COMPETITIVE INTERACTIONS BETWEEN THE SPRUCE BEETLE, *DENDROCTONUS RUFIPENNIS* KIRBY, AND TWO SECONDARY SPECIES, *IPS TRIDENS* MANNERHEIM AND *DRYOCOETES AFFABER* MANNERHEIM (COLEOPTERA: SCOLYTIDAE)

by

Therese M. Poland

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Examining Committee:

Chair: Dr. A. Beckenbach, Professor

Dr. J. H. Borden, Professor, Senior Supervisor
Department of Biological Sciences, SFU

Dr. G. Gries, Associate Professor
Department of Biological Sciences, SFU

Dr. L. Safranyik, Research Scientist
Pacific Forestry Centre, Canadian Forest Service

Dr. B. S. Lindgren, Associate Professor
Faculty of Natural Resources and Environmental Studies, UNBC

Dr. F. Breden, Associate Professor
Department of Biological Sciences, SFU
Public Examiner

Dr. T. Paine, Professor
Department of Entomology
Univ. of California, Riverside
External Examiner

Date Approved:

Abstract

The spruce beetle, *Dendroctonus rufipennis* Kirby, is the most destructive insect of mature spruce trees in Western North America. Interspecific competition by secondary scolytids has been found to be a significant mortality factor for the spruce beetle . *Ips tridens* Mannerheim and *Dryocoetes affaber* Mannerheim are the most common secondary species associated with the spruce beetle in Southern British Columbia. They are not considered to be economically important because they are generally unable to kill healthy trees. My ultimate objective was to determine the potential for managing the spruce beetle using semiochemical-induced competitive displacement or exclusion by *I. tridens* and *D. affaber*. I investigated the pheromone system of *I. tridens*, explored the role of semiochemicals in interspecific communication between the spruce beetle, *I. tridens*, and *D. affaber*, and tested the hypotheses that spruce beetle attack density and brood success are reduced in felled spruce trees that are baited with pheromones of the secondary species either after spruce beetle establishment or prior to spruce beetle attack. The pheromones for *I. tridens* were found to be ipsdienol and (-)-*cis*-verbenol. In field trapping experiments, *D. affaber* pheromones, ($\pm$)-*exo*- and (+)-*endo*-brevicomin, and *I. tridens* pheromones reduced attraction of the spruce beetle to frontalin and α-pinene as did individual components, (+) and ($\pm$)-ipsdienol, (+)- and ($\pm$)-*exo*-brevicomin, and (+)- and ($\pm$)-*endo*-brevicomin. Spruce beetle attack density, gallery length per m^2, and progeny density were significantly reduced in trees that were baited with *D. affaber* pheromones, or *D. affaber* pheromones plus *I. tridens* pheromones after spruce beetle establishment. Indirect interference with subsequent spruce beetle attacks and resource exploitation were the primary mechanisms of competition. Competitive effects were strongest when trees were baited prior to spruce beetle attack. Baiting individual felled spruce trees with pheromones of either or both secondary species, or the individual component ($\pm$)-*endo*-brevicomin prior to spruce beetle attack resulted in significantly reduced spruce beetle attack density, gallery length per m^2, and progeny density .

Baiting with *Ips tridens* pheromones also reduced spruce beetle attack and success in simulated patches of windthrown trees. Competitive exclusion of the spruce beetle may provide an alternative management tactic where traditional methods based on tree removal, widespread harvesting, and the use of insecticides are not feasible.

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1.0 General Introduction

1.1 Ecological and Economic Importance of Spruce Forests in British Columbia

British Columbia's spruce forests are extremely important to the province's natural history, wildlife ecology, environmental quality, and economy. They cover a large area of the province's forest land base and include forest types in four biogeoclimatic zones: Engelmann spruce - subalpine fir (ESSF); sub-boreal spruce (SBS); boreal white and black spruce (BWBS); and spruce-willow-birch (SWB). Within these forest types, the major tree species are Engelmann spruce, *Picea engelmannii* Parry, white spruce, *Picea glauca* (Moench.) Voss., hybrid white spruce, *Picea engelmannii* x *glauca*, and subalpine fir, *Abies lasiocarpa* (Hook) Nutt (Meidinger et al. 1991)

The ESSF is the highest elevation forest zone of the southern three quarters of the B.C. interior. It ranges in elevation from 900 to 1700 m in northern locations and from 1200 to 2300 m in southern B.C. (Coupé et al. 1991). Spruces are usually the most abundant trees in mature stands. At high elevations and in some wet areas subalpine fir can dominate the forest canopy. Lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, is a widespread seral species after fire, and can be dominant in the driest regions of the zone (Coupé et al. 1991). Old growth Engelmann spruce - subalpine fir forests in B.C. are the most productive regions for grizzly bears and fur-bearers including martins, fishers, red-squirrels, and wolverines. Ungulates, including moose, caribou, and black-tailed deer are also abundant in this zone. During the winter, caribou and black-tailed deer feed exclusively on arboreal lichens, which are abundant on old, slow-growing spruce trees (Bunnel and Kremsater 1990). At least 23 species of primary and secondary cavity nesting species depend on snags that are common in old growth spruce forests. Ungulates, snowshoe hares, grizzly and black bears, and several species of birds are common in young seral stands of the ESSF (Coupé et al. 1991).

Much of central B.C. falls within the SBS biogeoclimatic zone. It occurs at low and medium elevations ranging from valley bottoms up to 1100 to 1300 m. In the high parts of the SBS, hybrid white spruce and subalpine fir are the dominant climax tree species. At low elevations and in warm and dry regions, subalpine fir is replaced by lodgepole pine, Douglas-fir, *Pseudotsuga menzeisii* (Mirb.) Franco, birch, *Betula* spp., and willow, *Salix* spp. (Pojar et al. 1984). Sub-boreal spruce forests are the center of abundance for moose in B.C. Mammals including caribou, gray wolf, fisher, martin, and ermine as well as many birds such as the pine siskin, magnolia warbler, great grey owl, and boreal owl are abundant in old growth forests of the SBS. Moose, mule deer, voles, mice and predatory birds such as northern hawk owls are prevalent in early successional scrub (Pojar et al. 1991).

The BWBS zone is the most widespread zone in Canada, occurring from the Yukon territory across all the provinces to Newfoundland. It occurs in the northeastern portion of B.C. north from 54° N latitude and at elevations from 230 to 1300 m. White spruce, lodgepole pine, black spruce, *Picea mariana* (Mill.) B.S.P., subalpine fir, and trembling aspen, *Populus tremuloides* Michx., are the most common tree species. Despite a harsh climate, the BWBS zone is relatively rich in wildlife, including moose, caribou, mule deer, a wide selection of birds such as warblers and thrushes, and a variety of small mammals (DeLong et al. 1991).

The SWB zone is the most northerly subalpine zone in B.C., occurring north from 57° N latitude well into the Yukon territory. It ranges in elevation from 1100 to 1700 m in southern portions and from 900 to 1500 m in the northern part of the zone. At low elevations white spruce and sub-alpine fir are the dominant species. Upper elevations consist essentially of a scrub parkland dominated by deciduous shrubs including scrub birch, *Betula glandulosa*, and grey-leaved willow, *Salix glauca*. The SWB has the harshest climate of all the forested zones in B.C. Moose and caribou are the most abundant ungulates but they abandon much of the zone by mid-winter (Pojar and Stewart 1991).

Sub-boreal forests consist of a mosaic of microsites which may be in different states of successional development. The entire forest can be considered more or less stable and in dynamic balance with regional climate and disturbance regimes. The major natural disturbance in sub-boreal regions is recurrent fire (Pojar et al. 1984). It has been estimated that any given stand in the sub-boreal spruce forest would have burned at least once every 300 years, and most stands probably every 100 years (Rowe and Scotter 1973; VanWagner 1978; Stokes and Dietrich

1980). Past forest fires have been a dominant factor in determining the natural regeneration and distribution of tree species and in determining the pattern of ecosystem development over the sub-boreal landscape. The extent and impact of forest fires have been greatly reduced due to modern fire suppression activities (Pojar et al. 1984). Fire suppression efforts decrease the proportion of stands in early seral stages and result in a trend toward a homogenous pattern of communities across the landscape (Perry 1988; Hann 1990). Some of the impact of previously widespread wildfire has been taken up by industrial forestry in which clearcutting, often followed by broadcast burning, at least partially mimics the effects of natural fire (Pojar et al. 1984).

Spruce forests in the ESSF and SBS are very important for timber production in B.C. (Coupé et al. 1991; Pojar et al. 1991). Timber harvesting is relatively active in the BWBS but no harvesting occurs in the SWB (DeLong et al. 1991; Pojar and Stewart 1991). In 1995, 13 million m^3 of spruce were harvested, making up 26% of the total volume harvested in the interior and 19% of the provincial harvest (BCFS 1995). Contributions of spruce and subalpine fir to B.C.'s timber harvest are becoming increasingly important because of growing demands for forest products and the intensive past use of low elevation forests.

Spruce forests are also important for watershed quality. Through transpiration and interception of precipitation, trees influence water levels in rivers, lakes and streams (Holsten 1991). Watersheds and forested landscapes contribute to aesthetic quality and recreational opportunities throughout B.C. Many of B.C.'s provincial and national parks include ruggedly scenic portions of the ESSF. In the ESSF and SBS skiing, hiking, mountaineering, hunting, camping and fishing are important resource values (Coupé et al. 1991; Pojar et al. 1991). Hunting and trapping are the primary activities in the BWBS and SWB zones (DeLong et al. 1991; Pojar and Stewart 1991).

1.2 Biology, Chemical Ecology, Impact and Management of the Spruce Beetle

The spruce beetle, *Dendroctonus rufipennis* Kirby, is the most destructive insect pest of mature spruce forests in Western North America. It attacks all native species of spruce in its range. In northern B.C., overmature white spruce, Engelmann spruce and their hybrids are the preferred hosts (Safranyik 1988). At sub-outbreak levels, windthrow protected from the sun under the forest canopy is the primary source of breeding material. In cool, wet, shady areas, the bole of a downed tree may be attacked for most of its length. In windthrow, slash, or stumps exposed to the sun, most attacks occur on the underside or at the duff line. Standing trees stressed by drought, fire, flooding, disease, or physical damage may also be attacked. During favorable conditions, populations can build up to epidemic levels and beetles may attack healthy standing trees over extensive areas (Schmid and Frye 1977).

Overwintering beetles emerge as adults and fly in search of new hosts when air temperatures reach a threshold of 16 °C (Dyer 1973). Beetle flight lasts from early May through to the end of August, usually with a peak sometime in June and a second peak in July (Beckwith 1972; Dyer 1975). Spruce beetles are strong fliers, potentially capable of dispersing over long distances. Non-stop flights exceeding 11 km have been recorded on flight mills (Chansler 1960).

In B.C. spruce beetles usually have a two year life cycle; some populations may mature in one or three years depending on geographic location, and microclimatic conditions. The species is monogamous and females are the pioneer sex. They initiate attacks on suitable hosts and bore egg galleries underneath the bark in the phloem tissue. Larvae feed in the phloem, forming a common feeding front or individual galleries. Larvae develop through four instars and then pupate. Beetles may overwinter *in situ* as larvae, pupae, or adults. In standing trees, varying proportions of adult beetles emerge, drop to the base of the tree and burrow into the duff or bore into the root collar of the tree to overwinter (Safranyik 1988). In downed timber or stumps, adults overwinter *in situ*. All beetles must overwinter as adults before becoming reproductively mature (Safranyik 1983).

Spruce beetles vector mutualistic blue stain fungi belonging to the genera *Ophiostoma* or *Ceratocystis* (Safranyik and Linton 1983; Reynolds 1992). In live trees, bark beetles depend on the symbiotic fungi to overcome tree defenses and render the phloem suitable for brood development (Whitney 1982). Once introduced into the tree, the fungi spread rapidly through the phloem, disrupting water transport and killing the tree. Resulting brood mortality from defense mechanisms such as resinosis is thereby decreased (Berryman 1989). Without water translocation, phloem desiccates and gas exchange is disrupted, which also favors brood development (Whitney 1982). Colonization by fungi may also play a role in providing cues for the horizontal orientation of larval mining, setting boundaries to deter colonization by other species of scolytids, and providing a measure of phloem suitability for oviposition by females and for determining length of larval galleries (Fox et al. 1992).

