ANTIAGGREGANTS FOR THE PINE ENGRAVER

by

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ABSTRACT

The responses of pine engravers, *Ips pini* (Say), to ipsdienol-baited traps containing low, medium, and high dose rates of the antiaggregants, verbenone and ipsenol, released from impregnated, polyethylene and polypropylene beads, respectively, remained significantly lower than those to ipsdienol-baited, control traps throughout the spring experimental period. During the summer experimental period, the responses of pine engravers to traps containing the medium and high dose rates of impregnated beads remained significantly lower. Antiaggregant treatment densities of 100 and 400 bubble cap release points/ha reduced the numbers of pine engravers caught in ipsdienol-baited, multiple-funnel traps by 66.1 and 76.8 %, respectively. In 50 x 50 m thinning-simulation plots treated with a broadcast distribution of antiaggregant-impregnated beads in 1990, 32.9 % of the felled lodgepole pines were attacked; in untreated control plots, the proportion of attack was 53.1 %. On randomly-selected, 1 m-long bole sections of the felled pines, the mean attack/m^2 of available bark surface in the treated plots (1.3) was significantly lower than that in the untreated plots (1.9); however, in those bole sections sustaining attack by the pine engraver, the difference was not significant (8.8 and 9.4 attacks/m^2, respectively). In a 1991 experiment, verbenone- and ipsenol-impregnated beads were applied to 15 x 15 m thinning-simulation plots at rates of 2.5 mg of verbenone and

0.05 mg of ipsenol/m^2 of ground surface/day, and at double these rates. For both low and high rates 3 weeks prior to first attack by *I. pini*, and at a high rate 2 weeks prior to attack, these treatments reduced the mean attack/m^2 of availal 'e bark surface/week by 77.1, 82.9, and 97.1 %, respectively, compared to that on felled pines in untreated control plots. The results of these experiments suggest that a timely application of the antiaggregants would prevent the development of an outbreak population of the pine engraver by dispersing an attacking population over a large area and reserving unutilized host material for re-colonization by emergent brood.

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1.0 INTRODUCTION

1.1 Distribution and Hosts

The pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), is a common bark beetle in pine forests throughout most of North America (Sartwell et al. 1971). In western North America, its preferred hosts are ponderosa pine, *Pinus ponderosa* Dougl., Jeffrey pine, *P. jeffreyi* Grev. and Balf., and lodgepole pine, *P. contorta* Dougl. (Furniss and Carolin 1977). *P. contorta* var. *latifolia* Engelm. is the most common host in British Columbia (Andrews 1987; Humphreys and Ferris 1987).

1.2 Damage and Management

Ips pini seldom attacks healthy pines; rather, it usually invades pine hosts predisposed to attack by primary abiotic and/or biotic agents (Sartwell et al. 1971). In undisturbed forests, there is usually sufficient breeding material to absorb and maintain a below outbreak population (Thomas 1961). Infestations of *I. pini* are commonly found in wind-felled, fire- and snow-damaged, drought-stressed, suppressed, and insect- and disease- weakened pines (Kennedy 1969; Dewey et al. 1974; Geiszler et al. 1984; Andrews 1987; Humphreys and Ferris 1987; Rankin and Borden 1991).

The post-disturbance environments created by forest harvesting and improvement practices, in certain circumstances, may enhance the life requirements of normally innocuous insects. In such settings, the development of epidemic populations of these insects becomes detrimental to the regenerating or remaining forest. Thus, the pine engraver becomes an economically significant pest in forests disturbed by logging and thinning operations and other man-related intrusions (Thomas 1961; Kennedy 1969; Sartwell et al. 1971; Schmitz 1979). For example, 84 % of the pines killed by *I. pini* in Michigan in 1966 were killed by beetles emerging from pine host material created by logging and man-initiated fires (Kennedy 1969). Outbreak populations can also cause significant damage after natural disturbances (e.g. windstorms) have created an abundance of breeding material (Furniss and Carolin 1977).

The abundance of suitable slash created by logging and thinning operations allows local pine engraver populations to increase rapidly (Kennedy 1969; Sartwell et al. 1971; Livingston 1979; Furniss and Livingston 1979). If slash is scarce after these operations, the pine engraver may attack and kill pines adjacent to slash accumulations containing large brood populations. Drought-stressed pines are especially vulnerable to attack in such situations. In British Columbia, *I. pini* occasionally kills lodgepole pines in stands beside recently-logged cutblocks (Andrews 1988). Most attacks occur within 15 m of the cutblock boundary but some may extend 50 m into the surrounding stands. Such outbreaks seldom last more than 1-2 years (Furniss and Carolin 1977; Andrews 1988).

Pine engraver outbreaks can be prevented by proper management of pine slash (Sartwell et al. 1971; Livingston 1979). Windrowing of slash in cutblocks and piling slash on landings create host environments favorable for the production and survival of brood (Knopf 1982; Andrews 1988; Unger and Stewart 1988). Conversely, if the slash is left scattered and exposed it dries rapidly, making it unsuitable or suboptimal for colonization. Broadcast burning of a cutblock and burning of slash piles at landings will eliminate much of the logging residue, and may also kill resident beetles, preventing a population buildup. Because disposal of slash from thinning is often impractical, thinning operations can be timed to provide fresh breeding material for newly-developed adults, maintaining the population in the slash, and preventing attack of the remaining, standing pines (Livingston 1979). Unfortunately, proper slash management is not always logistically feasible, silviculturally desirable, or commonly practiced.

1.3 Host Selection and Biology

In British Columbia, *I. pini* has two major flight periods each year (Andrews 1988; Miller 1990). The first, consisting of adults which have overwintered in the forest duff, usually begins in early May and concludes by about mid-June. The second, larger flight, from about mid-July to mid-September, consists initially of re-emerging adults from the spring flight, and later consists mainly of newly-developed, brood beetles from the spring generation.

In the absence of secondary attractants (mainly pheromones) (Nordlund and Lewis 1976), it is thought that dispersing, attack-initiating males are initially drawn to a host by primary attractants (host kairomones) (Brown et al. 1970; Gries et al. 1989). The pine engraver may be attracted to lodgepole pine monoterpenes such as ß-phellandrene (Miller and Borden 1990), and/or stress-induced and metabolites of weakened and wind-felled pines (Anderson 1948). As beetles approach the potential host, visual cues appear to aid in host selection; *I. pini* will preferentially colonize horizontal over vertical logs (Seybert and Gara 1970).

Shortly after pine engraver males penetrate to the inner bark, they begin to emit aggregation pheromones (Anderson 1948). *Ips pini* has two pheromone components: ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (Vité et al. 1972; Lanier et al. 1972; Stewart 1975; Miller 1990), and lanierone (2-hydroxy-4,4,6-tri-methyl-2,5-cyclohexadien-1-one) (Teale et al. 1991). These pheromones supplement primary olfactory and visual stimuli, causing mass-attacks of unexploited hosts.

Male *I. pini* construct nuptial chambers in the phloem and outer sapwood where they usually mate with 3 females, but as many as 8 in some circumstances (Anderson 1948; Thomas 1961; Schenk and Benjamin 1969; Sartwell et al. 1971; Schmitz 1972; Livingston 1979). Mated females mine egg galleries that radiate from the nuptial chamber. Between 30 and 60 eggs per female are laid in niches cut alternately in the sides of the egg galleries. Newly-hatched larvae mine feeding tunnels perpendicular to the egg galleries. Pupation occurs in cells constructed at the end of the tunnels. Following pupation, callow adults feed for 5-10 days before emerging from the pine host to begin the life cycle anew. Generation time can range from 40-100 days.

1.4 Semiochemical-Mediated Interactions Between Sympatric Bark Beetles

Sympatric species of bark beetles utilizing a common conifer host employ mechanisms that reduce competition for host breeding material and ensure reproductive isolation. Discriminatory host selection based on physiological vigor and disparate mating periods contribute to the isolation of competing species (Dixon and Payne 1979; Furniss and Carolin 1977). Intra- and interspecific encounters are further minimized through mutual inhibition to the aggregation pheromones of competing species (Birch and Light 1977; Birch 1978; Byers and Wood 1980, 1981; Miller 1990).

In northern California, *Ips paraconfusus* Lanier and *I. pini* are sympatric, have common flight periods, and colonize fallen ponderosa pine (Birch and Light 1975). The temporal and spatial overlap between life cycles and reproductive strategies of the two species invites competitive interaction; yet, beetles of both species are seldom found within the same host. Specific separation appears to be maintained through reciprocal inhibition to components of their aggregation pheromones; *I. pini* is repelled by S-(+)-ipsdienol and S-(-)-ipsenol produced by *I.*

paraconfusus (Birch and Light 1977; Birch et al. 1977; Birch et al. 1980a), and R-(-)-ipsdienol produced by *I. pini* inhibits *I. paraconfusus* (Light and Birch 1979). Thus, a pheromone for conspecifics also acts as an interspecific synomone (Nordlund and Lewis 1976). In this context, a synomone benefits members of a late-arriving species by indicating that a host has been colonized by another species, while at the same time benefiting members of the first-attacking species by precluding competition with the second species.

A similar relationship exists between *Ips latidens* (LeConte) and *I. pini* in the lodgepole pine forests of British Columbia (Miller and Borden 1985; Miller 1990). While members of both species colonize pine slash, the former commonly attacks the tops and limbs of weakened or dead pines and the latter infests the lower boles of such pines (Reid 1955; Bright 1976; Furniss and Carolin 1977). The aggregation pheromones of *I. latidens* and *I. pini*, ipsenol (2-methyl-6-methylene-7-octen-4-ol) (Miller 1991; S. Seybold, Dept. of Entomology, Univ. of CA, Berkeley, pers. comm.) and ipsdienol, respectively, have been demonstrated to be mutually inhibitory (Miller 1990), and therefore, may contribute in part to the differential host utilization habits of these species.

