *S. ventralis* and *P. elegans* exhibit partial resource partitioning within the tree and a moderate level of competitive interaction expressed through exploitative competition (Macías-Sámano and Borden 2000).

Pityokteines elegans and *P. pseudotsugae* are commonly cited as competitors of the fir engraver (Struble 1957, Stark and Borden, 1995, Berryman 1973, Berryman and Ferrell 1988). Berryman (1973) reported that attack densities of *P. elegans* in grand fir were inversely related to the overall population trend of the fir engraver and directly related to its within-tree density. An increased density of attacks by *P. elegans* during the decline of a fir engraver outbreak was assumed to occur because of a decrease in numbers of trees killed by *S. ventralis*.

Scolytus ventralis exhibits a strong primary attraction toward its host, relying on a complex blend of host kairomones to achieve host colonization (Macías-Sámano et al. 1998a). There is no evidence for pheromone-based secondary attraction (Macías-Sámano et al. 1998b). On the other hand, *P. elegans* clearly possesses an aggregation pheromone that involves a synergistic interaction between (–)-ipsenol and (+)- and (–)-ipsdienol and an inactive role for (+)-ipsenol (Macías-Sámano et al. 1997).

The different type of semiochemicals used in host selection by *S. ventralis* and *P. elegans* is reflected in the orientation of their main predator species. In the field, *Thanasimus undatulus* Say is as attracted to the complex blend of host kairomones as its prey *S. ventralis*, while *Enoclerus lecontei* Wolcot is attracted to the pheromone blend of its host *P. elegans* (Macías-Sámano 1997).

We investigated the potential semiochemical-based interactions that could exist between *S. ventralis* and *P. elegans* in the field by using proven blends of attractants for both species.

Materials and Methods

Experiments were conducted in a mature *Abies grandis* (Douglas ex D. Don) Lindl. - *Acer rubrum* L. forest with well represented *Pseudotsuga menziesii* (Mirb.) Franco (Steel and Gier-Hayes 1992), located 10 km north of Coeur d'Alene, ID.

Two experiments evaluated the effect on attack by both species of baiting uninfested grand fir logs (Experiment 1) and trees undergoing initial attack by *S. ventralis* (Experiment 2) with *P. elegans* pheromone. For Experiment 1, on 30 June 1996 five pairs of green logs (130 cm long, 15-20 cm diam) were set upright in two rows with 15 m between rows and logs. At each position along the rows, one randomly selected log of the pair was baited with (±)-ipsenol and (±)-ipsdienol, released at 0.8 and 0.4 mg per 24 h, respectively, from bubble caps (Phero Tech Inc., Delta, B.C., Canada) stapled to the log. The other log at the position was an unbaited control. On 11 October 1996, all logs were transported to the laboratory, where the bark was peeled off and the successful (with brood) and unsuccessful attacks for each species were counted. One pair of logs was discarded because neither log was attacked.

In Experiment 2, 10 standing trees under initial attack by the fir engraver were baited as above on 14 July 1996, with one *P. elegans* bait stapled 2 m high on the north face of the tree and a second at 4 m. Ten control trees, also undergoing attack by *S. ventralis*, were selected $\geq$8 m from each of the treated trees. All trees were girdled with an axe frill at approximately 50 cm above ground to reduce the tree's ability to resist attack. On 11 October, all trees were felled and evaluated for attack;

seven baited and seven control trees were attacked heavily enough to justify sampling.

From these trees 20 bolts (40 cm long) were cut at regular intervals along the stem from the butt to the top. The bolts were pooled by tree and placed in rearing cages at 24°C. The numbers of emerged beetles of each species was recorded.