Semiochemicals play an important role in host location by bark beetles. Insect- and host-produced volatiles provide cues to host-seeking beetles which aid in evaluating a potential host based on whether it is an appropriate host species, whether it is susceptible or resistant to attack, and whether an adequate amount of suitable phloem is available for successful colonization or if the tree is already fully colonized by con- or heterospecific competitors (Borden 1996).

Spruce beetles are attracted to volatiles from white spruce (Moeck 1978) indicating a long-range influence of primary attraction in host selection. Two host kairomones, α-pinene (Dyer and Lawko 1978; Furniss et al. 1976) and ethanol (Moeck 1981) have been implicated in spruce beetle attraction. Spruce beetles also rely on secondary attraction by insect-produced semiochemicals to aid in the location of suitable hosts. Female beetles produce frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane) (Gries et al. 1988), seudenol (3-methyl-2-cyclohexen-1-ol) (Vité et al. 1972), MCOL (1-methyl-2-cyclohexen-1-ol) (Wieser et al. 1991), and verbenene (4-methylene-6,6-dimethylbicyclo[3.2.1]hept-2-ene) (Gries et al. 1992). Frontalin plus α-pinene attracts spruce beetles to traps (Furniss et al. 1976) and can be used to contain and concentrate an infestation in a grid-baited stand prior to sanitation-salvage harvesting (Shore et al. 1990). Addition of seudenol did not enhance attraction to frontalin (Dyer and Lawko 1978). Responses to MCOL and verbenene were regionally specific when tested in trapping experiments (Borden et al. 1996). (±)- or (+)-MCOL was highly attractive in Alaska, only (+)-MCOL was attractive in south-central B.C. and MCOL of any chirality was weakly attractive in southeastern B.C. or northern Alberta and in recent results (Setter, personal communication) in north central B.C. Verbenene was attractive only in Alaska.

Late in the colonization process antiaggregation pheromones are produced to deter additional beetles from attacking and overcrowding a mass-attacked tree (Borden 1982). The spruce beetle produces the antiaggregation pheromone, 3,2-methylcyclohexenone (3,2-MCH) (Rudinsky et al. 1974) which is effective in repressing spruce beetle attraction to female-infested logs (Kline et al. 1974) and to frontalin or seudenol (Furniss et al. 1976).

Normally trees resist invasion by beetles and blue stain fungi by a nonspecific reaction which involves primary resinosis, necrosis of the wounded area, development of callus tissue, wound periderm and resin-producing tissue, and eventual secondary resin envelopment which occurs only in fully resistant trees (Safranyik 1983). Spruce beetles are apparently able to recognize and attack trees under moisture stress. They normally prefer downed host materials or weakened decadent trees. Successful establishment in living tissue appears to depend on the speed of colonization by beetles and their blue stain fungi. Large numbers of beetles and the presence of susceptible stands can lead to attack of healthy standing trees and large epidemics (Safranyik 1983).

Spruce beetle outbreaks usually develop during hot dry years following extensive blowdown or large accumulations of suitable logging slash. However, these conditions do not necessarily result in outbreaks. Outbreaks are dependent on the interaction of beetle population size, density and spatial distribution of host material, and temperature conditions (Safranyik et al. 1990). When emergence of the beetle population from large-scale windthrow coincides with increased stand susceptibility, widespread outbreaks develop (Safranyik 1983). They average approximately four years in duration, during which most of the large-diameter trees are attacked and killed (Werner and Holsten 1983). Slow-growing trees of the largest diameter classes are most susceptible and are attacked first. As the outbreak continues and populations build, increasing numbers of fast-growing, small diameter trees are attacked and killed (Hard et al. 1983).

Spruce beetle outbreaks in B.C. have been reported since the 1940s. At that time over 37,500 ha were infested, killing an estimated 879,000 m^3 of spruce. Since then periodic major outbreaks have occurred. In the 1960s over 14 million m^3 of spruce were killed in the Prince George and Prince Rupert Forest Regions. In the late 1970s more than 60,000 ha were infested in the Bowron, Willow, and McGregor river drainages. Large-scale salvage operations were undertaken, removing over 2 million m^3 of mature spruce (Wood et al. 1987). After eight years of restocking, with over 5 million seedlings planted, this area is now considered the largest contiguous plantation in North America. In the Prince George Forest Region a resurgence of spruce beetle activity was recorded in 1990 and 1991. Between the years 1990 and 1993 171,060 ha of mature spruce have been infested (Wood and Van Sickle 1991, 1992, 1993a,b). The spruce beetle continues to threaten mature and healthy spruce in British Columbia and recurring large-scale outbreaks are inevitable where fire protection has resulted in large homogenous stands of overmature spruce. Catastrophic spruce beetle infestations result in enormous economic losses due to reduced revenue as a result of unsalvaged timber losses, degraded lumber values, reduced stumpage values, degradation of non-timber resources, disruptions in forest planning, and long term impacts on timber supply.

In addition to the direct effects of mortality (and related harvesting activities), spruce beetle outbreaks affect tree growth rates and establishment patterns, which in turn may alter stand productivity, structure, and composition. Severe beetle outbreaks shift dominance of spruce-fir forests towards subalpine fir. The shift in species composition was found to be accompanied by an overall reduction in live basal area in Colorado (Veblen et al. 1991). New seedling establishment is scarce because of the presence of advance regeneration of shade-tolerant trees and the lack of bare mineral soil and seeds. Subalpine fir is typically more abundant than spruce as a subcanopy tree. Therefore, recruitment of subalpine fir into the canopy is favored after a spruce beetle outbreak. However, the subalpine fir dominance is short lived because it becomes susceptible to pathogenic fungi (Schmid and Hinds 1974) and the western balsam bark beetle, *Dryocoetes confusus* Swaine, as it reaches maturity (Stock 1991). Subcanopy trees of both spruce and fir grow into the canopy gaps. Due to its greater maximum size and longevity, spruce eventually regains basal area dominance and the stand becomes increasingly susceptible to another major spruce beetle outbreak. Thus, in old growth spruce - fir forests, periodic spruce beetle outbreaks and wave-like oscillations in species dominance and basal area are common in the absence of fire (Schmid and Hinds 1974).

Between spruce beetle outbreaks, a gap dynamics disturbance regime is hypothesized (Stock 1991). Indigenous low-level spruce beetle populations create gaps by killing one or two dominant spruce trees. Shade-tolerant subalpine fir matures in the small openings with little advance regeneration growing under its dense canopy. The western balsam bark beetle then kills the resultant pockets of mature sub-alpine fir allowing less tolerant spruce to regenerate in the larger open gaps.

The massive mortality of canopy trees from beetle infestations has a major influence on the forest ecosystem. For instance, wildlife habitat, watershed relationships, biodiversity, ecosystem resilience, and scenic quality are affected in beetle-impacted areas. Plant composition changes following spruce beetle outbreaks may benefit some wildlife such as moose (Werner and Holsten 1983); however, animals such as bear, deer, and caribou, that depend on mature spruce for habitat may be adversely affected. Mortality of canopy trees causes water gains in rivers, lakes and streams (Holsten et al. 1991). Dead, red-topped trees and gray snags detract from scenic quality and constitute a safety hazard, thus reducing the quality of recreational areas. Fire risks also increase after spruce beetle outbreaks due to the increased rates of spread, probability of ignition, and high burning index (Werner and Holsten 1983). In 1994 my field research fell victim to such a fire.

Historically, spruce beetle populations have been managed by initiating action after infestations reached outbreak status. Techniques used for management are based on survey, detection, and treatment (Forest Practices Code of B.C. Act 1995a). Detection is carried out through aerial and ground surveys. An overview flight is completed first and is a broad reconnaissance of a Forest District using fixed-wing aircraft. The location and extent of damage caused by bark beetles and other agents are recorded and sketched onto 1:50,000 maps. Additional detailed flights are conducted using fixed- and rotary-wing aircraft. Color aerial photographs at scales no smaller than 1:15,000 are taken to facilitate intensive ground probing. Ground surveys are required to determine the exact location of infestations and the number of current year's (green) attacks. Infested trees are marked along a flagged path according to year of attack and action required. In addition, blowdown may be surveyed by removing sections of bark and recording the number of spruce beetle entrance holes, larvae, pupae, callow adults, and parent adults (B.C.F.S. 1994).

Ground probe data indicating the extent of infested area and the stage of infestation allow treatment protocols to be prescribed. Treatment options currently available include sanitation and salvage cutting, conventional and lethal trap trees, felling and burning, single tree chemical treatment with monosodium methane arsenate (MSMA), bark peeling, or no treatment. The most commonly used tactics are sanitation and salvage cutting, and felled trap trees (B.C.F.S. 1994).

Salvage cuts remove stands of timber after beetle infestations have killed or seriously damaged many trees. The purpose of salvage cutting is to retain as much value as possible from the timber before it deteriorates (Smith 1986). If salvaged trees are removed from overmature stands that are not increasing in value, there is a subsequent gain of production, because vacancies will be claimed by young vigorous trees. Plantations that replace large clear cuts may grow exponentially, but unlike mature stands they often lack the characteristics required to support diverse wildlife.

Sanitation cuts remove recently infested and susceptible trees to reduce pest populations and protect surrounding trees. Sanitation cuts may take the form of light partial cuts or may be combined with salvage operations with the intent of removing as many beetles as possible with the trees (Smith 1986).

In northern B.C., most sanitation and salvage operations are restricted to winter when wet sensitive soils are frozen and protected by snow. However, at this time much of the beetle population may be overwintering in the duff or base of trees and is also protected below the snow. A significant proportion of the population may, therefore, be left behind in logging slash and stumps. In the following spring, increased temperatures in clearcut areas may lead to synchronous emergence and flight of beetles, resulting in increased beetle pressure on surrounding forest margins. Blowdown is plentiful along the margins of cutblocks; therefore, breeding material is available over long periods of time. Favorable climatic conditions can then lead to recurrent outbreaks and the necessity to expand cutblocks with successive sanitation-salvage cuts.

The primary purpose of trap trees is to attract flying beetles away from living trees (Nagel et al. 1957). The brood developing in trap trees is subsequently destroyed by removing and milling or burning the trees, or by chemical treatment. All trap trees for the spruce beetle are living, large diameter host trees felled into the shade before the beetle flight period and left unlimbed and unbucked (Hodgkinson 1985). Adequate numbers of trap trees must be felled in appropriate locations to protect standing trees. In accessible locations, trap trees are removed and processed before the next beetle emergence period. In inaccessible areas, trap trees must be treated with approved insecticides to kill beetles under the bark (Hodgkinson 1985). Operational trap tree programs often suffer from reduced effectiveness due to poor selection of trap trees, felling trap trees in unsuitable locations, and failing to remove trap trees prior to beetle emergence. Trap tree programs are very costly because two entries are required, one for felling, and one for extraction. In inaccessible areas, helicopters are required to drop crews to poison lethal trap trees and then to fell them (Hall 1985).

In British Columbia, the extent to which current management tactics can be practiced is limited by forest practice regulations that restrict the size of cutblocks and prohibit harvesting and the use of conventional insecticides within riparian management zones (Forest Practices Code of B.C. Act 1995b). New strategies are needed for spruce beetle management that are compatible with forest practice regulations and that promote forest health, biodiversity, and all resource values including timber production.

1.3 The Role of Interspecific Competition in Spruce Beetle Mortality

Interspecific competition can be exploited for pest management if an economically important pest species can be artificially replaced by a less aggressive, secondary species (Payne and Richerson 1985; Borden 1992).