Another semiochemical, verbenone [4,6,6-trimethyl-bicyclo (3.1.1)hept-3-en-2-one] (Renwick 1967), is an antiaggregation pheromone for several species of *Ips* and *Dendroctonus*, including the mountain pine beetle, *Dendroctonus ponderosae* Hopk., in British Columbia (Pitman et al. 1969; Renwick and Vité 1970;

Paine et al. 1970; Bedard 1980; Ryker and Yandell 1983; Byers et al. 1984; Leufvén et al. 1984; Hunt and Borden 1990). The antiaggregative effect of verbenone is thought to reduce intra- and interspecific competition for subcortical breeding area. Between conspecifics, verbenone may regulate attack density (Byers et al. 1984), or terminate mass attack (Renwick and Vité 1970; McNew 1970). Interspecifically, it may either prevent or partition the attack of a host (Birch et al. 1980b; Byers et al. 1984; Rankin and Borden 1991; Borden et al. 1992).

Verbenone can deter the response of *I. pini* to its aggregation pheromone, ipsdienol (Borden et al. 1992). The relegation of *I. pini* to the upper bole portions of lodgepole pines initially attacked by mountain pine beetle, (Furniss and Carolin 1977; Andrews 1987; Humphreys and Ferris 1987; Rankin and Borden 1991) might be explained in part by the inhibitory effect of verbenone. Thus, verbenone would be a synomone benefiting both *D. ponderosae* and *I. pini* by partitioning attack on a common lodgepole pine host, or by preventing *I. pini* attack completely.

1.5 Utilization of Antiaggregant Pheromones for Bark Beetle Management

Unlike conventional insecticides, which may be ecologically disruptive, semiochemicals are a normal part of a natural forest environment and therefore, provide an unobtrusive means of managing a pest population. For example, aggregation pheromones of the mountain pine beetle are employed at lower concentrations than would occur in nature (Burke 1992) to contain and concentrate populations of the beetle in susceptible stands of lodgepole pine. The subsequent harvest of these stands prior to beetle emergence serves to reduce the local population, and thereby, lower the incidence of attack on the surrounding, remaining pines (Borden and Lindgren 1988; Borden 1990). The application of verbenone to mountain pine beetle-infested stands in Idaho and British Columbia has reduced the attack of lodgepole pines (Amman et al. 1989; Lindgren et al. 1989), and potentially, could be employed to protect susceptible stands that cannot be harvested.

The antiaggregant synomones, verbenone and ipsenol, could provide a means to prevent the entry of the pine engraver into a stand or, if already present, to cause it to disperse. The combination of verbenone and ipsenol shows promise for the inhibition of attack by *I. typographus* L. (Bakke 1981). Similarly, the western pine beetle, *D. brevicomis* LeConte is inhibited by the combination of verbenone and ipsdienol (Paine and Hanlon 1991).

In Idaho, ipsenol inhibited the response of *I. pini* to ponderosa pine logs baited with *I. pini* males (Furniss and Livingston 1979). Similarly, ipsdienol-baited, standing pines surrounded by a grid of verbenone bubble cap release devices had significantly less attack by *I. pini* than baited pines with no surrounding grid (Borden et al. 1992). Although neither verbenone nor ipsenol deployed separately could adequately protect felled lodgepole pines from mass attack by *I. pini*, verbenone and ipsenol applied together to felled and standing lodgepole pines dramatically reduced *I. pini* attack (Borden et al. 1992). It is necessary however, to determine if this success can be duplicated in operational settings before the antiaggregants can be employed as a routine management tool for the pine engraver.

The application of verbenone and ipsenol in a forest setting presumably would indicate to *I. pini* that a stand of lodgepole pines or slash is already heavily colonized by *I. latidens* and *D. ponderosae*, a situation that is probably uncommon in nature (Miller 1990). An effective semiochemical treatment depends on the mechanism of semiochemical release by the devices used to dispense the antiaggregants, density (dose rate) and placement of the devices in the forest, and the time of application in relation to the life activity of the pine engraver. Two devices are readily available: bubble caps, which dispense the antiaggregants at constant, temperature-dependent rates from discrete points and semiochemical-impregnated beads, which release the antiaggregants at declining, temperature-dependent rates from the ground over a broad area (Phero Tech Inc., Delta, B.C.).

The experiments described herein were designed to test the efficacy of the verbenone and ipsenol antiaggregant combination, and to evaluate the utility of the bubble cap and impregnated bead release devices deployed in simulated operational settings. The specific objectives were to determine:

1) the minimum density of verbenone and ipsenol bubble

cap release points at which the response of *I. pini* is effectively inhibited;

2) the inhibitory efficacy and longevity of impregnated beads dispensing verbenone and ipsenol at different dose rates from multiple funnel traps (Lindgren 1983), and the forest floor; and,

3) the capability of verbenone and ipsenol deployed in a simulated thinning environment to protect:

   a) standing lodgepole pines when antiaggregants are dispensed from grid and broadcast distributions of bubble caps and impregnated beads;

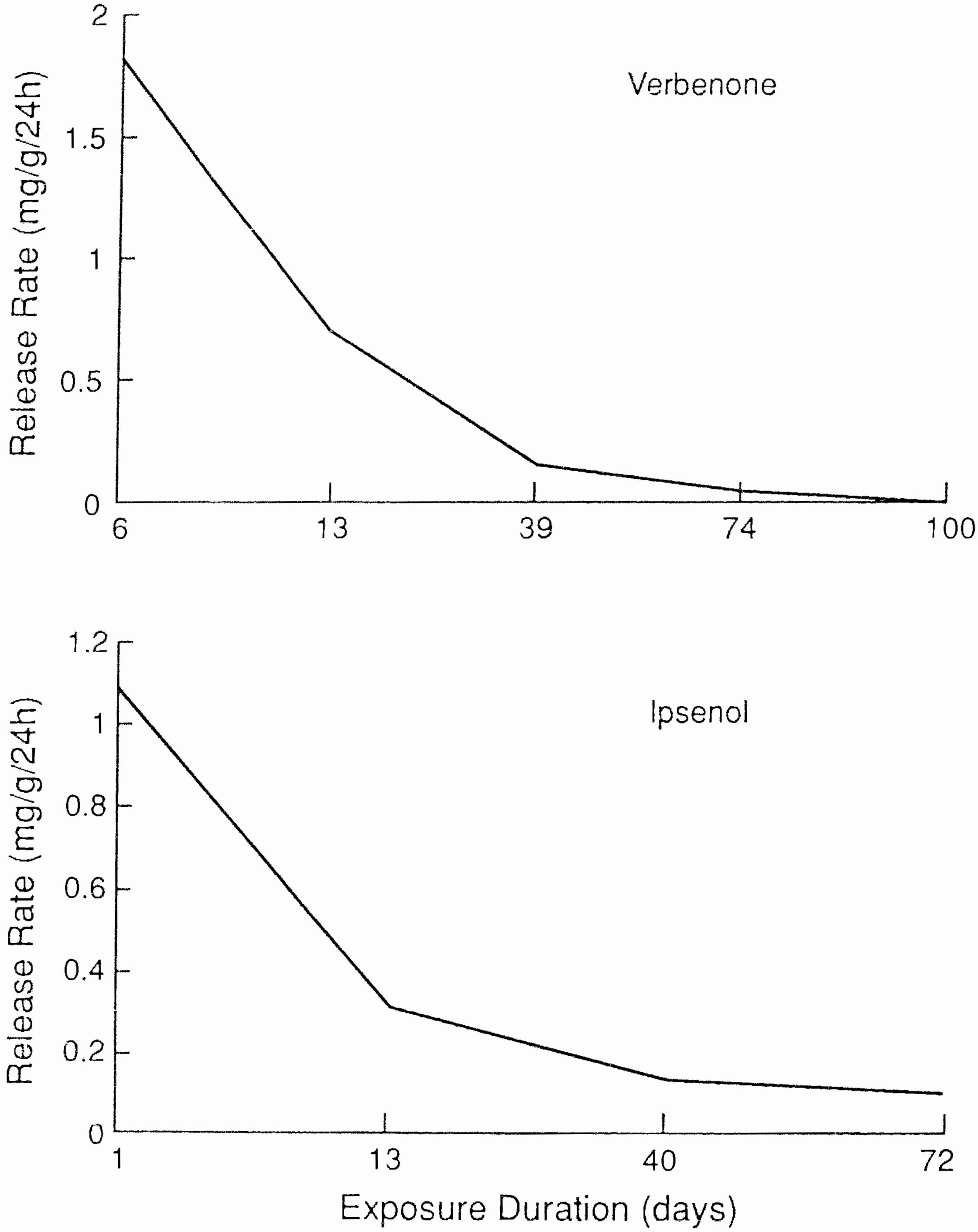
   b) felled pines when antiaggregants are dispensed from a broadcast distribution of impregnated beads; and,

   c) felled pines when antiaggregants, applied at various times prior to attack, are dispensed at different dose rates from broadcast distributions of impregnated beads.

2.0 MATERIALS AND METHODS

(±)-Ipsdienol, (±)-ipsenol, and (±)-verbenone (chemical purities 97, 97, and 98 %, respectively) and semiochemical-impregnated bead and bubble cap release devices were obtained from Phero Tech Inc., Delta, B.C. The beads were made from polyethylene (verbenone) and polypropylene (ipsenol) materials

Fig. 1. Release rates of verbenone and ipsenol from impregnated, polyethylene and polypropylene beads, respectively, at 24°C under laboratory conditions. Verbenone release rate data prior to day 6 is unavailable. Data obtained from Phero Tech Inc., Delta, B.C.