Two field trapping experiments were conducted in 1997 to assess the effect of semiochemicals used in aggregation by each species on the response to aggregants by the other species. Experiments 3 and 4 tested the effect of the 13-component synthetic blend of terpenoids resembling grand fir bark oil (Macías-Sámano et al. 1998a) and (±)-*exo*-brevicomin produced by female *S. ventralis* (Macías-Sámano et al. 1998b), respectively, on the catches of *P. elegans* in multiple-funnel traps baited with (±)-ipsenol and (±)-ipsdienol released as above from bubble cap lures. The synthetic bark oil was dispensed from microcentrifuge tubes at 762 mg per 24 h. The *exo*-brevicomin was dispensed from a flexure (Phero Tech Inc., Delta, B.C. Canada) at 0.28 mg per 24 h. These experiments had the following treatments: unbaited control, *P. elegans* pheromone [(±)-ipsenol and (±)-ipsdienol], and *P. elegans* pheromone with the synthetic bark oil (Experiment 3) or (±)-*exo*-brevicomin (Experiment 4). The experiments were laid out as randomized complete blocks, with 10 replicates each on the following dates: Experiment 3, 25 May-24 June; and Experiment 4, 26 June-7 July, 1997. All captured beetles were stored frozen until counted. The sex of *P. elegans* was determined by the presence (females) or absence (males) of a setal brush on their frons (Bright 1976).

Numbers of parental galleries (Experiment 1) and emerged insects (Experiment 2) were transformed by $\sqrt{(x + 0.5)}$ to normalize the data and stabilize the variances between replicates, and results for baited and control treatments for each species were compared using t-tests (Zar 1984). The numbers of insects captured in traps (Experiments 3 and 4) were transformed by $\log_{10}(x+1)$ and analyzed by ANOVA followed by the Ryan-Einot-Gabriel-Welsh (REGW) Multiple Range test (Day and Quinn 1989). All analyses employed SAS computer software (SAS Institute 1990).

Results and Discussion

In Experiment 1 (Fig. 1), unattacked logs baited with *P. elegans* pheromone sustained similar numbers of *S. ventralis* attacks as unbaited control logs, indicating that (±)-ipsenol and (±)-ipsdienol had no inhibitory or stimulatory effect on attack by *S. ventralis.* Attack by *P. elegans* occurred only on baited logs. Both baited and unbaited logs were attacked at low levels by *S. opacus.*

Bolts taken from trees that were baited with *P. elegans* pheromone at the time they were under initial attack by *S. ventralis* produced significantly lower numbers of emergent *S. ventralis* than bolts from unbaited control trees (Fig. 1, Experiment 2). The opposite effect occurred for *P. elegans.* Small numbers of *Crypturgus borealis* Swaine emerged from the baited trees while equivalent numbers of *S. opacus* emerged from the control trees.

Pityokteines elegans was strongly attracted to the blend of (±)-ipsenol and (±)-ipsdienol in Experiments 3 and 4 (Fig. 2), confirming their role as pheromone components (Macías-Sámano et al. 1997). Neither synthetic bark oil (Experiment 3) nor *exo*-brevicomin (Experiment 4) caused a significant change in the catches of *P. elegans* in traps baited with its pheromone (Fig. 2). Very few *S. ventralis* were captured in traps baited with synthetic bark oil, apparently because they were attracted to