Competition occurs when a number of organisms utilize a scarce resource; or if the resource is not limited, competition occurs if the organisms seeking the resource harm each other in the process (Birch 1957). Because most bark beetles feed and breed completely enclosed within the spatially-restricted inner bark of the bole of their host trees, intra- and inter-specific encounters are maximized, thereby promoting competition (Stiling and Strong 1984). Although some species, such as the pine engraver, *Ips pini* Say, and *Pityogenes knechteli* Swaine, may apparently infest the same habitat without competing (Poland and Borden 1994), interspecific competition can decrease brood production and increase mortality in many bark beetle species. Competition by *Pityophthorus pseudotsugae* Swaine was found to be a significant mortality factor for the fir engraver, *Scolytus ventralis* LeConte (Stark and Borden 1965). *Pityokteines elegans* (Swaine) may also regulate the abundance of the fir engraver, especially during the final stages of an outbreak when it serves as an important factor in the rate of decline of fir engraver populations to sub-outbreak levels (Ashraf and Berryman 1969; Berryman 1973). The presence of small southern pine engravers, *Ips avulsus* Eichhoff, reduced the area of phloem colonized by the southern pine beetle, *Dendroctonus frontalis* Zimmerman (Paine et al. 1981) and significantly reduced the number of emergent *D. frontalis* in lightning struck trees (Hodges and Pickard 1971). Interspecific competition between *I. pini* and the California fivespined ips, *Ips paraconfusus* Lanier, resulted in reduced larval survivorship and numbers of emergent brood of both species (Light et al. 1983).

Interspecific competition by secondary scolytids has been found to be a major mortality factor for the spruce beetle. For instance, competition for food by secondary species, including *Scierus annectans* LeConte, the four-eyed spruce beetle, *Polygraphus rufipennis* Kirby, and *Ips* spp., primarily *Ips pilifrons* Swaine, was a major cause of spruce beetle larval mortality and contributed to the decline of a small outbreak in Colorado (McCambridge and Knight 1972).

The spruce beetle is also associated with numerous other natural enemies including avian predators such as northern three-toed, hairy, and downy woodpeckers (McCambridge and Knight 1972), nematodes (Massey 1956) and arthropod predators and parasites (Whitmore 1983, Gara et al. 1995). Natural enemies may help to regulate spruce beetle populations at sub-outbreak levels. The most important mortality factor for spruce beetle larvae in felled Alaskan white spruce was interspecific competition by secondary scolytids, especially *Dryocoetes affaber* Mannerheim. The impact of dipteran and coleopteran predators and hymenopteran parasites on spruce beetle survival was of less importance than interspecific competition (Whitmore 1983; Gara et al. 1995).

Wood boring beetles in the families Cerambycidae and Buprestidae also feed beneath the bark of spruce trees. Larvae mine extensively in the phloem before entering the sapwood and heartwood of dying or dead trees. They may cause severe damage to wood and wood products due to larval tunnels and the establishment of wood staining and decaying fungi (Safranyik and Moeck 1995). They may also compete with bark beetles while tunneling in the limited phloem resource. For instance, the cerambycid *Monochamus titillator* was found to be a potential competitor of southern pine beetle larvae in the inner bark tissue (Coulson et al. 1976).

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

If secondary species can be induced by semiochemicals to pre-empt the resource and outcompete or exclude the spruce beetle, the phenomenon would have considerable potential for spruce beetle management and prevention of large-scale outbreaks. Such an effect has been demonstrated experimentally for *I. pini*, a secondary bark beetle capable of outcompeting the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, a major pest of lodgepole pine (Rankin and Borden 1991; Safranyik at al. 1995, 1996).

1.4 Biology and Importance of Secondary Bark Beetles Associated with the Spruce Beetle

The spruce beetle is frequently associated with several species of secondary bark beetles including *Ips tridens* Mannerheim, *Ips perturbatus* Eichhoff, *D. affaber, P. rufipennis*, and *S. annectans* (Whitmore 1983; Werner and Holsten 1984). The secondary species are not generally considered to be economically important because they are incapable of killing healthy trees; they attack only downed material or trees which have already been overcome and killed by the spruce beetle (Bright 1976). Interactions among all associated species within the phloem resource may be important in influencing their population dynamics and sucesss. I restricted my investigations to the interactions between the spruce beetle, *I. tridens*, and *D. affaber* because *I. tridens* and *D. affaber* are the most common secondary species in southern and interior B.C. and both secondary species have been successfully captured in semiochemical-baited traps (Moeck 1983; Camacho et al. 1994). Therefore, among the secondary associates of the spruce beetle, *I. tridens* and *D. affaber* were most amenable to semiochemical-based studies and population manipulations. An aggregation pheromone is also known for *P. rufipennis* (Bowers 1991). Therefore, *P. rufipennis* was included in initial experiments; however, insufficient numbers were captured to allow for data analysis and it was not included in subsequent experiments.

Ips tridens ranges from the Rocky Mountains west to the Pacific, from Alaska to northern California. It infests all native *Picea* spp., including Sitka spruce, *Picea sitchensis* (Bong.) Carr., white spruce, Engelmann spruce, and their hybrids (Bright and Stark 1973). It is generally not economically important because it preferentially attacks windthrown trees, logging slash, or trees that are severely weakened by fire, flooding, drought or physical damage (Bright 1976). However, it breeds abundantly in the tops of trees that have been killed by the spruce beetle, and has recently been reported killing young white spruce in Alaska following heavy thinning and pruning treatments and selective logging to minimize spruce beetle-caused tree mortality and reduce fuel ladders in sensitive areas (Holsten et al. 1996).

Flight by *I. tridens* begins in May, and attacks by re-emerging parent adults continue through July. Males are polygamous and are the pioneer sex, initiating attacks on suitable hosts, and attracting both males and females to the breeding site (Bright and Stark 1973). Each male is joined by four to six females which construct egg galleries approximately parallel to the grain. Egg galleries usually appear in contiguous pairs with only a thin septum of phloem between them (Hopping 1965). Eggs are laid in niches along the sides of the galleries. Larvae mine in the phloem, engraving the xylem, and pass through four larval instars before pupating. At low elevations on the coast, teneral adults may emerge and initiate new attacks, resulting in two complete generations annually. At higher elevations and further north *I. tridens* is univoltine; parent beetles may produce two or three successive broods but new adults do not participate in attacks. Teneral adults feed in the brood host through the summer and either overwinter *in situ* or emerge to overwinter in the forest litter (Bright and Stark 1973).

Dryocoetes affaber is the most widespread member of its genus in North America; its distribution is transcontinental in Canada, and it ranges from Alaska south to New Mexico (Bright 1976). It infests mainly *Picea* spp., but has also been reported from *Pinus* spp., *Larix* spp., and *Abies* spp. The males are the pioneer sex and are polygamous. They locate suitable hosts, excavate an entrance hole and nuptial chamber, and produce aggregation pheromones to attract three or four females. Each female constructs an egg gallery radiating from the nuptial chamber (Bright 1976; Furniss and Carolin 1977). Little is known about the life cycle of *D. affaber*; however, it appears to have one generation per year in Colorado where it overwinters as an adult (McCambridge and Knight 1972). Flight activity by *D. affaber* began at the end of May or early June following snowmelt and rose to a peak in mid-July to early August and continued well into September near Merritt, B.C. (Camacho-Vera 1993).

1.5 Thesis Objectives

There were three general objectives in my thesis research: 1) to identify the pheromones of *I. tridens*; 2) to explore the roles of semiochemicals in interspecific communication between the spruce beetle and two associated secondary scolytids, *I. tridens* and *D. affaber*; and 3) to determine the potential for developing tactics of managing the spruce beetle using semiochemical-induced competitive displacement or exclusion.

2.0 Identification of Aggregation Pheromones for *Ips tridens*

2.1 Introduction

To maximize the potential for semiochemical-based management, optimal pheromone blends should be used. Often a complex blend of species-specific pheromones is required for optimal attraction. Tactics involving semiochemical-induced competitive displacement or exclusion of the spruce beetle by *I. tridens* and *D. affaber* may require the use of species-specific pheromones for the secondary species. The enantiospecific blend for attracting *D. affaber* has been well studied and the optimal blend determined (Camacho-Vera 1993). In British Columbia, *I. tridens* was attracted by (±)-ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) and (-)-*cis*-verbenol (*cis*-4,6,6-trimethyl-bicyclo[3.1.1]hept-3-en2-ol), two components of the commercial pheromone lure for the European spruce bark beetle, *Ips typographus* (L.) (Moeck et al. 1985). However, production of, and response to, pheromones in *I. tridens* has not been investigated. Alternative or additional pheromones may be produced by *I. tridens* that might enhance *I. tridens* attraction.

With the prospect of developing semiochemical-based management of the spruce beetle using competitive displacement or exclusion by secondary species (including *I. tridens*), my objectives were: 1) to identify the major antennally active volatiles produced by *I. tridens* males feeding in hosts and exposed to host vapors; 2) to determine the most attractive combination of the insect-produced volatiles for *I. tridens*; and 3) to determine the effect of exposure to spruce beetle semiochemicals (frontalin and α-pinene) on the response of *I. tridens* to its aggregation pheromone.

2.2 Materials and Methods

2.2.1 Collection of Insects and Host

Engelmann spruce bolts, both uninfested and infested with *I. tridens*, were obtained from trees felled near Princeton, B.C. The infested bolts were placed in screen cages at approximately 20°C. Emerging beetles were collected from the cages daily, separated by sex, and held on layers of moistened tissue paper in sealed jars at room temperature for up to five days.

2.2.2 Collection and Analysis of Volatiles

Three fresh Engelmann spruce bolts into which artificial entrance holes [1.5 mm internal diam (ID)] had been drilled were placed in separate glass chambers (28 cm long, 15 cm ID). One hundred and fifty male *I. tridens* were placed on one bolt, 150 females on another, and the third was left as an uninfested control. Beetles were allowed to select their own attack sites and feed in the phloem. Humidified air was drawn for 7 days at 2 L/min through a charcoal filter, the chamber, and a glass trap [20cm x 13 mm outside diam. (OD)] containing Porapak-Q (Byrne et al. 1975). Volatiles were eluted from the trap with distilled pentane and the eluent was concentrated to ca. 5 mL by distilling off solvent through a Dufton column.

Whole body extracts were prepared from 20 beetles of each sex exposed to the host compound α-pinene. Twenty glass cylinders (2:0 cm OD and 2.0 cm high) were arranged in each of two 14 cm diam. glass petri dishes. A 100 μg dose of (±)-α-pinene diluted in pentane to 10 μg per μl was delivered on filter paper placed in the bottom of each glass cylinder, making up a dose of 2.0 mg of α-pinene per dish. The petri dish was closed with a moist filter paper-lined lid and vapors were allowed to dissipate for 5 min. One beetle was dropped into each cylinder with males and females in separate petri dishes. The covered petri dishes were stored in a dark cupboard at approximately 20 °C for 24 h. Beetles were then removed and crushed in distilled pentane contained in a vial set on dry ice. After removal from the dry ice the extract was allowed to warm to room temperature and the supernatant was transferred to a clean vial. The extract was concentrated to ca. 100 μl under a stream of nitrogen and placed on glass wool in a small glass chamber to which a Porapak-Q trap (6 mm OD packed with ca. a 30 mm length of absorbent) was attached. The volatiles were transferred from the glass wool to the

Porapak-Q with nitrogen for 30 min and recovered by eluting the Porapak-Q trap with 1 mL of pentane.

The whole body extracts and volatiles from aerated logs were analyzed by gas chromatography (GC) using Hewlett Packard 5830A and 5890A instruments equipped with capillary inlet systems, flame-ionization detectors, and fused silica columns (30 m x 0.25 mm ID) coated with SP-1000 (Supelco, Bellefonte, Pennsylvania) or DB-5 (J &W Scientific Inc., Folsom, California). Coupled GC-mass spectrometry (GC-MS) was performed with a Hewlett Packard 5895B instrument fitted with a fused silica column (30 m x 0.25 mm ID) coated with SP-1000. Mass spectra were compared with those of authentic samples to confirm compound identification. The enantiomeric composition of male *I. tridens* produced ipsdienol was determined by GC analyses using a Cyclodex-B column (30 m x 0.25 mm ID) (J & W Scientific, Folsom, California).

Captured volatiles were also subjected to coupled gas chromatographic-electroantennographic detection (GC-EAD) analyses (Arn et al. 1975) adapted for intact bark beetles (Gries 1995). Responses of female *I. tridens* antennae to compounds of interest were verified with at least two antennae. For GC-EAD analyses a DB-23 (30m x 0.32 mm ID) (J & W Scientific, Folsom, California) column was employed.