Verbenone
Release Rate (mg/g/24h)
2
1.5
1
0.5
0
6
13
39
74
100
Ipsenol
Release Rate (mg/g/24h)
1.2
1
0.8
0.6
0.4
0.2
0
1
13
40
72
Exposure Duration (days)

best suited for dispensing the antiaggregants. The pill-shaped beads were impregnated with verbenone or ipsenol by means of a heat-treating process. The dimensions of the black (verbenone-impregnated) and white (ipsenol-impregnated) beads were 4.2 x 1.7 mm and 3.0 x 1.9 mm, respectively.

The release rate of antiaggregants from the beads declines with time (Fig. 1). Because the rate of decline in the field will vary with daily ambient temperature, type of polymer material, and the semiochemical involved, only the initial release rates (Fig. 1) were used to establish a 50:1 ratio of verbenone:ipsenol for operational experiments.

The release rates of ipsdienol, ipsenol, and verbenone through the semi-permeable membranes of polyvinyl chloride (ipsdienol and ipsenol) and polyethylene (verbenone) bubble caps were 0.2, 0.2, and 10 mg/day at 24°C, respectively. The actual rate of release in the field was dependent on the daily ambient temperature. To prevent the polymerization and rapid volatilization of the semiochemicals in direct sunlight, the verbenone bubble caps were placed over the ipsenol bubble caps and stapled to the north side of trees at a height of approximately 2 m. Ipsdienol bubble caps were stapled 1 m high on the north side of flat, cedar stakes driven into the ground.

All experiments were performed during 1990 and 1991 in homogeneous stands of mature lodgepole pine located adjacent to recently-logged cutblocks in the southern and central interior of British Columbia.

Experiment 1

Exp. 1 was designed to test the effect of antiaggregants deployed at different densities in inhibiting the ability of *I. pini* to orient to a source of attractive pheromone. It was established on 16 July, 1990 in the Cariboo Forest Region approximately 75 km northwest of Williams Lake. It consisted of 3 antiaggregant treatment density grids and an untreated control replicated 5 times in a randomized, complete block layout. The replicated blocks were established along 3 km of logging road on compass lines run at angles approximately perpendicular to the road and parallel to cutblock margins. All treatment density grids contained a total of 16 verbenone and ipsenol bubble cap release points in a 4 x 4 layout. Grid densities of 44, 100, and 400 elevated release points/ha were obtained by stapling bubble caps to pine boles located approximately 15, 10, and 5 m apart, respectively. The edges of the grids were separated by a distance of at least 50 m. An ipsdienol-baited, multiple-funnel trap was suspended between two trees in the approximate center of each grid. Control traps, also baited with ipsdienol, were not surrounded by a grid of bubble caps releasing verbenone and ipsenol. The trap catches were collected on 28 August. The captured beetles were separated by sex, counted and preserved in 70 % ethanol.

Experiments 2 and 3

Experiments 2 and 3 tested different doses of antiaggregants as treatments to inhibit responses of *I. pini* to ipsdienol-baited traps. They were conducted in 1990 from 3 May to 3 July (Exp. 2) and 4 July to 5 September (Exp. 3) in the Kamloops Forest Region approximately 60 km northeast of Princeton.

Each experiment consisted of 3 antiaggregant release rate treatments and an untreated control replicated 10 times in randomized, complete blocks. Treatment traps contained antiaggregant-impregnated beads placed within separate compartments of plastic mesh tubes suspended in the central column of multiple-funnel traps. Verbenone and ipsenol were dispensed from the beads at 5 and 0.1 mg/day, respectively, and at 2 and 4 times these rates. All traps, including the controls, contained a single bubble cap releasing ipsdienol. The traps were suspended between two trees and spaced at least 15 m apart. The beads and bubble caps initially placed in the traps at the start of the spring and summer experiments were employed for the duration of each experiment. Captured beetles were collected 3 and 5 times during the spring and summer experiments, respectively, and processed as in Exp. 1.

Experiments 4 and 5

The objective of Experiments 4 and 5 was to evaluate different doses of antiaggregants as inhibitors of attack by *I. pini* on lodgepole pine logs. Exp. 4 was set up on 5 May, 1990 approximately 50 km northeast of Princeton, and Exp. 5 on 19 July, 1990 approximately 90 km west of Williams Lake. Both experiments consisted of 3 antiaggregant dose rate treatments and an untreated control replicated 12 times in randomized, complete blocks.

Forty-eight, 2 m-long bolts (4 per replicate) of freshly-cut lodgepole pines (15-20 cm diameter at breast height, dbh, 1.3 m) were placed at 20 m intervals, starting at 0 and ending at 220 m, along four, straight lines spaced 20 m apart. Antiaggregant-impregnated beads were spread by hand over 8 m^2 of ground in a 2 m-wide band surrounding each bolt. Verbenone and ipsenol were dispensed from the impregnated beads at initial rates of 0.625 and 0.125 mg/m^2 of ground surface/day, respectively, and at 2 and 4 times these rates. A straight line containing 6 ipsdienol-baited stakes was positioned midway between the first and second and another between the third and fourth lines. Thus, each ipsdienol bait was centered in a 20 x 20 m square, equidistant from 4 bolts. In Exp. 4, the beads were applied the day after the pines were felled and cut, and in Exp. 5, 3 days after cutting. The experiments were assessed by counting the numbers of attacks on each bolt 8 and 6 weeks after treatment for Exp. 4 and 5, respectively.

Experiment 6

Exp. 6 was intended to evaluate the efficacy of antiaggregants to inhibit attack by *I. pini* on standing trees following simulated silvicultural thinnings. It was set up from 6 to 17 May, 1990 approximately 40 km northeast of Princeton. Fifteen 50 x 50 m plots, spaced at least 50 m apart, were laid out in lodgepole pine forests ≥ 60 years old. Four replicates of 3 plots each were grouped together at one location and a fifth replicate was established approximately 1 km away.

Simulated operational thinnings were done in each plot to reduce the stand density to 800 trees/ha. To determine stand density before and after thinning, 5 circular sample plots (50 m^2/plot, 10 % sampling intensity) were systematically located within each thinned plot. The stand densities before thinning ranged from 960 to 3280 trees/ha. After thinning, the mean density had been reduced to 803 trees/ha (range 520-920). The mean dbh of the remaining trees was 17.1 cm (range 13.7-20.6).

Attack of the slash by *I. pini* did not occur until about mid-June, probably because the spring of 1990 was unusually cool and wet. Therefore, application of the antiaggregants was delayed until spring 1991, in an attempt to ensure that a pine engraver population large enough to threaten the standing pines was created within each plot. In early August another 20 trees/plot were felled to provide additional host material in which populations of the pine engraver could build up.

When the site was visited in April 1991, numerous, fresh wind-felled pines were found within and between the blocks. Moreover, winter logging immediately adjacent to the experimental site had created an abundance of pine slash. Because the presence of this preferred host material could have diverted *I. pini* away from within the plots, application of the antiaggregants was delayed once more until summer 1991.

The antiaggregants were finally applied on 16 August, 1991. A 10 x 10 m grid of verbenone and ipsenol bubble cap release points (100/ha) was established in 5 of the plots, and a broadcast distribution of verbenone- and ipsenol-impregnated beads was applied to another 5 plots using a hand-held fertilizer spreader. Verbenone and ipsenol were dispensed from the beads at initial rates of 2.5 and 0.05 mg/m^2 of ground surface/day, respectively. Because very few ipsenol-impregnated beads were required to achieve the desired release rate, impregnated beads were mixed with unimpregnated beads at a ratio of 5:1 to ensure that the impregnated beads were evenly distributed on the forest floor. The remaining 5 plots were left as untreated controls.

Ipsdienol bubble caps were applied on 5 stakes distributed uniformly within each of the 15 plots in mid-May and again in mid-August, 1990, before the antiaggregants were applied, and on 16 August, 1991, when the antiaggregant treatments were applied. The experiment was assessed by counting the number of attacks/m^2 of bark surface on the first 2 m of a pine bole approximately 7 weeks after treatment.

Experiment 7

Exp. 7 tested the efficacy of broadcast antiaggregants for inhibiting attack by *I. pini* on slash in simulated thinnings. It consisted of an antiaggregant treatment of impregnated beads and an untreated control replicated 5 times in a randomized, complete block layout. Two and 3 replicates were respectively established approximately 80 and 100 km west of Williams Lake.

Ten 50 x 50 m plots, separated by at least 50 m, were established on 24 and 25 May, 1990. Two lodgepole pines were felled and baited with 2 ipsdienol bubble caps each just outside and on opposite sides of each plot to create a small local population of the pine engraver. From 11 to 15 July, selected lodgepole pines within the plots were felled to simulate a thinning with a constant density of felled pines (15-20 cm dbh). As determined in 5 systematically located, circular sample plots (50 m^2/plot, 10 % sampling intensity) within the thinned plots, the mean stand density before thinning was 2272 trees/ha (range 1400-3200), and the mean density of felled pines was 528 trees/ha (range 360-640). The numbers of felled pines in treated and untreated plots ($\bar{x} \pm SE$) were 134.4 ± 5.0 and 127.4 ± 8.9, respectively. The mean dbh (± SE) of felled pines was 15.3 ± 0.3 cm (range 13.7-17.7).

On 18 July, antiaggregant-laden beads were distributed as in Exp. 6 using the hand-held spreader in 5 of the plots. Verbenone and ipsenol were released at 2.5 and 0.05 mg/m^2 of ground surface/day, respectively. To challenge *I. pini* to break through the antiaggregant treatment, and to ensure attack on the control blocks, stakes baited with the attractive pheromone, ipsdienol, were uniformly distributed within each plot.

The efficacy of the antiaggregant treatment was evaluated by determining the number of attacks/m^2 of available bark surface on a randomly-selected 1 m-long section in the first 5 m of each felled-pine bole ≥ 10 cm dbh. The distance from the sampled bole section to the nearest baited stake was estimated visually to the nearest meter. The full length of each pine bole was examined for the presence or absence of pine engraver attack. An attack by *I. pini* was evidenced by the presence of frass of a certain texture and colour. A frass pile not thought to be produced by the pine engraver was examined by exposing the gallery and identifying the beetle therein. Only pine engraver attacks were counted.