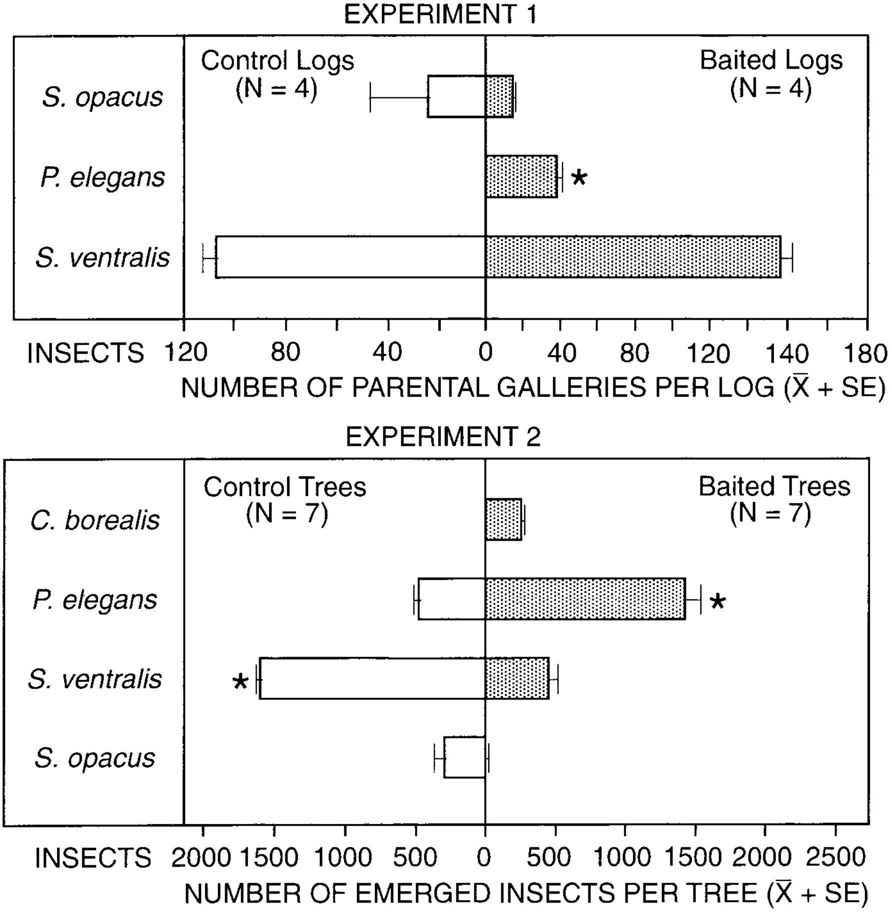

Fig. 1. Numbers of galleries of three species of bark beetles in unbaited grand fir logs or logs baited with *P. elegans* pheromone (Experiment 1), and numbers of *S. ventralis* and *P. elegans* (Experiment 2) that emerged from bolts taken from grand fir trees that were under initial attack by *S. ventralis* and then were baited 2 and 4 m high on the bole with *P. elegans* pheromone. Baits contained (±)-ipsenol and (±)-ipsdienol released at 0.8 and 0.4 mg per 24 h, respectively. Bars with asterisks indicate significant differences in paired values between baited and control treatments, *t*-test, $P < 0.05$.

trees unexpectedly felled approximately 10 m from the experiment; hundreds of *S. ventralis* of were observed crawling on the boles of the felled trees. However, the predator *Enoclerus sphegeus* F. was captured at significant levels in Experiment 3 in traps baited with the combination of *P. elegans* pheromone and synthetic bark oil, and in Experiment 4 *T. undatulus* was captured at significant levels in traps baited with *exo*-brevicomin alone or combined with *P. elegans* pheromone (Fig. 2).