2.2.3 Laboratory Experiments

Behavioral activity of the antennally active components identified in the aeration volatiles was determined through single-choice bioassays in an open arena olfactometer (Stock and Borden 1983). Groups of 10 males or 10 females were released in the center of a filter paper arena (18.5 cm diam.) and the beetles were allowed 2 min to walk upwind against a gentle stream (500 mL per min) of medical air, released through a filter paper-lined glass tube (1.0 cm diam.) impregnated with test compounds diluted in pentane or a pentane control. Beetles that entered an area within 2 cm of the outlet of the glass tube were classed as responders. Bioassays were conducted over a 4 day period with various combinations and doses of (±)-ipsdienol and amitinol (*trans*-2-methyl-6-methylene-3,7-

octadien-2-ol), with all treatments as well as pentane control stimulus tested on any particular day. Fifty beetles of each sex were tested to each experimental treatment and 200 beetles of each sex were tested against the pentane control stimulus.

(±)-Ipsdienol (96.9% pure) was purchased from Phero Tech Inc., Delta, B.C. Amitinol was prepared by the method of Francke et al. (1980) from (±)-ipsdienol (BRI, Danbury, Connecticut) and purified to 98% by flash chromatography on silica gel using pentane-ether (2:1, v/v) as eluent (H.D. Pierce, Jr., Dept. of Biological Sciences, S.F.U.).

2.2.4 Field Experiments

Trapping experiments were conducted in a forest of Engelmann spruce, subalpine fir, and lodgepole pine 60 km west of Princeton, B.C. Candidate pheromones were tested in 12-unit multiple funnel traps (Lindgren 1983) (Phero Tech, Inc.) placed 15 m apart in randomized complete blocks. Compounds were released from bubble cap or Eppendorf tube dispensers (Phero Tech, Inc). (±)-Ipsdienol and *cis*-verbenol [83% R-(-)] were released from bubble caps at 0.2 and 0.6 mg per 24 h, respectively. Butanediol was added to ipsdienol as a stabilizer. Amitinol was released from bubble caps at 0.02 mg per 24 h with butanediol added as a stabilizer (Phero Tech, Inc.). Spruce beetle baits consisted of frontalin released at 2.6 mg per 24 h from 0.5 mL Eppendorf tubes and α-pinene released at 1.5 mg per 24 h from 1.5 mL Eppendorf tubes.

Experiment 1, conducted from 7 - 21 July 1995 tested *I. tridens* responses to antennally active volatiles individually and in all possible combinations that contained the major component, ipsdienol. It comprised seven replicates of seven treatments: 1) unbaited control; 2) ipsdienol; 3) *cis*-verbenol; 4) amitinol; 5) ipsdienol and *cis*-verbenol; 6) ipsdienol and amitinol; and 7) ipsdienol, *cis*-verbenol, and amitinol.

Experiment 2, conducted from 3 - 11 July 1996 tested whether or not the addition of attractants for the spruce beetle interfered with the attraction of *I. tridens* to its own pheromone. Spruce beetle lures consisted of a 1.5 mL Eppendorf tube containing α-pinene released at 1.5 mg per 24 h and a 400 μl tube containing frontalin released at 2.6

mg per 24 h (Phero-Tech, Inc.). The experiment comprised 10 replicates of six treatments: 1) unbaited control; 2) spruce beetle lure; 3) ipsdienol and *cis*-verbenol; 4) ipsdienol, *cis*-verbenol, and amitinol; 5) spruce beetle lure combined with ipsdienol and *cis*-verbenol; and 6) spruce beetle lure combined with ipsdienol, *cis*-verbenol, and amitinol.

2.2.5 Statistical Analyses

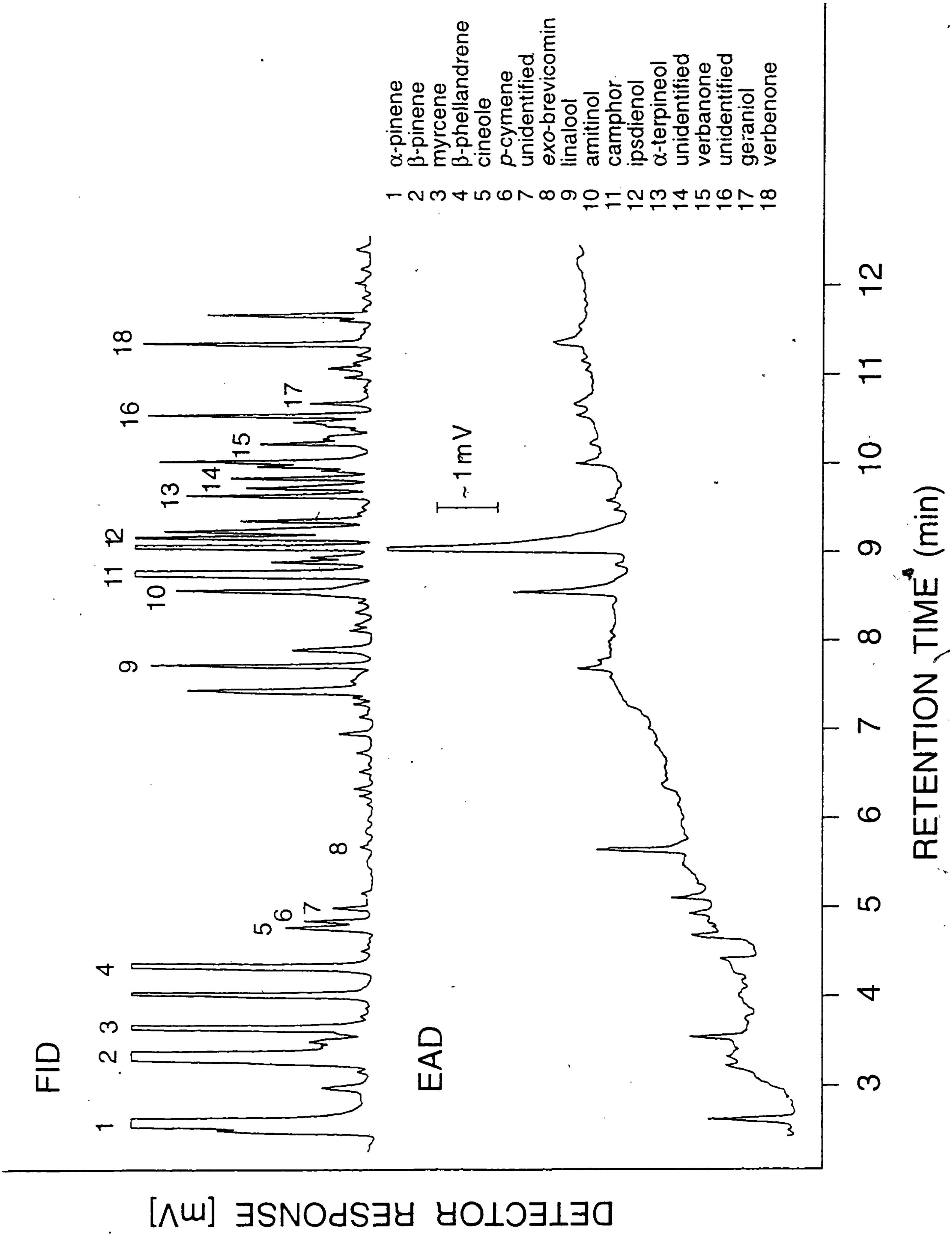
Percentages of beetles responding in laboratory bioassays were analyzed by a chi-square test comparing responses to test volatiles with the average response to pentane over the testing period. Data from the field experiments were transformed by $x' = \log (x + 1)$ to satisfy assumpations of normality and homoscedasticity (Zar 1984) and then analyzed using ANOVA for randomized complete block design treating replicates as blocks. Treatment means were compared by the Ryan-Einot-Gabriel-Welsch (REGW) multiple *F*-test. In these and all subsequent experiments, normality and homoscedasticity of transformed data were verified by examining residual plots and employing Bartlett's test (Zar 1984). In all cases $\alpha = 0.05$. All analyses employed SAS computer software (SAS Institute 1990).

2.3 Results

2.3.1 Identification of Candidate Pheromones

GC-Analysis of volatiles from aerated logs revealed the presence of ipsdienol and amitinol produced by male *I. tridens*. The enantiomeric composition of ipsdienol was found to be 82 % (*R*)-(-) by GC analysis using a chiral column. Ipsdienol and amitinol consistently elicited antennal responses in GC-EAD analyses (Figure 1). *exo*-Brevicomin (*exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane) was also produced by male *I. tridens* and consistently elicited antennal responses. However, its identity was not confirmed until after completion of all behavioral laboratory and field experiments, therefore, its role remains unknown. Several host compounds, including α-pinene, β-

Figure 1. Representative recording of flame-ionization detector (FID) and electroantennographic detector (EAD: female *I. tridens* antenna) responses to captured volatiles released from an Engelmann spruce bolt infested with *I. tridens* males. Chromatography: Varian MS Saturn ion trap fitted with DB-23 column; temperature program: 50°C (1 min.), 10°C/min to 200 °C.


FID
EAD
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
~1mV
3
4
5
6
7
8
9
10
11
12
RETENTION TIME (min)
DETECTOR RESPONSE [mV]
1 α-pinene
2 β-pinene
3 myrcene
4 β-phellandrene
5 cineole
6 *p*-cymene
7 unidentified
8 *exo*-brevicomin
9 linalool
10 amitinol
11 camphor
12 ipsdienol
13 α-terpineol
14 unidentified
15 verbanone
16 unidentified
17 geraniol
18 verbenone

pinene, β-phellandrene, and linalool, also elicited antennal responses. The previously known attractant *cis*-verbenol was not detected in the volatiles obtained from feeding beetles of either sex. However, both males and females exposed to (+)-α-pinene vapors produced *cis*- and *trans*-verbenol. When subjected to GC-EAD analysis, both *cis*-verbenol and (+)-ipsdienol elicited antennal responses when co-injected in a 5:1 ratio.

2.3.2 Laboratory Experiments

Both males and females were attracted to 10 ng doses of ipsdienol or amitinol in olfactometer bioassays (Table 1). Males were also attracted to 1 ng of amitinol, and females responded to a 1 ng dose of ipsdienol. Both sexes responded most strongly to stimuli composed of 1 ng of each compound, indicating a synergistic interaction. Responses by males peaked at ipsdienol:amitinol ratios of 5:1 and 7:1, whereas there was no evident trend in the responses by females at ratios ranging from 1:1 to 10:1.

2.3.3 Field Experiments

In Experiment 1, both male and female *I. tridens* were attracted at significant levels to traps baited with the three-component blend of ipsdienol, *cis*-verbenol, and amitinol (Figure 2). Responses to traps baited with the two-component blend of ipsdienol plus *cis*-verbenol were intermediate between those to the three-component blend and the unbaited control traps. The two-component blend of ipsdienol with amitinol was not attractive nor was any of the components tested alone.

Both male and female *I. tridens* were attracted in Experiment 2 at significant levels to the three-component blend of ipsdienol, *cis*-verbenol and amitinol (Figure 3). Elimination of amitinol did not cause a significant reduction in attraction by either sex. Addition of the spruce beetle bait to the three-component blend caused a significant reduction in the attraction of females, whereas its inclusion with the two-component bait of ipsdienol and *cis*-verbenol caused the attraction of females to fall to a level intermediate between that to the two-component bait and the combined three-component

Table 1 Responses of walking male or female *I. tridens* in laboratory bioassays

Sex	Treatment	Dose	Number tested	Percent response	χ^2 *P* compared to pentane control
Males					
	pentane	10 µl	200	6.5	-
	(±) ipsdienol	1 ng	50	8.0	.7063
		10 ng	50	22.0	.0009
	amitinol	1 ng	50	30.0	<.0001
		10 ng	50	22.0	.0009
	(±) ipsdienol:amitinol	1:1 ng	50	24.0	.0002
		3:1 ng	50	18.0	.0102
		5:1 ng	50	44.0	<.0001
		7:1 ng	50	42.0	<.0001
		10:1 ng	50	34.0	<.0001
Females					
	pentane	10 µl	200	5.5	-
	(±) ipsdienol	1 ng	50	26.0	<.0001
		10 ng	50	26.0	<.0001
	amitinol	1 ng	50	12.0	.1025
		10 ng	50	22.0	.0002
	(±) ipsdienol:amitinol	1:1 ng	50	36.0	<.0001
		3:1 ng	50	20.0	.0009
		5:1 ng	50	26.0	<.0001
		7:1 ng	50	22.0	.0002
		10:1 ng	50	38.0	<.0001

Figure 2. Numbers of male and female *I. tridens* caught in multiple funnel traps in Experiment 1 (7-21 July 1995), Britton Creek, Tulameen, B.C. (±)-Ipsdienol, (-)-*cis*-verbenol, and amitinol released from bubble caps at 0.2, 0.6, and 0.02 mg per 24 h respectively. N=7. Bars for each sex with the same letter are not significantly different, REGW test, $P < 0.05$.