Experiment 8

The objective of Exp. 8 was to evaluate further the efficacy of broadcast antiaggregants as inhibitors of attack on slash by testing different doses and application times prior to attack. It was located approximately 50 km northeast of Princeton, and consisted of 6 antiaggregant-impregnated bead treatments and an untreated control replicated 5 times in randomized, complete blocks.

Between 13 and 15 May, 1991, 35, 15 x 15 m plots were established at 60 m centers. Within each plot, 6 lodgepole pines (15-20 cm dbh) were felled. Commencing on 16 May and for 3 consecutive weeks, antiaggregant-impregnated beads were applied as in Exp. 6 and 7 so as to release verbenone and ipsenol respectively at 2.5 and 0.05 mg/m^2 of ground surface/day, or at twice these rates. Thus, 5 plots/dose rate/week were treated; 5 plots were left as untreated controls. Treatment on 3 consecutive weeks resulted in applications 4, 3, and 2 weeks prior to the first observed attack by *I. pini* on a control plot on 13 June. On June 13, an ipsdienol-baited stake was placed in the center of each thinning-simulation plot to challenge *I. pini* to overcome the antiaggregant treatment.

The experiment was assessed by counting the number of attacks/m^2 of available bark surface on the first 10 m of all 6 pine boles in the plots every week for ten weeks, from 13 June to 15 August. At the completion of the experiment, 0.5 m-long bolts were cut from each 1 m bole section along the first 10 m of randomly-selected felled pines (6 from each of the 10-1 m sections) from the plots of 5 treatments and the control. The 60 bolts were debarked and the exposed galleries identified for species and counted.

Statistical Analyses

Statistical analyses were performed using the SAS statistical package ver. 5.0 (SAS Institute Inc., Cary, NC). All data were tested for heteroscedasticity and non-normality. Homoscedastic and normalized transformed data (as noted in the results) were subjected to two-way ANOVA, using block and treatment as model factors, and Bonferroni (Dunn) t-tests to determine differences among treatment means. When transformation failed to correct for heteroscedasticity and non-normality, the data were analyzed using Friedman's test (Conover 1980; SAS 1985) and a nonparametric multiple comparisons test (Zar 1984). In Exp. 1, regression analysis was performed on treatment densities and trap catch data. Gallery counts were regressed against their corresponding surface attack counts to assess the accuracy of the surface attack density evaluation in Exp. 8. A comparison of two proportions test (Zar 1984) was employed to detect the effect of treatment on the proportion of attacked pine boles in Exp. 7.

3.0 RESULTS

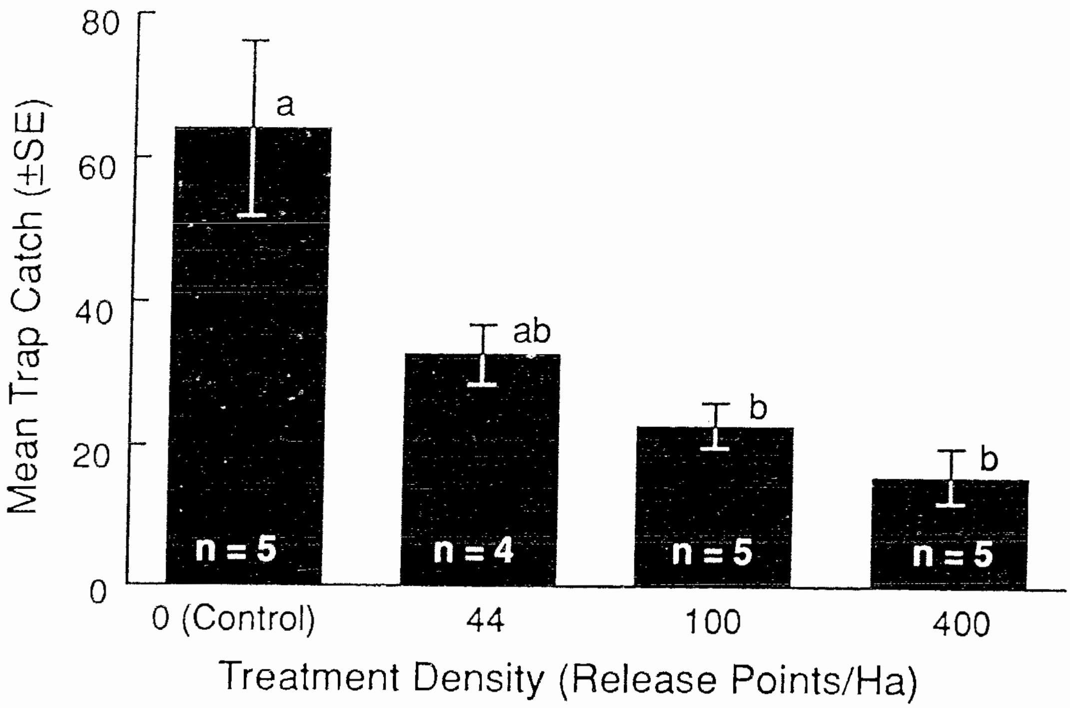
Experiment 1

The responses of *I. pini* to ipsdienol-baited traps were significantly reduced from those of control traps by antiaggregant-containing bubble caps deployed at densities of 100 and 400/ha (Fig. 2). There was a reasonably strong curvi-linear relationship between antiaggregant treatment density and the trap catches (r^2=0.60, log y=1.8-0.24 log x, P<0.0001, data transformed by $\log_{10}$ x+1 and y+1). The mean female to male ratios for the 4 increasing treatment densities were 3.3:1, 4.2:1, 4.4:1, and 4.7:1, respectively.

Experiments 2 and 3

The responses of *I. pini* in Exp. 2 to ipsdienol-baited traps containing antiaggregant-impregnated beads were lower than to the control traps (Table 1). There was no difference among catches in traps treated with the low, medium, and high rates of verbenone and ipsenol during any of the three collection periods. The mean ratios of control to treatment trap catches for the low, medium, and high rates at the end of the first collection period were 39:1, 35:1, and 129:1, respectively, and 24:1 and 47:1 for the low and medium rates, respectively, during the final collection period. No beetles were caught in the high rate treatment traps during the final collection period. Catches in the treated traps were too low for calculation of meaningful female to male ratios.

Fig. 2. The effect of verbenone and ipsenol dispensed at ca. 10 and 0.2 mg/day, respectively, from 4 x 4 grid distributions of elevated, bubble cap release points on the numbers of *Ips pini* responding to centrally-positioned, multiple-funnel traps in stands of lodgepole pine near Williams Lake, B.C., 16 July to 27 August, 1990. Bars topped by the same letter are not significantly different, $P<0.005$, Bonferroni (Dunn) t-tests on data transformed by $y^{0.2296}$.



80
60
40
20
0
Mean Trap Catch (±SE)
a
ab
b
b
n = 5
n = 4
n = 5
n = 5
0 (Control)
44
100
400
Treatment Density (Release Points/Ha)

Table 1. Numbers of *Ips pini* caught in Exp. 2 during three collection periods in ipsdienol-baited, multiple-funnel traps containing 3 doses of verbenone- and ipsenol-impregnated beads, 3 May to 3 July, 1990 in stands of lodgepole pine near Princeton, B.C. The initial low, medium, and high release rates from beads were ca. 5, 10, and 20 mg verbenone/day and 0.1, 0.2, and 0.4 mg ipsenol/day, respectively.

	Trap Catch ($\bar{x} \pm$ SE)[a]		
Treatment dose rate	**Bead exposure period, days 1 - 8**	**Bead exposure period, days 9 - 50**	**Bead exposure period, days 51 - 62**
Control	38.8 ± 9.9a	32.2 ± 5.6a	14.2 ± 3.0a
Low	1.0 ± 0.5b	2.2 ± 0.7ab	0.6 ± 0.4b
Medium	1.1 ± 0.7b	0.8 ± 0.3b	0.3 ± 0.2b
High	0.3 ± 0.2b	0.3 ± 0.3b	0.0 ± 0.0b

[a] Means within a column followed by the same letter are not significantly different, P<0.05, nonparametric multiple comparisons test (Zar 1984); n=9 for medium and high doses, days 9 - 50 and high dose, days 51 - 62; otherwise n=10.

During the first 42 days of bead exposure in the summer, the mean catches of *I. pini* in traps treated with low, medium, and high doses of antiaggregants were significantly lower than those in the control traps (Table 2). After 49 days, catches for the low rate did not differ from the untreated traps. Catches for both the medium and high rates remained significantly lower than in the controls for the duration of the experiment. There was no difference between the catches for the medium and high rates until the final collection period and, except for the third collection period, no difference between those for the low and medium rates. Peak flight activity of the pine engraver occurred during the second and third collection periods. By the end of the fifth collection period, the mean ratios of control to treatment trap catches for the low, medium, and high rates had declined to 2:1, 2:1, and 3:1 from 8:1, 25:1, and 22:1, respectively, at the completion of the first collection period. The mean female to male ratios for all collection periods combined were 2.5:1, 3.6:1, 2.8:1, and 2.7:1 for the low, medium, and high rates and control, respectively.

Experiments 4 and 5

Attack by *I. pini* on the 2 m-long lodgepole pine bolts in Exp. 4 and 5 was negligible. In the spring experiment (Exp. 4), only one of 12 control bolts was infested (59 attacks). In one instance, an unattacked, control bolt was within 1 m of a heavily-attacked, wind-felled pine. Four attacks occurred on bolts in the 8 m^2 plots treated with the verbenone- and

Table 2. Numbers of *Ips pini* caught in Exp. 3 during five collection periods in ipsdienol-baited, multiple-funnel traps containing 3 doses of verbenone- and ipsenol-impregnated beads, 4 July to 5 September, 1990 in stands of lodgepole pine near Princeton, B.C. The initial low, medium, and high release rates from beads were ca. 5, 10, and 20 mg verbenone/day and 0.1, 0.2, 0.4 mg ipsenol/day, respectively.