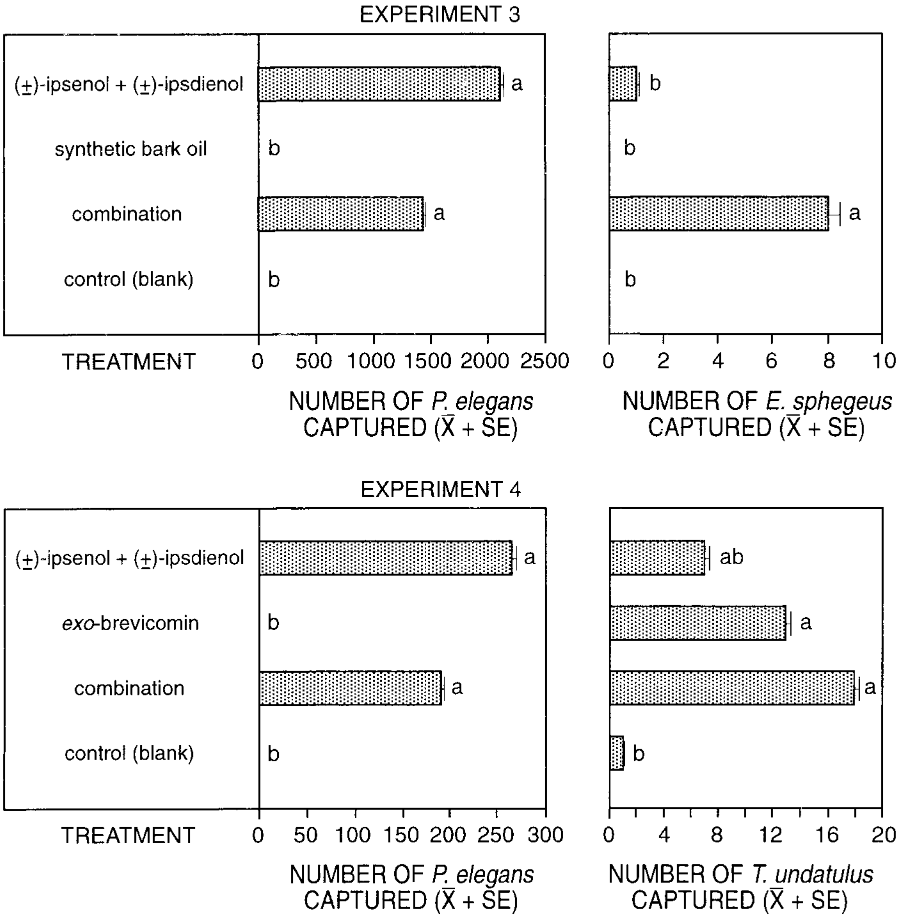

Fig. 2. Numbers of beetles captured in multiple-funnel traps in Experiment 3 (25 May-24 June 1997) which tested the effect of synthetic bark oil (blend of 13 terpenoid components), and Experiment 4 (26 June-7 July 1997) which tested the effect of *exo*-brevicomin on the response of *P. elegans* to its own pheromone. N = 10 for each experiment. Release rates as follows: (±)-ipsenol and (±)-ipsdienol, 0.8 and 0.4 mg per 24 h, respectively; synthetic bark oil 762 mg per 24 h, *exo*-brevicomin, 0.28 mg per 24 h. Bars for each species within an experiment with the same letter are not significantly different, REGW test, $P < 0.05$.

Our results do not support the hypothesis that semiochemical-based interference competition occurs between the two species. *Scolytus ventralis* colonized *P. elegans* pheromone-baited logs to the same extent as unbaited control logs (Fig. 1, Experiment 1) and neither *exo*-brevicomin produced by *S. ventralis* (Macías-Sámano et al. 1998b) nor synthetic bark oil, to which *S. ventralis* responds (Macías-Sámano et al.

1998a), had any effect on *P. elegans* (Fig. 2). Our results differ from those of Poland and Borden (1998a,b,c) who found that response by the spruce beetle, *Dendroctonus rufipennis* (Kirby), to traps or logs baited with its pheromone was reduced by the presence of the pheromones of two secondary bark beetles, *Dryocoetes affaber* Mannerheim and *Ips tridens* Mannerheim, clear evidence of interference competition.

Analyses of attack distribution and gallery development by *P. elegans* and *S. ventralis*, as well as field observations, suggest the occurrence of weak exploitative competition (Macías-Sámano and Borden 2000), but support the absence of interference competition. In the early spring (May), *P. elegans* flies and colonizes mainly winter-fallen material. Because *P. elegans* utilizes an aggregation pheromone, it can concentrate its attack in very defined hosts or areas therein. In mid-summer, during the peak flight period of *S. ventralis*, most of the remaining host material would be drying out, and *S. ventralis* would attempt to colonize standing trees. The mechanisms of recognizing suitable hosts also differ between the two species and probably are associated with resource partitioning. *Scolytus ventralis* strongly responds to host volatiles from living trees with a preference for those weakened by root rot (Macías-Sámano et al. 1998a). On the other hand, *P. elegans* did not respond at all to synthetic bark oil, suggesting that it is adapted to attack only deteriorating bark, including that attacked by *S. ventralis.* Such bark is apparently recognized and avoided by *S. ventralis.* For example, we observed two trees that were completely colonized by last instars of *P. elegans*, on which many *S. ventralis* adults landed, and left soon thereafter, presumably because they recognized a deteriorated phloem resource that was already colonized by a heterospecific competitor. When *S. ventralis* attacks a vigorous tree at low density, causing the tree to create reaction zones around the sites of beetle and fungal invasion (Raffa 1991), *P. elegans* and other bark beetles do not superimpose their attacks on these zones and recognize and avoid them when mining through the phloem.