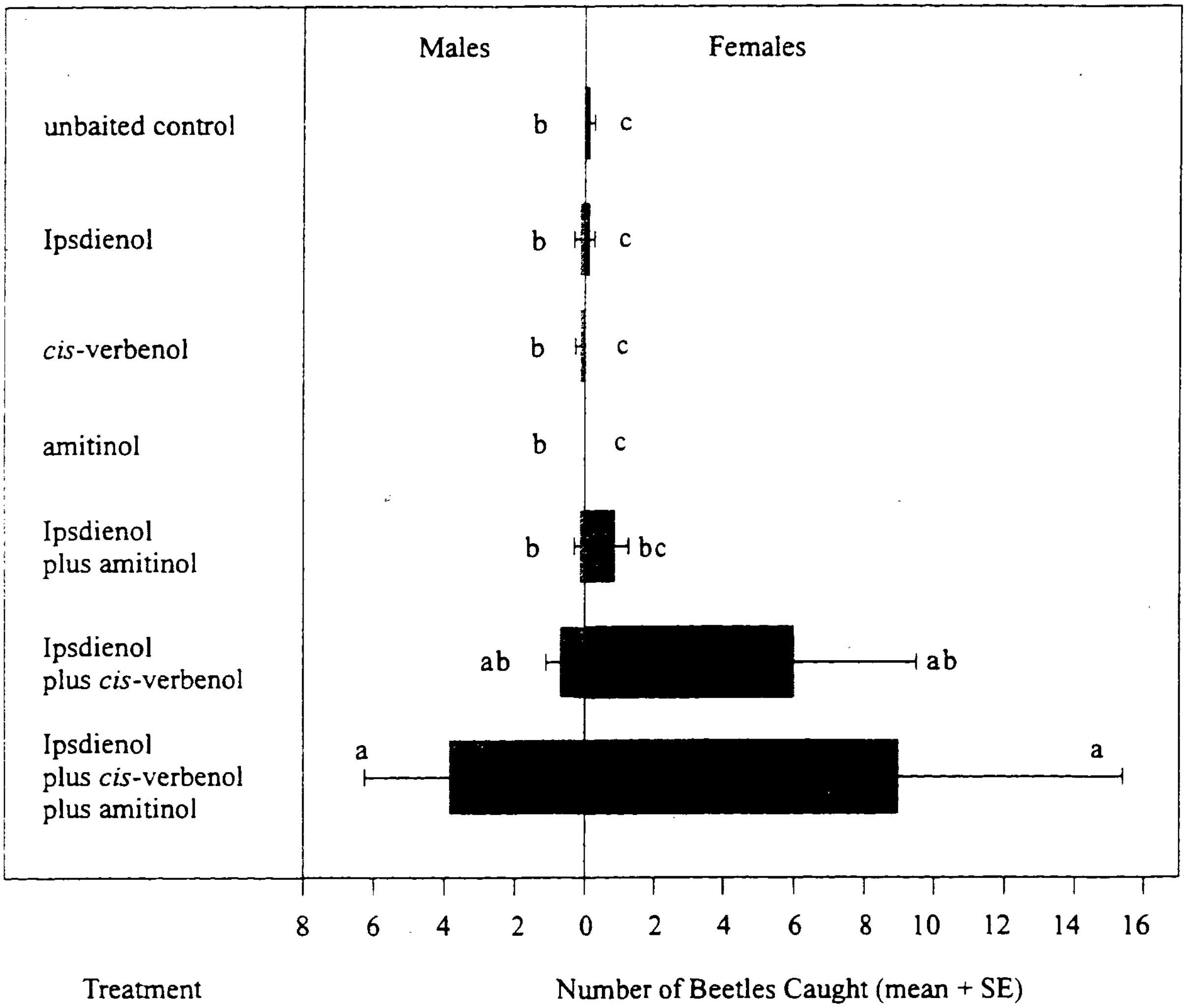
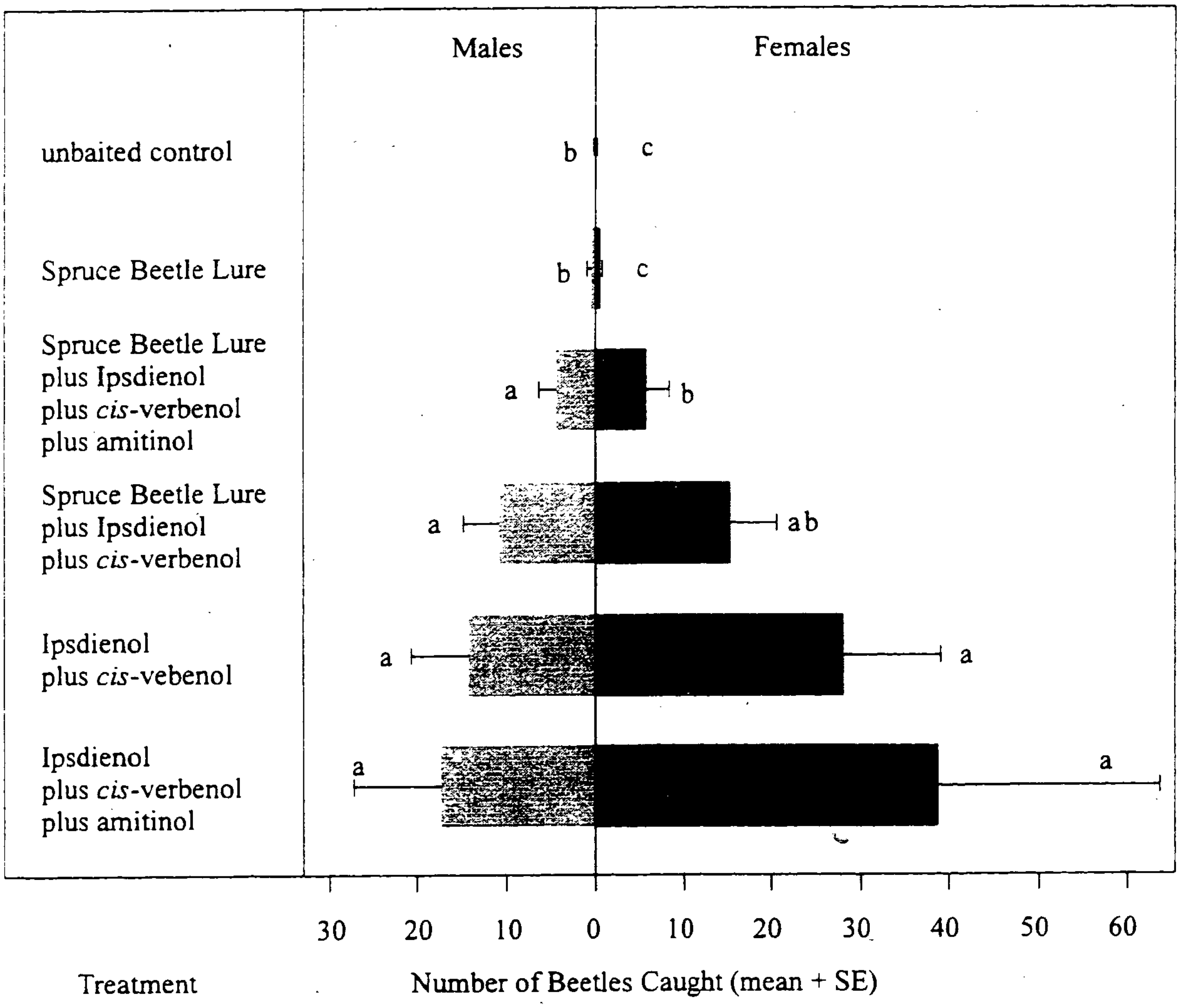

Males
Females
unbaited control
Ipsdienol
cis-verbenol
amitinol
Ipsdienol plus amitinol
Ipsdienol plus *cis*-verbenol
Ipsdienol plus *cis*-verbenol plus amitinol
b
c
b
c
b
c
b
c
b
bc
ab
ab
a
a
8
6
4
2
0
2
4
6
8
10
12
14
16
Treatment
Number of Beetles Caught (mean + SE)

Figure 3. Numbers of male and female *I. tridens* caught in multiple funnel traps in Experiment 2 (3-11 July 1996), Granite Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. (±)-Ipsdienol, (-)-*cis*-verbenol, and amitinol released from bubble caps at 0.2, 0.6, and 0.02 mg per 24 h respectively. N=10. Bars for each sex with the same letter are not significantly different, REGW test, $P < 0.05$.


Males
Females
unbaited control
b
c
Spruce Beetle Lure
b
c
Spruce Beetle Lure
plus Ipsdienol
plus *cis*-verbenol
plus amitinol
a
b
Spruce Beetle Lure
plus Ipsdienol
plus *cis*-verbenol
a
ab
Ipsdienol
plus *cis*-vebenol
a
a
Ipsdienol
plus *cis*-verbenol
plus amitinol
a
a
30
20
10
0
10
20
30
40
50
60
Treatment
Number of Beetles Caught (mean + SE)

and spruce beetle baits. Spruce beetle bait alone elicited no response. Spruce beetle catches were so low that any differences between treatments were obscured.

2.4 Discussion

These results confirm that the previously known attractant ipsdienol (Moeck et al. 1985) is a pheromone produced by male *I. tridens* boring in spruce bark. Although *cis*-verbenol was not detected in the captured volatiles from logs infested by either sex, its production by both sexes when exposed to vapors of (±)-α-pinene, its ability to stimulate antennae in GC-EAD recordings, and it synergistic activity with ipsdienol in field experiments (Figures 2,3) (Moeck et al. 1985) strongly support its designation as a pheromone for *I. tridens*.

α-Pinene, present in uninfested Engelmann spruce logs, would be readily encountered by *I. tridens* when boring into hosts. The enantiomeric composition of α-pinene influences the isomerism of verbenol produced. Male *I. paraconfusus*, produced *cis-* and *trans*-verbenol when treated with (-)- and (+)-α-pinene respectively (Renwick et al. 1976). My results support this finding because males and females produced both *cis-* and *trans*-verbenol when exposed to (±)-α-pinene. It is probable that *I. tridens* also produced *cis*-verbenol when boring in logs but that it was present at levels below the detection threshold of the flame ionization detector. Although amitinol was produced by male *I. tridens* boring in logs, elicited antennal responses (Figure 1) and was attractive in laboratory bioassays (Table 1), it contributed marginally to attraction of *I. tridens* to baited traps in the field (Figures 2,3). The weak field response to amitinol may be partially explained by its similarity in structure to ipsdienol; thus while it elicited antennal responses its role in long range attraction in the field may be redundant to that of ipsdienol. Further research, testing responses to trees baited with ipsdienol, *cis*-verbenol, and amitinol are required to determine whether amitinol plays a role in attraction to baited hosts or in close range attraction to the entrance of gallery systems.

exo-Brevicomin is an important pheromone in several scolytids including members of the genera *Dendroctonus* and *Dryocoetes* (Borden 1982) but has not previously been reported as a pheromone in *Ips*. Therefore, its potential role as a pheromone in *I. tridens* warrants further investigation. Individual host compounds or multicomponent blends may also attract bark beetles (Dyer et al. 1978; Furniss et al. 1976) or synergize pheromone attraction (Furniss et al. 1976). In particular, β-phelladrene acts as a kairomonal synergist for pheromones of *I. latidens* and *I. pini* (Miller and Borden 1990a,b). The potential behavioral role of antennally active host volatiles thus requires additional research.

The pronounced and constant responses to ipsdienol and *cis*-verbenol indicate that this two-component blend should be sufficient for use in inducing attack by *I. tridens* in competitive displacement or exclusion tactics (Payne and Richerson 1985; Borden 1992) employed against the spruce beetle.