	Trap Catch ($\bar{x} \pm SE$)[a]				
Treatment dose rate	**Bead exposure period, days 1 - 21**	**Bead exposure period, days, 22 - 34**	**Bead exposure period, days 35 - 42**	**Bead exposure period, days 43 - 49**	**Bead exposure period, days 50 - 63**
Control	15.1 ± 3.2a	68.5 ± 18.1a	72.4 ± 17.5a	22.7 ± 3.8a	33.9 ± 8.5a
Low	1.9 ± 0.5b	21.5 ± 5.8b	22.9 ± 4.6b	16.6 ± 3.3ab	20.6 ± 5.0ab
Medium	0.6 ± 0.3b	10.1 ± 2.9bc	9.7 ± 2.6c	9.2 ± 2.2bc	16.5 ± 5.4b
High	0.7 ± 0.3b	5.9 ± 1.9c	6.5 ± 2.7c	7.0 ± 1.8c	10.7 ± 3.9c

[a] Means within a column followed by the same letter are not significantly different, $P<0.05$, Bonferroni (Dunn) t-tests, data transformed by $\log_{10} y+1$; n=9 for control, days 22 - 34; otherwise n=10.

ipsenol-impregnated beads. Only one attack by *I. pini* was observed in the summer (Exp. 5). The data were too few for statistical analysis.

Some attack by *Ips mexicanus* (Hopk.) was observed on the bolts, the majority in antiaggregant-treated plots. Other scolytid species observed attacking the pine bolts were *Pityogenes knechteli* Swaine, *Ips latidens*, *Dendroctonus sp.* and *Hylurgops sp.*

Experiment 6

The hypothesis that verbenone and ipsenol dispensed from impregnated beads and bubble caps could protect standing trees from attack by *I. pini* was not evaluated because none of the standing lodgepole pines within the treated or control plots was attacked.

Experiment 7

The pines felled and baited prior to the spring flight period were heavily attacked by the pine engraver. The summer flight of *I. pini* was estimated to have begun during the second week of August.

The proportion of felled pines having at least one attack by *I. pini* in the untreated plots was significantly higher than that in the plots treated with the verbenone- and ipsenol-impregnated beads (Table 3). The application of the antiaggregant-impregnated beads in the treated plots significantly reduced the mean attack/m^2 of available bark surface on the felled pines

Table 3. Proportions of felled pines attacked by *Ips pini* in Exp. 7 in ipsdienol-baited, thinning-simulation plots broadcast-treated with verbenone- and ipsenol-impregnated beads having initial release rates of ca. 2.5 and 0.05 mg/m^2 of ground surface/day, respectively, near Williams Lake, B.C., 18 July to 27 August, 1990. Pooled data from 5 replicates.

Treatment	**Total number of felled pines**	**Proportion of felled pines attacked**[a]
Untreated control	637	0.531
Verbenone- and ipsenol-impregnated beads	672	0.329

[a] Proportions significantly different, P<0.001, comparison of two proportions test (Zar 1984).

Table 4. Densities of attack by *Ips pini* in Exp. 7 on felled lodgepole pines in ipsdienol-baited, thinning-simulation plots broadcast-treated with verbenone- and ipsenol-impregnated beads having initial release rates of ca. 2.5 and 0.05 mg/m^2 of ground surface/day, respectively, near Williams Lake, B.C., 18 July to 27 August, 1990 (n=5).

	Randomly-selected, 1 m-long sections from first 5 m of each felled pine		**1 m-Long sections that sustained attack by *Ips pini***	
Treatment	**Number of pines**	**Attack/m^2 ($\bar{x}$ ± SE)[a]**	**Number of pines**	**Attack/m^2 ($\bar{x}$ ± SE)[b]**
Untreated control	637	1.9 ± 0.2	129	9.4 ± 0.8
Verbenone- and ipsenol-impregnated beads	672	1.3 ± 0.2	102	8.8 ± 0.8

[a] Means significantly different, P=0.0168, Friedman's test, $F_{(1,1303)}$ (SAS 1985; Conover 1980).

[b] Means not significantly different, P=0.8589, Friedman's test, $F_{(1,225)}$ (SAS 1985; Conover 1980).

(Table 4). However, when unattacked 1 m bole sections are excluded from the mean, there is no difference between the attack densities on the felled pines in the untreated and treated plots (Table 4).

The mean attack/m^2 of available bark surface/m^2 of ground surface was highest within 1 m of an ipsdienol bait, and then decreased with increasing distance from the bait in both the untreated and treated plots (Fig. 3). The mean number of unattacked 1 m-long bole sections/m^2 of ground surface steadily increased with distance from the ipsdienol baits, plateaued, and then decreased (Fig. 3). In all but 1 distance class (9-10 m), the mean number of unattacked sections was higher in the treated plots than in the untreated plots.

Experiment 8

The mean cumulative attack/m^2 of available bark surface increased steadily after first attack by *I. pini* on the felled lodgepole pines in the untreated plots (Fig. 4). In contrast, impregnated beads dispensing verbenone and ipsenol at a high rate applied 2 weeks (H2) before first attack provided almost complete protection from attack throughout the 10-week observation period. All other treatments provided partial protection, but gradually began to break down (Fig. 4).

Verbenone and ipsenol applied at low and high rates 3 weeks prior to attack, and at the high rate 2 weeks prior to attack (L3, H3, and H2, respectively), reduced the mean attack/m^2 of available bark surface/week to a level significantly lower than

Fig. 3. The effect in Exp. 7 of ipsdienol dispensed at ca. 0.2 mg/day from a bubble cap on the distribution of the intensity of attack and numbers of unattacked 1 m-long bole sections in lodgepole pine thinning-simulation plots treated with verbenone- and ipsenol-impregnated beads near Williams Lake, B.C., 18 July to 27 August, 1990.