It is evident that *S. ventralis* and *P. elegans* occupy overlapping, but not identical niches, and thus neither species will competitively exclude the other (Begon and Mortimer 1982). Based on this interpretation, pheromone-induced competitive displacement (Poland and Borden 1998b) of *S. ventralis* by *P. elegans* may occur (Fig. 1, Experiment 2) but would have limited potential for regulating the size of *S. ventralis* populations.

The captures of the two predators (Fig. 2) supports the plasticity of semiochemical perception and response systems used in host selection by entomophagous insects. Unlike previous studies in the same location (Macías-Sámano 1997, Macías-Sámano et al. 1998a), *T. undatulus* was not captured in traps baited with synthetic bark oil, possibly because Experiment 3 was run early in the spring, and *E. sphegus*, not *E. lecontei*, was captured in traps baited with (±)-ipsenol and (±)-ipsdienol.

Acknowledgments

We thank D. R. Miller, A. Savoie and T. M. Poland for their comments and discussion of some of the ideas presented in this work: L. J. Chong and G. A. Yakel for field assistance; S. J. Kegley, J. Schwandt, and J. L. Wallace, USDA, Forest Service, Idaho Panhandle National Forest, for advice and support with field sites and laboratory facilities. The research was supported by the Natural Sciences and Engineering Council of Canada, the Canadian Forest Service, the Science Council of B.C., the Cost Forest and Lumber Sector, the Interior Lumber Manufacturers' Association, the Cariboo Lumber Manufacturers' Association, Phero Tech Inc., Canadian Forest Products Ltd., International Forest Products Ltd., Northwood Pulp and Timber Ltd., TimberWest Ltd., Tolko Industries Ltd., Western Forest Products Ltd., Weyerhaeuser Canada Ltd., and by scholarships to J.E. Macías-Sámano from the Comisión Nacional de la Ciencia y la Technología (CONACyT), México and Organization of American States, Washington, DC.

References Cited

Ashraf, M. and A. A. Berryman. 1969. Biology of *Scolytus ventralis* (Coleoptera: Scolytidae) attacking *Abies grandis* in Northern Idaho. Melanderia 2: 1-23.

Begon, M. and M. Mortimer. 1982. Population ecology. Blackwell, Boston.

Berryman, A. A. 1968. Distribution of *Scolytus ventralis* attacks, emergence, and parasites in grand fir. Can. Entomol. 100: 57-68.

1973. Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera Scolytidae). I. Analysis of population behavior and survival from 1964 to 1971. Can. Entomol. 105: 1465-1488.

Berryman, A. A. and G. T. Ferrell, 1988. The fir engraver beetle in Western States, Pp. 555-577. *In* A. A. Berryman (ed.), Dynamics of Forest Insect Populations, Plenum, NY.

Birch, M. C., P. Svihra, T. D. Paine and J. C. Miller. 1980. Influence of chemically mediated behavior on host tree colonization by four cohabiting species of bark beetles. J. Chem. Ecol. 2: 395-414.

Bright, D. E., Jr. 1976. The insects and arachnids of Canada and Alaska. 2. Coleoptera: Scolytidae. Can. Dep. Agric., Ottawa, Pub. No. 1576.

Day, R. W. and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Mongr. 59: 433-463.