3.0 Interspecific Semiochemical Communication Between the Spruce Beetle, *Ips tridens*, and *Dryocoetes affaber*

3.1 Introduction

Potential management of the spruce beetle using semiochemical-based competitive displacement or exclusion by secondary bark beetles would be enhanced if the pheromones that induce attack by the secondary species also disrupted attraction of the spruce beetle. Specificity in pheromone-based communication is of major importance as a mechanism for reproductive isolation (Roelofs and Cardé 1974, West Eberhard 1984, Cardé 1986) and resource partitioning (Birch 1978; Svihra et al. 1980). Interruption of pheromonal attraaction by sympatric species has been observed for several scolytids. For instance, in California, *I. pini* and *I. paraconfusus* compete for breeding material in weakened or fallen ponderosa pine, *Pinus ponderosae* Laws. Attraction of beetles in each species to their conspecifics was disrupted in the presence of heterospecifics (Birch and Wood 1975). Aggregation pheromones, ipsenol (2-methyl-6-methylene-7-octen-4-ol) and (+)-ipsdienol, produced by *I. paraconfusus*, disrupted attraction of *I. pini* to logs containing conspecific males (Birch and Light 1977; Birch et al. 1980). (-)-Ipsdienol produced by *I. pini* inhibited attraction of *I. paraconfusus* to conspecifics (Birch et al. 1980). Similarly, attraction of western pine beetles, *Dendroctonus brevicomis* LeConte, and *I. paraconfusus* to ponderosa pine bolts infested with conspecifics was mutually inhibited in the presence of nearby bolts infested with beetles of the other species (Byers and Wood 1980). A blend of ipsenol, ipsdienol, and *cis*-verbenol, the aggregation pheromones for *I. paraconfusus*, inhibited attraction of *D. brevicomis* to its pheromones *exo*-brevicomin and frontalin plus kairomonal myrcene (2-methyl-6-methylene-2,7-octadiene). The attraction of *I. paraconfusus* to its pheromones was unaffected by the aggregation pheromones of *D. brevicomis* but was disrupted by the antiaggregation pheromone verbenone, 4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one (Byers and Wood 1980). In British Colulmbia, *I. pini* co-exists with the mountain pine beetle and *Ips* *latidens* LeConte. Attraction of *I. pini* to synthetic ipsdienol, and attacks on felled lodgepole pine were reduced by ipsenol, an aggregation pheromone for *I. latidens*, and verbenone, an antiaggregation pheromone for the mountain pine beetle (Borden et al. 1991; Devlin and Borden 1994). Blends of antiaggregation pheromones and repellent synomones produced by sympatric competitors may be even more effective. For instance, verbenone and ipsdienol acted synergistically in inhibiting attraction by the western pine beetle (Paine and Hanlon 1991).

Because secondary species may coattack trees that have been weakened or killed by aggressive primary attacking species, it is possible that they exploit the pheromone of the primary species as an attractant alone, or that the semiochemical blends of primary and secondary species interact in an additive or synergistic mode in attracting the secondary species.

The aggregation pheromone for *D. affaber* consists of a 1:2 mixture of (+)-*exo*- and (+)-*endo*-brevicomin (Camacho et al. 1994). The results of Chapter 2 confirm that (±)-ipsdienol and (-)-*cis*-verbenol are sufficient for attracting *I. tridens*. Enantiospecific pheromones are expensive and unlikely to be economically viable as management tools. Racemic mixtures are cheaper and would be preferred for operational use if they were effective in eliciting appropriate beetle responses.

My objectives were to test the hypotheses that: 1) *D. affaber* and *I. tridens* pheromone baits inhibit attraction of the spruce beetle to spruce beetle lures; 2) racemic mixtures of *D. affaber* and *I. tridens* pheromones inhibit spruce beetle attraction to spruce beetle lures as effectively as blends of chirally pure compounds; and 3) attraction of secondary species is enhanced when their pheromone baits are combined with that of the spruce beetle.

3.2 Materials and Methods

Five field trapping experiments were conducted near Princeton, B.C. in mature stands composed of Engelmann spruce, lodgepole pine, and subalpine fir. All experiments utilized twelve-unit multiple funnel traps (Lindgren 1983) set out in randomized complete blocks with at least 15 m between traps. Captured beetles were collected and stored in plastic bags at - 18 °C before they were sexed and counted. Ten replicates were set up initially for each experiment. For some experiments treatment positions were re-randomized between collection periods to provide an additional 10 replicates.

Spruce beetle funnel lures (Phero Tech Inc., Delta B.C.) were used as the attractive semiochemical bait. The lures consisted of a 1.5 mL Eppendorf tube containing α-pinene released at 1.5 mg per 24 h and a 400 μl tube containing frontalin released at 2.6 mg per 24 h.

The attractive lure for *I. tridens* consisted of 3 bubble caps each releasing (+)- and (-)-*cis*-verbenol in a 17:83 ratio at 0.6 mg per 24 h, and 3 bubble caps each releasing (±)-ipsdienol at 0.2 mg per 24 h. (+)- or (-)-Ipsdienol (97% chirally pure) were released at 0.2 mg per 24 h from bubble caps. All release devices were obtained from Phero Tech.

Pheromone baits for *D. affaber* consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h from glass capillary tubes (1.0 mm ID) sealed at one end and placed in perforated Eppendorf tubes (Stock et al. 1990). The presence of (-)-*exo*-brevicomin does not affect attraction of *D. affaber*; however, (-)-*endo*-brevicomin is inhibitory. Therefore, (±)-*exo*-brevicomin and (+)-*endo*-brevicomin were used in a mixture that delivered a 1:2 ratio of the (+)-enantiomers (Camacho et al. 1994). Enantiomers of *exo*- and *endo*-brevicomin were released separately from devices prepared in the same manner as the *D. affaber* lures. Respective chemical and optical purities were: (+)-*exo*-brevicomin 98.1% and 94.0%; (-)-*exo*-brevicomin 97.9% and 95.0%; (+)-*endo*-brevicomin 98.8% and 90.2%; and (-)-*endo*-brevicomin 91.1% and

88.0%. Racemic *exo*- and *endo*-brevicomin (98.0% and 95.6% chemical purity, respectively) were obtained from Phero Tech. All chiral compounds were synthesized by B.D. Johnston (Department of Chemistry, Simon Fraser University) according to procedures developed by Johnston and Oehlschlager (1982).

Experiment 3 tested whether attraction of the spruce beetle to the spruce beetle lure is inhibited in the presence of the *D. affaber* pheromone. It comprised 10 replicates of four treatments: 1) unbaited control; 2) spruce beetle lure; 3) *D. affaber* lure; and 4) spruce beetle plus *D. affaber* lures.

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

Experiment 6 compared (±)-*exo*- and (±)-*endo*-brevicomin alone and combined in 20 replicates of 5 treatments: 1) unbaited control; 2) spruce beetle lure; 3) spruce beetle lure plus (±)-*exo*-brevicomin; 4) spruce beetle lure plus (±)-*endo*-brevicomin; and 5) spruce beetle lure plus both (±)-*exo*- and (±)-*endo*-brevicomin.

Experiment 7 tested whether attraction of the spruce beetle to the spruce beetle lure is inhibited by the presence of *I. tridens* pheromone. It was identical to Experiment 3 except that *I. tridens* lures replaced *D. affaber* lures.

Experiment 8 tested whether the different enantiomers of ipsdienol disrupted attraction of the spruce beetle to the spruce beetle lure. It comprised 10 replicates of five treatments: 1) unbaited control; 2) spruce beetle lure; 3) spruce beetle lure plus (+)-ipsdienol; 4) spruce beetle lure plus (-)-ipsdienol; and 5) spruce beetle lure plus (±)-ipsdienol.

The numbers of beetles of each species captured were transformed by $\log_{10}(x+1)$ to satisfy assumptions of normality and homoscedasticity (Zar 1984), and were then analyzed using ANOVA for randomized complete block design treating replicates as blocks (SAS 1990). An additional blocking factor for collection time was included for experiments in which treatments were re-randomized. The means were compared by the Ryan-Einot-Gabriel-Welsh (REGW) multiple range test. In Experiments 3 and 7 captures of male and female beetles were not significantly different from each other ANOVA; therefore, data for the two sexes were pooled. In all cases $\alpha = 0.05$.

3.3 Results

In Experiment 3, spruce beetles were significantly more attracted to spruce beetle lures than to unbaited controls or traps baited with the pheromone of *D. affaber* (Figure 4). Attraction of spruce beetles to their own pheromone with the pheromone of *D. affaber* was intermediate between that to unbaited controls and spruce beetle lures alone. *Dryocoetes affaber* was significantly attracted to its own pheromone but not to spruce beetle lures (Figure 4). Attraction to its own pheromone was significantly enhanced in the presence of the spruce beetle lure.

In Experiments 4-6, the numbers of beetles captured differed significantly between the two randomization periods resulting in large overall variances. However, differences between treatments were similar for both collection periods and were significant when the data for the two collection periods were combined and analyzed with a model factor included for randomization period.

In Experiment 4, spruce beetles of both sexes were significantly attracted to traps baited with spruce beetle lures alone or combined with (-)- or ($\pm$)-*exo*-brevicomin (Figure 5). The presence of (+)-*exo*-brevicomin reduced the catches slightly, but significantly to a

Figure 4. Numbers of spruce beetles and *Dryocoetes affaber* captured in multiple funnel traps in Experiment 3 (28 May - 7 July 1993), Slate Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. *Dryocoete*[illegible]*ffaber* pheromone consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. N=10. Bars for each species with the same letter are not significantly different, REGW test, *P*<0.05.