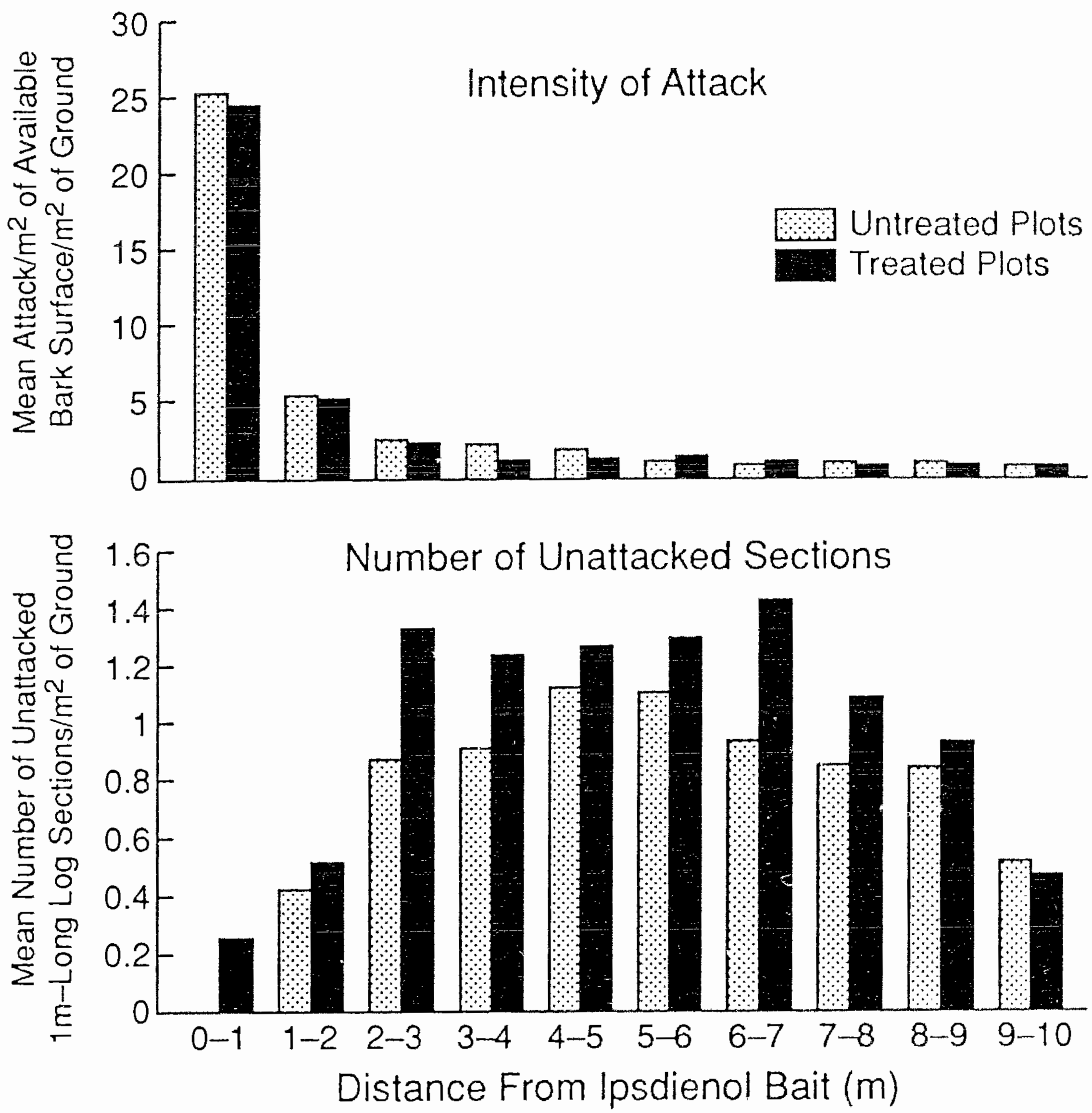
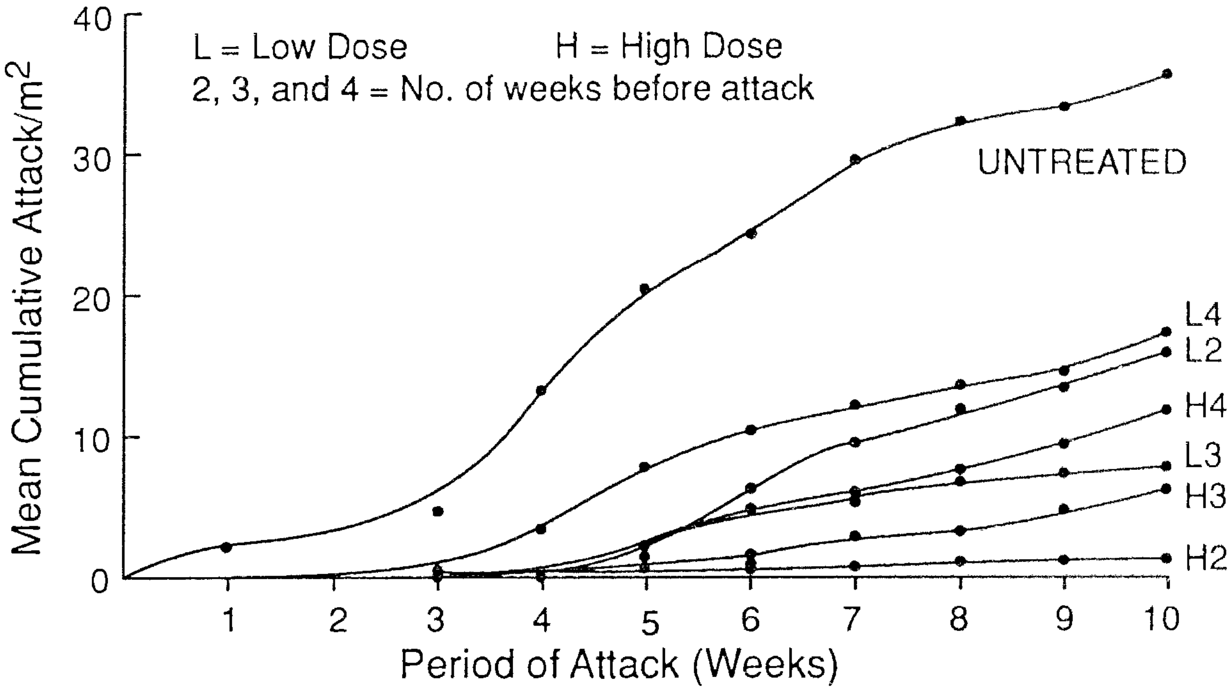
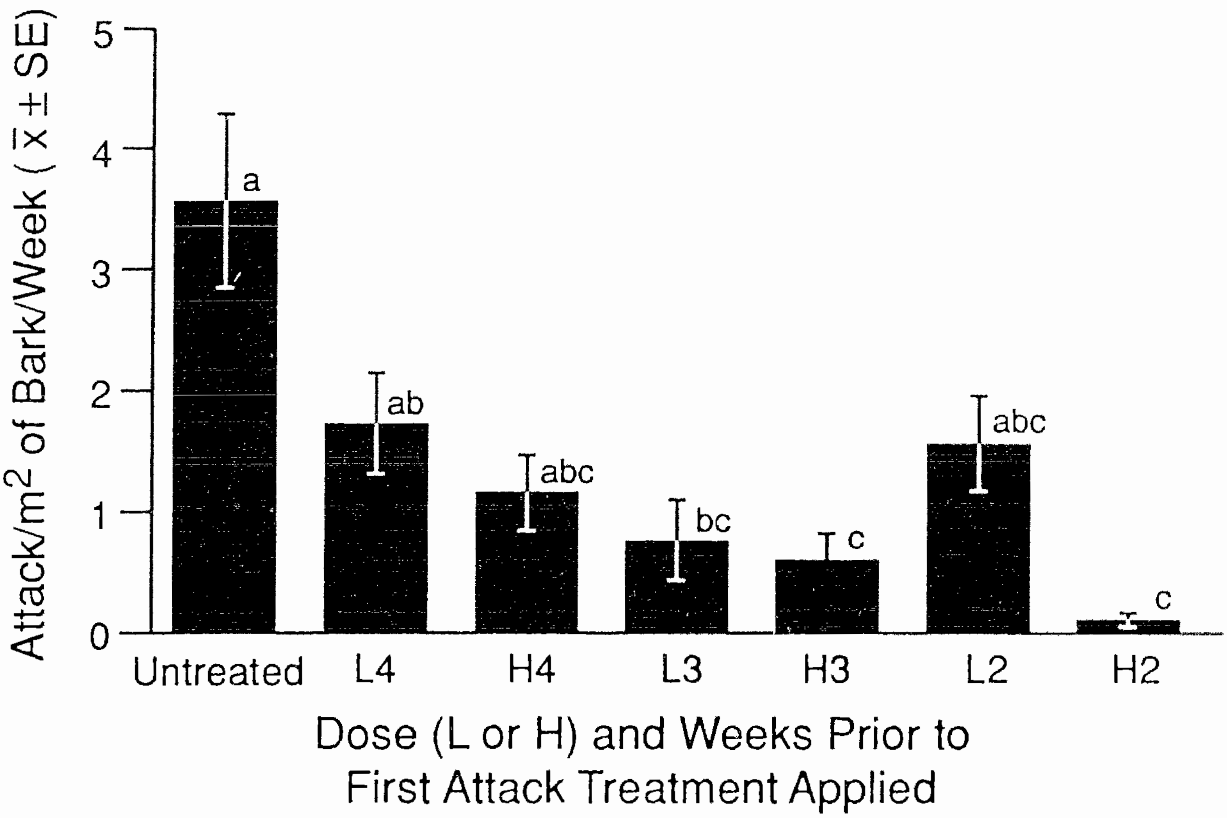

Intensity of Attack
Mean Attack/m2 of Available Bark Surface/m2 of Ground
30
25
20
15
10
5
0
Untreated Plots
Treated Plots
Number of Unattacked Sections
Mean Number of Unattacked 1m–Long Log Sections/m2 of Ground
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0–1
1–2
2–3
3–4
4–5
5–6
6–7
7–8
8–9
9–10
Distance From Ipsdienol Bait (m)

Fig. 4. The effect in Exp. 8 of verbenone and ipsenol at 2 doses dispensed from a broadcast distribution of impregnated beads applied to lodgepole pine, thinning-simulation plots 4, 3, and 2 weeks prior to first attack by *Ips pini* on the mean cumulative attack/m^2 of available bark surface, near Princeton, B.C., 13 June to 15 August, 1991. The initial low (L) and high (H) release rates from the beads were ca. 2.5 and 5.0 mg verbenone/m^2 of ground surface/day and 0.05 and 0.1 mg ipsenol/m^2 of ground surface/day, respectively.



L = Low Dose
H = High Dose
2, 3, and 4 = No. of weeks before attack
Mean Cumulative Attack/m²
0
10
20
30
40
1
2
3
4
5
6
7
8
9
10
Period of Attack (Weeks)
UNTREATED
L4
L2
H4
L3
H3
H2

Fig. 5. Attack/m^2 of available bark surface in Exp. 8 by *Ips pini* on felled lodgepole pines following broadcast applications of verbenone and ipsenol at 2 doses, 4, 3, and 2 weeks prior to first attack, near Princeton, B.C., 13 June to 15 August, 1991. The initial low (L) and high (H) release rates from the beads were ca. 2.5 and 5.0 mg verbenone/m^2 of ground surface/day and 0.05 and 0.1 mg ipsenol/m^2 of ground surface/day, respectively. Bars topped by the same letter are not significantly different, $P<0.05$, nonparametric multiple comparisons test (Zar 1984).



Attack/m^2 of Bark/Week ($\bar{x}$ ± SE)
5
4
3
2
1
0
a
ab
abc
bc
c
abc
c
Untreated
L4
H4
L3
H3
L2
H2
Dose (L or H) and Weeks Prior to First Attack Treatment Applied

that on pines in the untreated plots at the completion of the experiment (Fig. 5). The L4, H4, and L2 treatments provided an intermediate level of protection. There was no difference in the weekly attacks/m^2 between the low and high rates applied to the plots the same week.

There was a reasonably strong linear relationship between the number of attacks counted on the bark surface and number of galleries observed in the 0.5 m-long bolts cut from the felled pines (r^2=0.68, y=1.56+1.0x, P<0.0001). The proportion of *I. pini* galleries was 86.8 %, *P. knechteli* accounted for 12.7 %, and the remainder were occupied by *I. mexicanus* or *Dendroctonus sp.*

4.0 DISCUSSION

Trap catches can be interpreted as a direct measure of the inhibitory capability of the verbenone and ipsenol antiaggregant combination. This inhibitory effect increased with increasing initial dose rate and decreased with increasing time of bead exposure in the field in the summer.

Differences in environmental conditions between the spring and summer experiments appear to have affected bead performance. In the spring, antiaggregants at all 3 dosages were equally efficacious throughout the cool and wet experimental period (Table 1). The combination of low temperature and high precipitation would have retarded the rate of antiaggregant release and reduced the numbers of flying pine engravers. In comparison with the summer experiment when it was warm and dry, the lack of significant differences among the treatment trap catches and decline in the mean ratios of control to treatment trap catch in the spring was probably the result of greater amounts of verbenone and ipsenol released throughout the experiment, and a pine engraver population too small to test rigorously the inhibitory strength of the antiaggregants.