Dixon, W. N. and T. L. Payne. 1979. Sequence of arrival and spatial distribution of entomophagous and associated insects on southern pine beetle-infested trees. Tex. Agric. Exp. Stn. Misc. Publ. No. 1432.

Hertert, H. D., D. L. Miller and A. D. Partridge. 1975. Interaction of bark beetles (Coleoptera: Scolytidae) and root-rot pathogens in grand fir in Northern Idaho. Can. Entomol. 107: 899-904.

Macías-Sámano, J. E. 1997. Chemical ecology of *Scolytus ventralis* LeConte and *Pityokteines elegans* (Swaine) two bark beetles of *Abies grandis* (Dougl.) Lindl. Ph.D. Diss., Simon Fraser University, Burnaby, British Columbia, Canada.

Macías-Sámano, J. E. and J. H. Borden. 2000. Interactions between *Scolytus ventralis* and *Pityokteines elegans* (Coleoptera: Scolytidae) in *Abies grandis.* Environ. Entomol. 29: 28-34.

Macías-Sámano, J. E., J. H. Borden, H. D. Pierce, Jr., R. Gries and G. Gries. 1997. Aggregation pheromone of *Pityokteines elegans* Swaine (Coleoptera: Scolytidae). J. Chem. Ecol. Ecol. 23: 1333-1347.

Macías-Sámano, J. E., J. H. Borden, R. Gries, H. D. Pierce, Jr., G. Gries, and G. G. S. King. 1998a. Primary attraction of the fir engraver, *Scolytus ventralis.* J. Chem. Ecol. 24: 1049-1075.

1998b. Lack of evidence for pheromone-mediated secondary attraction in the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). J. Entomol. Soc. Brit. Columbia 95: 117-125.

Paine, T. D., M. C. Birch and P. Svihra. 1981. Niche breath and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). Oecologia 48: 1-6.

Poland, T. M. and J. H. Borden. 1994. Attack dynamics of *Ips pini* (Say) and *Pityogenes knechteli* (Swaine) (Coleoptera: Scolytidae) in windthrown lodgepole pine trees. J. Appl. Entomol. 117: 434-443.

Poland, T. M. and J. H. Borden. 1998a. Disruption of secondary attraction of the spruce beetle, *Dendroctonus rufipennis*, by pheromones of two sympatric species. J. Chem. Ecol. 24: 151-166.

1998b. Semiochemical-induced competition between *Dendroctonus rufipennis* and two secondary species, *Ips tridens* and *Dryocoetes affaber* (Coleoptera: Scolytidae). J. Econ. Entomol. 91: 1142-1149.

1998c. Competitive exclusion of *Dendroctonus rufipennis* induced by pheromones of *Ips tridens* and *Dryocoetes affaber* (Coleoptera: Scolytidae). J. Econ. Entomol. 91: 1150-1161.

Raffa, K. F. 1991. Induced defensive reactions in conifer-bark beetles systems, Pp. 245-276. *In* D. W. Tallamy and M. J. Raupp (eds.), Phytochemical Induction by Herbivores, Wiley, NY.

Rankin, L. J. and J. H. Borden. 1991. Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. Can. J. For. Res. 21: 1029-1036.

SAS Institute. 1990. SAS System for personal computers, release 6.10. SAS Institute, Inc., Cary, NC.

Stark, R. W. and J. H. Borden. 1965. Observations on mortality factors of the fir engraver beetle *Scolytus ventralis* (Coleoptera: Scolytidae). J. Econ. Entomol. 58: 1162-1163.

Steel, R. and K. Gier-Hayes. The grand fir/mountain maple habitat type in Central Idaho: succession and management. USDA For. Serv. Gen. Tech. Rep. INT-284.

Struble, G. R. 1957. The fir engraver. A serious enemy of the western true firs. USDA-For. Serv., Calif. F or. Range Exp. Sta., Prod. Res. Rep. No. 11.

Zar, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall, Engelwood Cliffs, NJ.