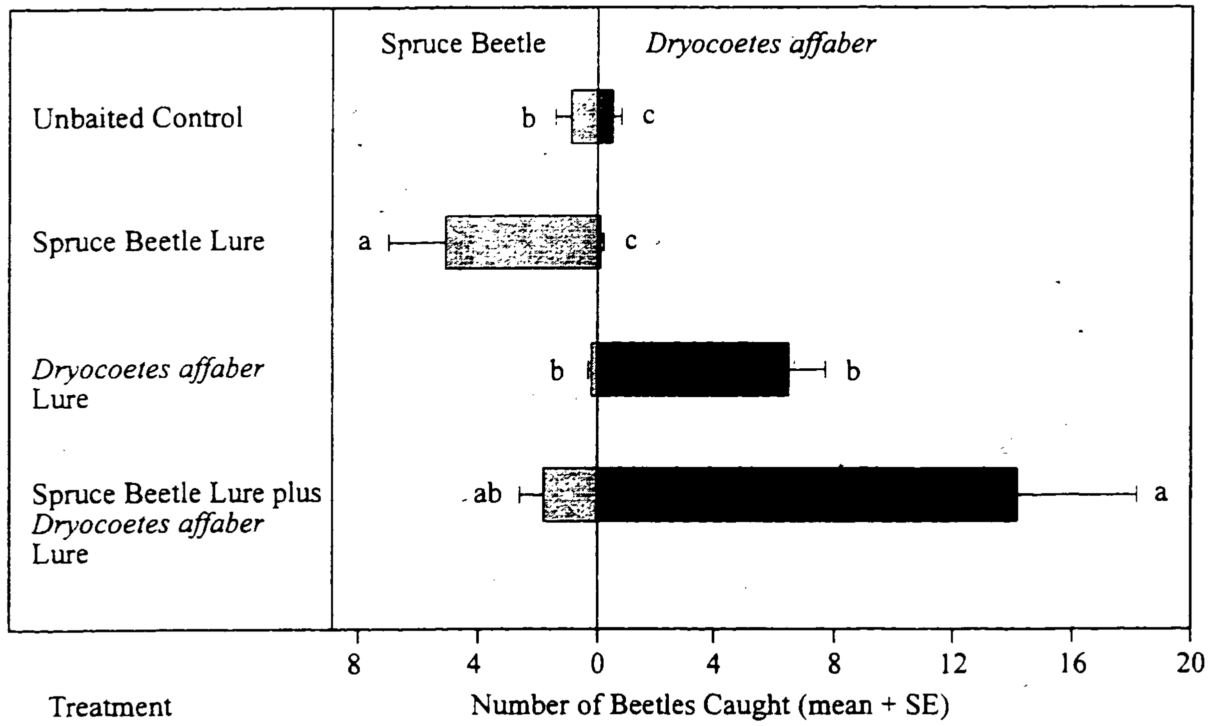
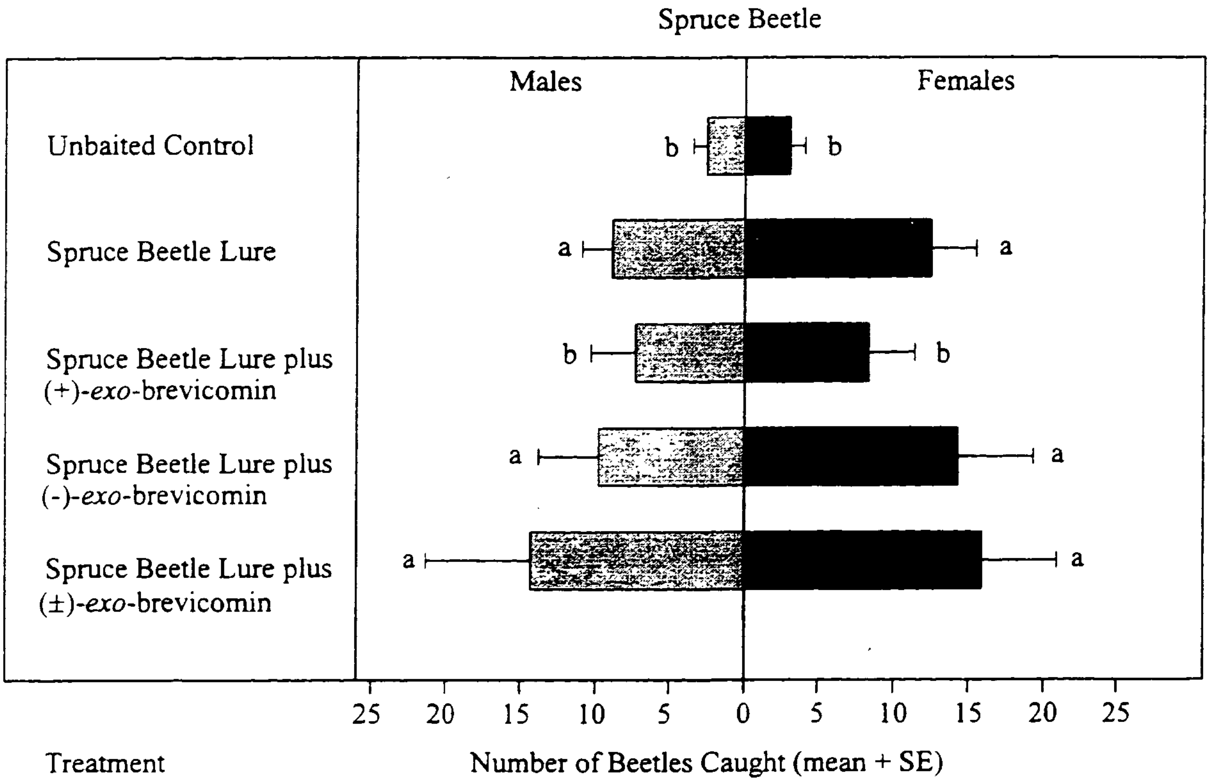

Spruce Beetle
Dryocoetes affaber
Unbaited Control
b
c
Spruce Beetle Lure
a
c
Dryocoetes affaber Lure
b
b
Spruce Beetle Lure plus *Dryocoetes affaber* Lure
ab
a
8
4
0
4
8
12
16
20
Treatment
Number of Beetles Caught (mean + SE)

Figure 5. Numbers of male and female spruce beetles captured in multiple funnel traps in Experiment 4 (26 April - 29 June 1994), Arastra Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. Enantiomers of *exo*-brevicomin were released at 0.2 mg per 24 h. N=20. Bars for each sex with the same letter are not significantly different, REGW test, *P*<0.05.


Spruce Beetle
Males
Females
Unbaited Control
Spruce Beetle Lure
Spruce Beetle Lure plus (+)-*exo*-brevicomin
Spruce Beetle Lure plus (-)-*exo*-brevicomin
Spruce Beetle Lure plus (±)-*exo*-brevicomin
b
b
a
a
b
b
a
a
a
a
25 20 15 10 5 0 5 10 15 20 25
Treatment
Number of Beetles Caught (mean + SE)

level not different from that to unbaited control traps (Figure 5). Catches of *D. affaber* were very low and were not significantly different between treatments.

Attraction of spruce beetles in Experiment 5 was similarly reduced when spruce beetle lures were combined with (+)- or (±)-*endo*-brevicomin (Figure 6). *Dryocoetes affaber* was attracted to spruce beetle lures combined with either (+)- and (±)-*endo*-brevicomin.

In Experiment 6, spruce beetles were attracted at significant levels only to traps baited with spruce beetle lures (Figure 7). Addition of (±)-*exo*-brevicomin, (±)-*endo*-brevicomin, or both to spruce beetle lures reduced attraction of both sexes by 75%, 87%, and 77% respectively, levels not significantly different from that to unbaited control traps (Figure 7). *Dryocoetes affaber* was significantly attracted to spruce beetle lures plus (±)-*endo*-brevicomin alone or combined with (±)-*exo*-brevicomin but not to spruce beetle lures plus (±)-*exo*-brevicomin alone.

The results of Experiment 7 were very similar to those of Experiment 3. The attraction of spruce beetles to the combination of spruce beetle and *I. tridens* lures was reduced to a level intermediate between that to unbaited controls and spruce beetle lures (Figure 8). *Ips tridens* was significantly attracted to *I. tridens* lures alone or in combination with spruce beetle lures, but unlike *D. affaber* its attraction was not significantly enhanced in the presence of the spruce beetle lure (Figure 8).

In Experiment 8, spruce beetles of both sexes were significantly more attracted to traps baited with spruce beetle lures than to unbaited controls. The presence of (+)- or (±)-ipsdienol significantly reduced spruce beetle attraction to a level that did not differ from that to unbaited control traps (Figure 9).

3.4 Discussion

The experimental results uphold all three hypotheses, at least in part. Attraction of spruce beetles to traps baited with the aggregation pheromone frontalin plus the host kairomone α-pinene was reduced by up to 87% by both pheromones of *D. affaber*

Figure 6. Numbers of male and female spruce beetles and *Dryocoetes affaber* captured in multiple funnel traps in Experiment 5 (26 April - 29 June 1994), Arastra Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. Enantiomers of *endo*-brevicomin were released at 0.2 mg per 24 h. N=20. Bars with the same letter within each species and sex are not significantly different, REGW test, $P<0.05$.

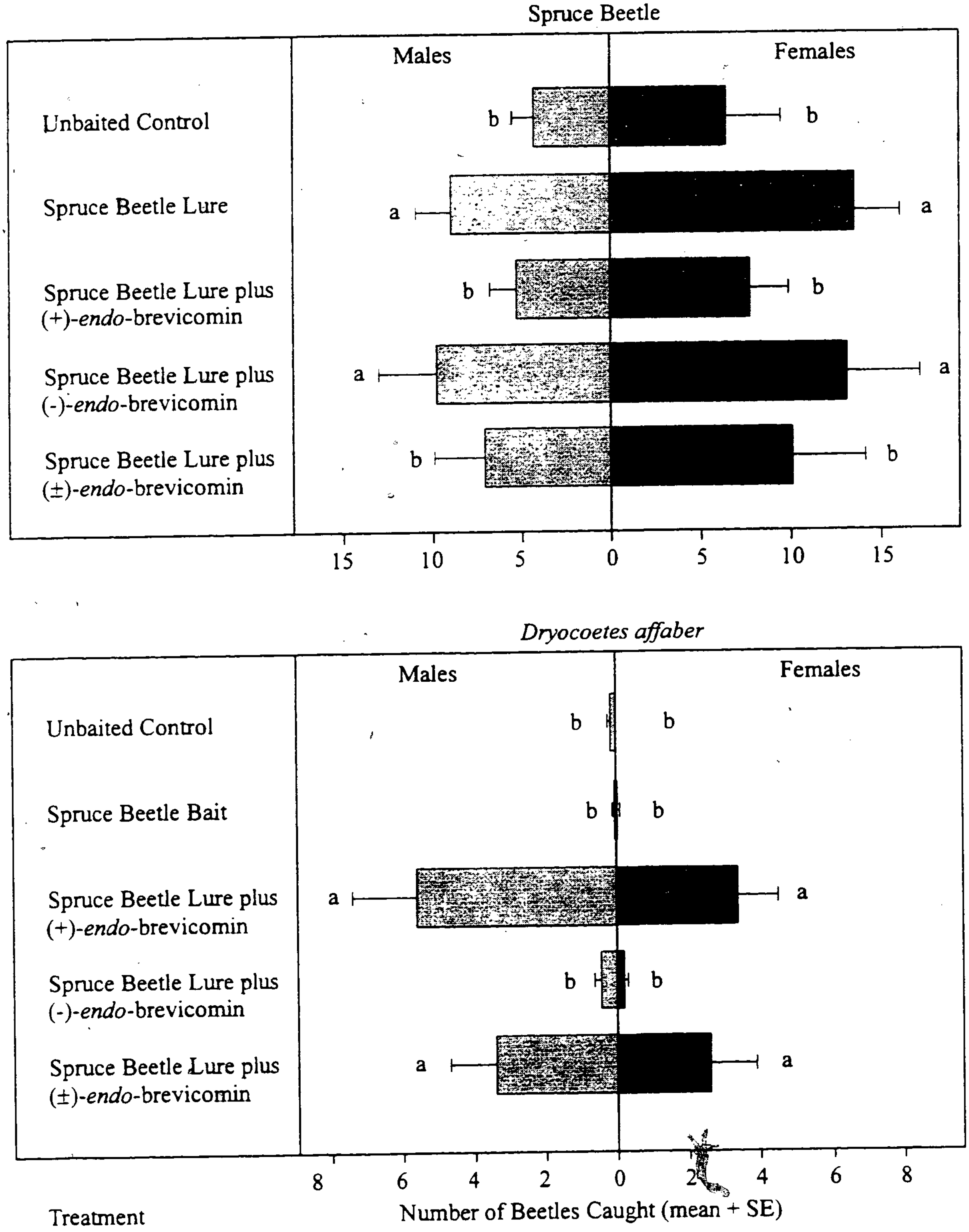

Spruce Beetle
Males
Females
Unbaited Control
Spruce Beetle Lure
Spruce Beetle Lure plus (+)-*endo*-brevicomin
Spruce Beetle Lure plus (-)-*endo*-brevicomin
Spruce Beetle Lure plus (±)-*endo*-brevicomin
b
b
a
a
b
b
a
a
b
b
15
10
5
0
5
10
15
Dryocoetes affaber
Males
Females
Unbaited Control
Spruce Beetle Bait
Spruce Beetle Lure plus (+)-*endo*-brevicomin
Spruce Beetle Lure plus (-)-*endo*-brevicomin
Spruce Beetle Lure plus (±)-*endo*-brevicomin
b
b
b
b
a
a
b
b
a
a
8
6
4
2
0
2
4
6
8
Treatment
Number of Beetles Caught (mean + SE)

Figure 7. Numbers of male and female spruce beetles and *Dryocoetes affaber* captured in multiple funnel traps in Experiment 6 (29 June - 17 Aug. 1994), Arastra Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. (±)-*exo* and (±)-*endo*-Brevicomin were released at 0.2 mg per 24 h. N=20. Bars with the same letter within each species and sex are not significantly different, REGW test, *P*<0.05.