An ill-timed application of the beads in Exp. 7 revealed the importance of timing an application so as to achieve maximal antiaggregant release during the period of peak attack by *I. pini*. The beads were applied an estimated 3 weeks prior to the summer flight of the pine engraver. However, the rate of antiaggregant release (Fig. 1) would have declined to a minimum during the period of attack. A later application would probably have resulted in a greater difference between the treatment and control attack proportions (Table 3).

The results of Exp. 3 (Table 2) suggest that if an initial antiaggregant dosage is sufficiently high, the rate of release will not decline to below an effective threshold level of inhibition. Thus, the treatment will have an extended effective longevity, despite a sharp decline in overall release rate (Fig. 1). Accordingly, Exp. 8 tested whether a high dose could compensate for the low treatment efficacy in Exp. 7, which probably resulted from a premature application of beads. In spite of highly variable weekly attack densities in Exp. 8, the high rates for each of the 3 application dates tended to cause lower attack densities than low rates (Fig. 5). Moreover, although all of the antiaggregant treatments delayed the onset of attack, breakthrough occurred first for the low-dosage treatment 4 weeks before attack (Fig. 4).

Premature application of the beads is most likely to occur in the spring when emergence of the pine engraver from the forest duff is difficult to predict (Schenk and Benjamin 1969). Emergence of the summer generation is more easily predicted because the development of brood in spring-infested pine slash can be monitored. Unless a more controlled release device can be found, synchronization of antiaggregant application with the onset and peak of pine engraver flight activity will be critical to the operational success of an antiaggregant treatment.

Furniss and Livingston (1979) suggested that a reduction in attack density would result in a compensatory increase in *I. pini* brood emergence, and therefore, no treatment benefit would be realized. Oviposition by *I. pini* females, and the size of the resultant brood, is dependent on the combined effect of male attack density and the female to male ratio (Light et al. 1983). When both are high, oviposition per female is reduced, but the rate of brood survival to the adult stage is increased. Thus, each larva will have a relatively uniform amount of food and space, and for any given density of colonization, brood production will be optimized (Coulson et al. 1976; Thomson and Sahota 1981; Light et al. 1983).

While the mean female to male ratios in the summer trap catches of Exp. 3 were not altered by the antiaggregants, those in Exp. 1 tended to be higher than that of the control and the 3:1 ratio commonly found in infested pine hosts (Schenk and

Benjamin 1969; Sartwell et al. 1971). Assuming that the effect of the antiaggregants is to decrease male attack density, but to increase the female to male ratio, brood production in the presence of the antiaggregants should be greater than normal. However, Borden et al. (1992) reported that the emergence from pine bolts treated with verbenone and ipsenol had both a significantly lower attack density and a lower amount of emergent brood than untreated bolts or those treated with ipsenol alone or ipsdienol alone.

In contrast, in the thinning-simulation plots of Exp. 7, the effect of the antiaggregants was to reduce the number of infested felled-pine boles (Table 3 and Fig. 3), rather than to decrease the attack density wherever attack occurred (Table 4 and Fig. 3). Thus, the effect of an antiaggregant treatment would be to disperse an attacking population over a larger area, and to reserve unutilized portions of the thinning residue for re-colonization by the emergent brood. The risk of attack on standing trees would be greatly reduced.

Ips latidens was rarely observed during the experiments. Presumably, the aggregating message conveyed by ipsenol was nullified by the inhibitory effect of both ipsdienol (Miller 1990) and verbenone (D.R. Miller, Phero Tech Inc., Delta, B.C., pers. comm.). *Pityogenes knechteli* seemed to be drawn to treatments and controls in proportion to the magnitude of the response by *I. pini*. *Pityogenes knechteli* is a secondary invader of pines previously attacked by *Dendroctonus* and *Ips* and seldom initiates attacks (Bright 1976; Furniss and Carolin 1977).

In Exp. 1, increasing the grid treatment density exponentially from 44 bubble caps/ha to 100 and 400/ha (2.3- and 9.1-fold increases, respectively) resulted in catch reductions of only about one-third for each increase in density (Fig. 2). The high catches at a density of 44 bubble caps/ha (Fig. 2), and the relationship between antiaggregant treatment density and trap catches (r^2=0.60), suggest that the effect of the antiaggregants may be near the limit of influence at a 15 m spacing. Although the efficacy of antiaggregants at a 15 m spacing could be improved by increasing the release rate from the bubble caps, it is unlikely that lower treatment densities would be efficacious and that higher densities would be cost effective.

In contrast to grid distributions of bubble cap release devices, broadcast distributions of impregnated beads are not as labour-intensive, and therefore, would be more cost effective. However, the beads usually penetrate into the duff, where air movement is impeded, and the efficiency of antiaggregant dispersion would be reduced. Development of beads or other devices with a higher surface area to volume ratio and a shape that allows them to be intercepted by and caught up in pine slash and ground vegetation should improve the efficiency of the antiaggregant deployment in the forest environment.

Even though populations of the beetles were known to exist at the locations where Exp. 4 and 5 were conducted, *I. pini* could not be induced to attack the 2 m-long bolts in significant numbers. Because short bole lengths dry out more rapidly than longer lengths, bolts of this length may not have been perceived as suitable hosts. *Ips pini* prefers pine hosts with high inner bark moisture content (Anderson 1948), and survivorship of brood is reduced in prematurely-dried host material (Knopf 1982). It was observed during the evaluation of Exp. 7 that *I. pini* tended to attack the intact bole of felled pines rather than short pine bolts (< 2 m) cut from the same trees.

In treatment L2 of Exp. 8 (Fig. 5), the inhibitory effect of the antiaggregants was apparently overridden by the aggregating signal emitted by a large number of attack-initiating males converging on 2 of the treatment plots. It may be necessary in some circumstances to provide *I. pini* with an alternative to treated host breeding material. Mass trapping with ipsdienol and lanierone in multiple-funnel traps might be employed to reduce an outbreak population, and thereby, to increase the ability of an antiaggregant treatment to protect a stand of drought-stressed pines.

For Exp. 6, which failed, it was necessary to create a large population of *I. pini* that would threaten to attack standing lodgepole pines. At the time of antiaggregant application, a large pine engraver population resided in the experimental area, but there was an unplanned abundance of wind-felled pines within the plots and pine slash from a nearby logging operation. *Ips pini* must have colonized these readily available hosts, rather than the apparently healthy standing pines within the thinning-simulation plots.

Ipsdienol was employed in all experiments to challenge the inhibitory strength of the antiaggregants by drawing *I. pini* to the treatments. Ideally, a thinned pine stand to be protected would have no attractant source, except for primary attractants emitted by the slash itself. Thus, it is expected that the efficacy of an antiaggregant treatment would be even greater than was demonstrated in these experiments.

As British Columbia's second growth lodgepole pine forests mature, pre-commercial thinning, to improve the yield of the harvest crop, will become more prevalent as will the occurrence of outbreak populations of *I. pini*. Thus, the employment of slash management techniques and aggregative and antiaggregative semiochemicals to control pine engraver populations will likely be a necessity.

5.0 REFERENCES

Amman, G.D., R.W. Their, M.D. McGregor, and R.F. Schmitz. 1989. Efficacy of verbenone in reducing lodgepole pine infestation by mountain pine beetles in Idaho. Can. J. For. Res. 19:60-64.

Anderson, R.F. 1948. Host selection by the pine engraver. J. Econ. Entomol. 41:596-602.

Andrews, R.J. 1987. Forest insect and disease conditions. Cariboo Forest Region 1986. Can. For. Serv., Pac. For. Ctr., Victoria, British Columbia. FIDS 87-1.

Andrews, R.J. 1988. Forest insect and disease conditions. Cariboo Forest Region 1987. Can. For. Serv., Pac. For. Ctr., Victoria, British Columbia. FIDS 88-1.

Bakke, A. 1981. Inhibition of the response in *Ips typographus* to the aggregation pheromone: field evaluation of verbenone and ipsenol. Z. angew. Entomol. 92:172-177.

Bedard, W.D., P.E. Tilden, K.Q. Lindahl, Jr., D.L. Wood, and P.A. Rauch. 1980. Effects of verbenone and trans-verbenol on the response of *Dendroctonus brevicomis* to natural and synthetic attractant in the field. J. Chem. Ecol. 6:997-1013.

Birch, M.C. 1978. Chemical communication in pine beetles. Am. Sci. 66:409-419.

Birch, M.C. and D.M. Light. 1977. Inhibition of the attractant pheromone in *Ips pini* and *I. paraconfusus* (Coleoptera: Scolytidae): field evaluation of ipsenol and linalool. J. Chem. Ecol. 3:257-267.

Birch, M.C., D.M. Light, and K. Mori. 1977. Selective inhibition of response of *Ips pini* to its pheromone by the S-(-)-enantiomer of ipsenol. Nature 170:738-739.

Birch, M.C., D.M. Light, D.L. Wood, L.E. Browne, R.M. Silverstein, B.J. Bergot, B. Ohloff, J.R. West, and J.C. Young. 1980a. Pheromonal attraction and allomonal interruption of *Ips pini* in California by the two enantiomers of ipsdienol. J. Chem. Ecol. 6:703-717.

Birch, M.C., P. Svihra, T.D. Paine, and J.C. Miller. 1980b. Influence of chemically mediated behavior on host tree colonization by four cohabiting species of bark beetles. J. Chem. Ecol. 6:395-414.

Birch, M.C. and D.L. Wood. 1975. Mutual inhibition of the attractant pheromone response by two species of *Ips* (Coleoptera: Scolytidae). J. Chem. Ecol. 1:101-113.

Borden, J.H. 1990. Use of semiochemicals to manage coniferous tree pests in western Canada. In Behavior-modifying chemicals for insect management: applications of pheromones and other attractants. R.L. Ridgway, R.M. Silverstein, and M.N. Inscoe (eds.). Marcel Dekker Inc., New York. pp. 281-315.

Borden, J.H., D.R. Devlin, and D.R. Miller. 1992. Synomones of two sympatric species deter attack by the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). Can. J. For. Res. (In press).

Borden, J.H. and B.S. Lindgren. 1988. The role of semiochemicals in IPM of the mountain pine beetle. In Integrated control of scolytid bark beetles. T.L. Payne and H. Saarenmaa (eds.). Virginia Polytech Inst. and State Univ., Blackburg, VA. pp. 247-255.

Bright, D.E. 1976. The insects and arachnids of Canada. Part 2: the bark beetles of Canada and Alaska (Coleoptera: Scolytidae). Can. Dept. Agr., Res. Branch, Ottawa, Ontario. Publ. 1576.

Brown, W.L.,Jr., T. Eisner, and R.H. Whittaker. 1970. Allomones and kairomones: transpecific chemical messengers. Bioscience 20:21-22.

Byers, J.A. and D.L. Wood. 1980. Interspecific inhibition of the response of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus*, to their pheromones in the field. J. Chem. Ecol. 6:149-164.

Byers, J.A. and D.L. Wood. 1981. Interspecific effects of pheromones on the attraction of the bark beetles *Dendroctonus brevicomis* and *Ips paraconfusus* in the laboratory. J. Chem. Ecol. 7:9-18.

Byers, J.A., D.L. Wood, J. Craig, and L.B. Hendry. 1984. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter- and intraspecific competition. J. Chem. Ecol. 10:861-877.

Burke, S. 1992. Use patterns and non-target effects of forest coleopteran semiochemicals. In Insect behavior-modifying chemicals: applications and regulation. R.L. Ridgway, M.N. Inscoe, and H. Arn (eds.). Proceedings of a symposium organized in assosciation with the British Crop Protection Conucil, 19 November 1990, Brighton, Sussex, UK. BCPE Publications, Bracknell, Berkshire, UK. (In press).

Conover, W.J. 1980. Practical nonparametric statistics. J. Wiley and Sons, 2nd Edition. New York.

Coulson, R.N., A.M. Mayysi, J.L. Foltz, F.P. Hain, and W.C. Martin. 1976. Resource utilization by the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). Can. Entmol. 108:353-362.

Dewey, J.E., W.M. Ciesla, and H.E. Meyer. 1974. Insect defoliation as a predisposing agent to a bark beetle outbreak in eastern Montana. Env. Entomol. 3:722.

Dixon, W.N. and T.L. Payne. 1979. Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees. Texas Agric. Expt. Stn., Misc. Publ. 1432.

Furniss, M.M. and R.L. Livingston. 1979. Inhibition by ipsenol of pine engraver attraction in northern Idaho. Env. Entomol. 8:369-372.

Furniss, R. L. and V.M. Carolin. 1977. Western forest insects. USDA, For. Serv. Publ. No. 1339.

Geiszler, D.R., R.I. Gara, and W.R. Littke. 1984. Bark beetle infestations of lodgepole pine following a fire in south-central Oregon. Z. angew. Entomol. 98:389-394.

Gries, G., R. Nolte, and W. Sanders. 1990. Computer simulated host selection in *Ips typographus*. Entomol. exp. appl. 53:211-217.

Humphreys, N. and R.L. Ferris. 1987. Forest insect and disease conditions. Vancouver Forest Region 1986. Can. For. Serv., Pac. For. Ctr., Victoria, British Columbia. FIDS 87-6.

Hunt, D.W.A. and J.H. Borden. 1989. Conversion of verbenols to verbenone by yeasts isolated from *Dendroctonus ponderosae* (Coleoptera: Scolytidae). J. Chem. Ecol. 16:1385-1397.

Kennedy, P.C. 1969. Causes of the 1966 *Ips pini* outbreaks. Mich. Acad. 2:87-92.

Knopf, J.A.E. 1982. Attraction and containment of *Ips* beetles by large slash piles. USDA, For. Serv., Intermountain Reg., For. Pest Mgt. 82-8.

Lanier, G.N., M.C. Birch, R.F. Schmitz, and M.M. Furniss. 1972. Pheromones of *Ips pini* (Coleoptera: Scolytidae): variation in response among three populations. Can. Entomol. 104:1917-1923.

Leufvén, A., G. Bergstrom, and E. Falsen. 1984. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. J. Chem. Ecol. 10:1349-1360.

Light, D.M. and M.C. Birch. 1979. Inhibition of the attractive pheromone response in *Ips paraconfusus* by R-(-)-ipsdienol. Naturwiss. 66:159-160.

Light, D.M., M.C. Birch, and T.D. Paine. 1983. Laboratory study of intraspecific and interspecific competition within and between two sympatric bark beetle species, *Ips pini* and *I. paraconfusus*. Z. angew. Entomol. 96:233-241.

Lindgren, B.S. 1983. A multiple-funnel trap for scolytid beetles. Can. Entomol. 115:299-302.

Livingston, R.L. 1979. The pine engraver, *Ips pini* (Say), in Idaho. Life history, habits, and management recommendations. Idaho Dept. Lands, For. Insect and Dis. Contr. Rep. 79-3.

McNew, G.L. 1970. The Boyce Thompson Institute in forest entomology that led to the discovery of pheromones in bark beetles. Contrib. Boyce Thompson Inst. 24:251-262.

Miller, D.R. 1990. Reproductive and ecological isolation: community structure in the use of semiochemicals by pine bark beetles (Coleoptera: Scolytidae). Ph. D. Thesis, Simon Fraser University, Burnaby, British Columbia.

Miller, D.R. and J.H. Borden. 1985. Life history of *Ips latidens* (Leconte) (Coleoptera: Scolytidae). Can. Entomol. 117:859-871.

Miller, D.R. and J.H. Borden. 1990. ß-Phellandrene: kairomone for the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). J. Chem. Ecol. 16:2519-2531.

Miller, D.R., J.H. Borden, G.G.S. King, and K.N. Slessor. 1991. Ipsenol: an aggregation pheromone for *Ips latidens* (LeConte) (Coleoptera: Scolytidae). J. Chem. Ecol. 17:1517-1527.

Nordlund, D.A. and W.J. Lewis. 1976. Terminology of chemical releasing stimuli in intraspecific and interspecific interactions. J. Chem. Ecol. 2:211-220.

Payne, T.L., J.E. Coster, J.V. Richerson, L.J. Edson, and E.R. Hart. 1978. Field response of the southern pine beetle to behavioral chemicals. Environ. Emtomol. 7:578-582.

Pitman, G.B., J.P. Vité, G.W. Kinzer, and A.F. Fentiman. 1969. Specificity of population-aggregating pheromones in *Dendroctonus*. J. Insect Physiol. 15:363-366.

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

Reid, R.W. 1955. The bark beetle complex association with lodgepole pine slash in Alberta. I. Notes on the biologies of some Scolytidae attacking lodgepole pine slash. Can. Entomol. 87:311-323.

Renwick, J.A.A. 1967. Identification of two oxygenated terpenes from the bark beetles *Dendroctonus frontalis* and *Dendroctonus brevicomis*. Contrib. Boyce Thompson Inst. 23:355-360.

Renwick, J.A.A. and J.P. Vité. 1970. Systems of chemical communication in *Dendroctonus*. Contrib. Boyce. Thompson Inst. 24:283-292.

Ryker, L.C. and K.L. Yandell. 1983. Effect of verbenone on aggregation of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) to synthetic attractant. Z. angew. Entomol. 96:452-459.

Sartwell, C., R.F. Schmitz, and W.J. Buckthorn. 1971. Pine engraver, *Ips pini*, in the Western States. USDA, For. Serv. Pest Leaflet 122.

SAS 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, NC. pp. 647-653.

Schenk, J.A. and D.M. Benjamin. 1969. Notes on the biology of *Ips pini* in central Wisconsin jack pine forests. Ann. Entomol. Soc. Amer. 62:480-485.

Schmitz, R.F. 1972. Behavior of *Ips pini* during mating, oviposition, and larval development (Coleoptera: Scolytidae). Can. Entomol. 104:1723-1728.

Schmitz, R.F. 1979. Dispersal of pine engraver beetles in second growth ponderosa pine forests. In Dispersal of forest insects: evaluation, theory, and management implications. A.A. Berryman and L. Safrenyik (eds.). Proceedings of the Second IUFRO Conference, Sandpoint, Idaho, 27-31 August 1979. pp. 41-50.

Seybert, J.P. and R.I. Gara. 1970. Notes on flight and host-selection behaviour of the pine engraver, *Ips pini* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Amer. 63:947-950.

Stewart, T.E. 1975. Volatiles isolated from *Ips pini*: isolation, identification, enantiometric composition, biological activity. M. Sc. Thesis. College of Env. Sc. and For., State University of New York, Syracuse, New York.

Teale, S.A., F.X. Webster, A. Zhang, and G.N. Lanier. 1991. Lanierone: a new pheromone component from *Ips pini* (Coleoptera: Scolytidae) in New York. J. Chem. Ecol. 17:1159-1176.

Thomas, J.B. 1961. The life history of *Ips pini*. Can. Entomol. 93:384-390.

Thomson, A.J. and T.S. Sahota. 1981. Competition and population quality in *Dendroctonus rufipennis* (Coleoptera: Scolytidae). Can. Entomol. 113:177-183.

Unger, L. and A. Stewart. 1988. Forest insect and disease conditions. Prince Rupert Forest Region 1987. Can. For. Serv., Pac. For. Ctr., Victoria, British Columbia. FIDS 88-5.

Vité, J.P., A. Bakke, and J.A.A. Renwick. 1972. Pheromones in *Ips* (Coleoptera: Scolytidae): occurrence and production. Can. Entomol. 104:1967-1975.

Wood, D.L. 1972. Selection and colonization of ponderosa pine by bark beetles. In Insect plant relationships. H.F. van Emden (ed.). Blackwell, London. pp. 101-117.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.