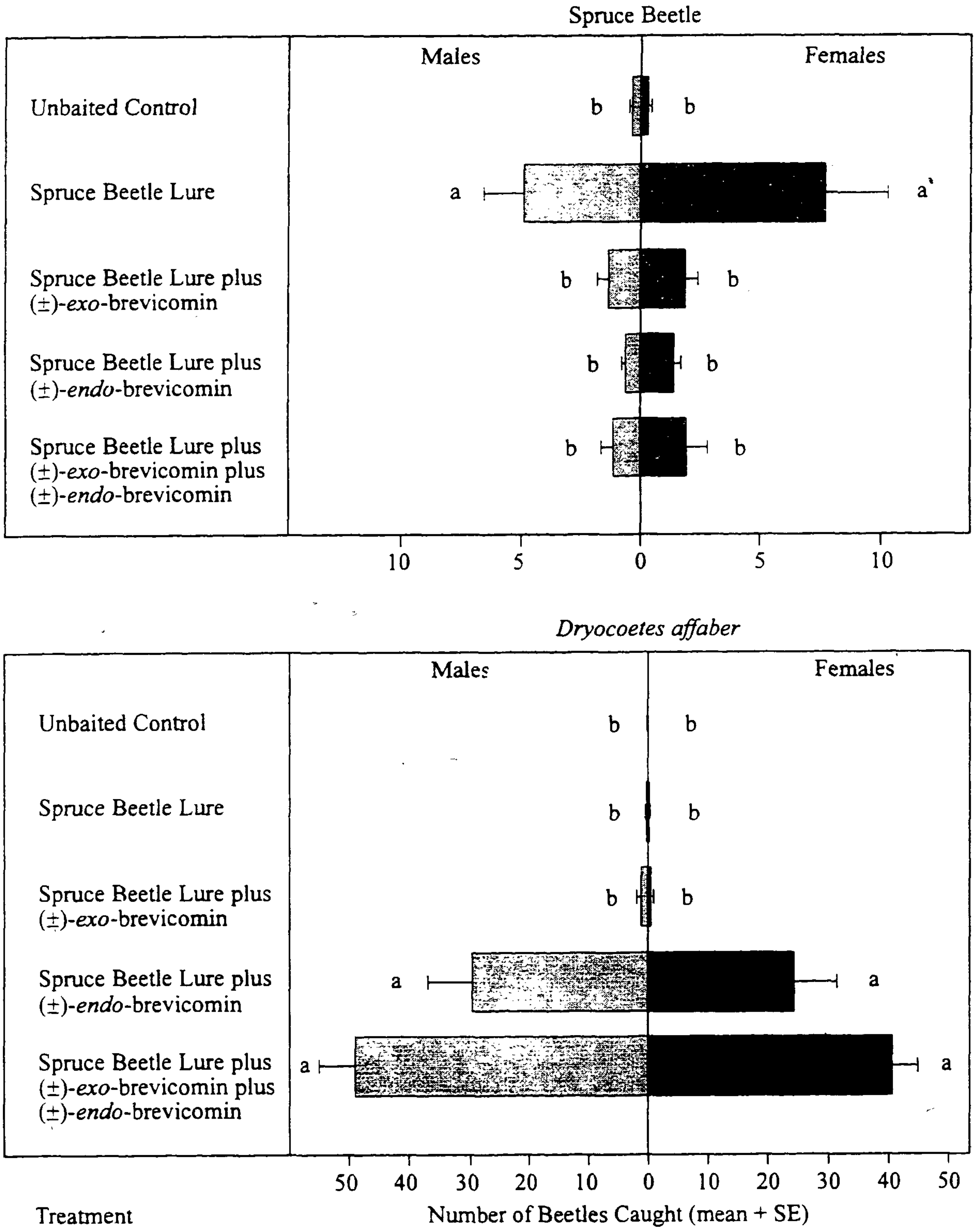

Spruce Beetle
Males
Females
Unbaited Control
b
b
Spruce Beetle Lure
a
a
Spruce Beetle Lure plus (±)-*exo*-brevicomin
b
b
Spruce Beetle Lure plus (±)-*endo*-brevicomin
b
b
Spruce Beetle Lure plus (±)-*exo*-brevicomin plus (±)-*endo*-brevicomin
b
b
10
5
0
5
10
Dryocoetes affaber
Males
Females
Unbaited Control
b
b
Spruce Beetle Lure
b
b
Spruce Beetle Lure plus (±)-*exo*-brevicomin
b
b
Spruce Beetle Lure plus (±)-*endo*-brevicomin
a
a
Spruce Beetle Lure plus (±)-*exo*-brevicomin plus (±)-*endo*-brevicomin
a
a
50
40
30
20
10
0
10
20
30
40
50
Treatment
Number of Beetles Caught (mean + SE)

Figure 8. Numbers of spruce beetles and *Ips tridens* captured in multiple funnel traps in Experiment 7 (28 May - 7 July 1993), Slate Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. *Ips tridens* lures consisted of a (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h respectively. N=10. Bars for each species with the same letter are not significantly different, REGW test, $P<0.05$.

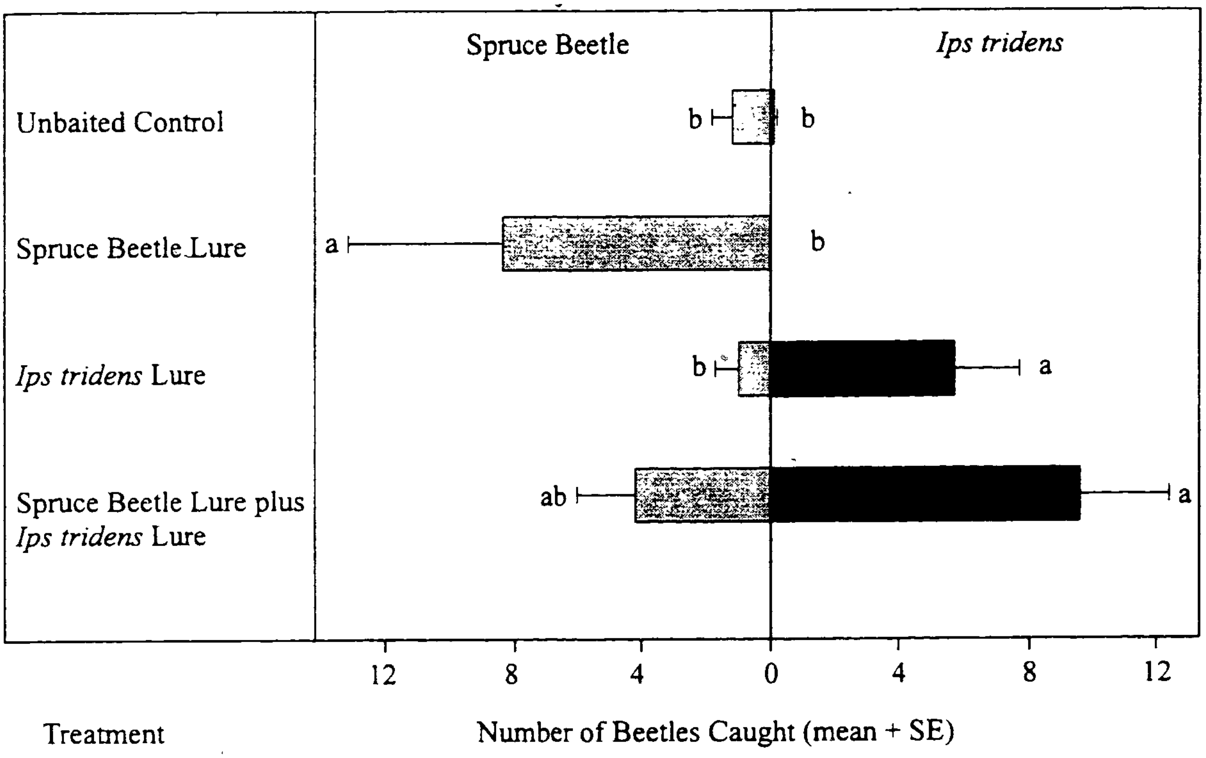
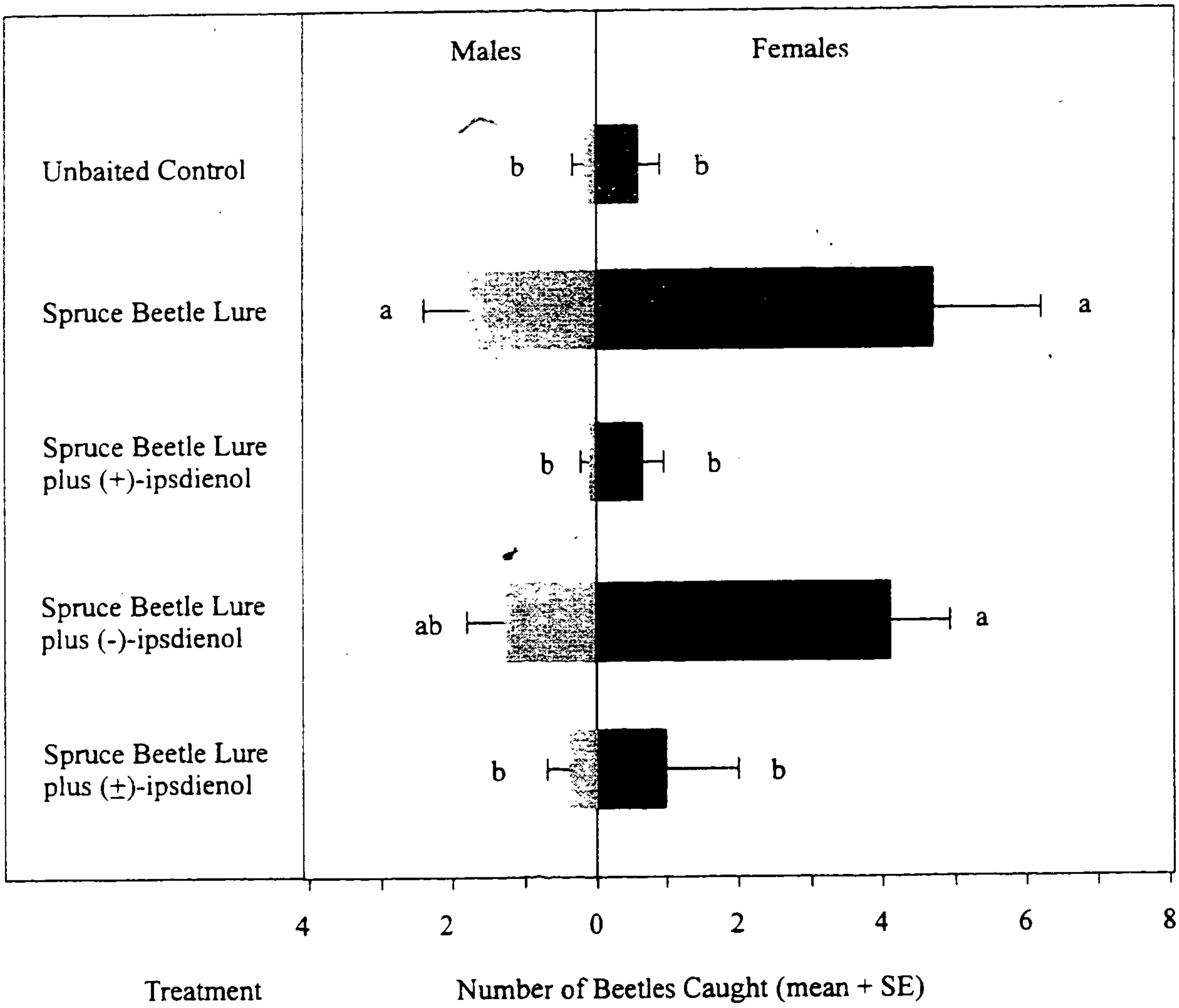

Spruce Beetle
Ips tridens
Unbaited Control
Spruce Beetle Lure
Ips tridens Lure
Spruce Beetle Lure plus Ips tridens Lure
b
b
a
b
b
a
ab
a
12
8
4
0
4
8
12
Treatment
Number of Beetles Caught (mean + SE)

Figure 9. Mean numbers of male and female spruce beetles captured in multiple funnel traps in Experiment 8 (14 July - 17 August 1994), Arastra Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. Enantiomers of ipsdienol were released at 0.2 mg per 24 h. N=10. Bars for each sex with the same letter are not significantly different, REGW test, $P<0.05$.

Spruce Beetle



(Figure 4). Spruce beetle attraction was reduced by the naturally produced (+)-enantiomers of both *exo-* and *endo*-brevicomin (Figures 5,6). (±)-*endo*-Brevicomin also reduced attractiveness of the spruce beetle bait in Experiments 5 and 6 (Figures 6,7) and (±)-*exo*-brevicomin in Experiment 6 (Figure 7). (±)-Ipsdienol as well as its (+)-enantiomer reduced attraction of the spruce beetle to the spruce beetle lure (Figure 9). On the other hand, spruce beetle lures enhanced attraction of *D. affaber* to its pheromone (Figure 4), but no such effect was observed for *I. tridens* (Figure 8).

Several species of bark beetles are known to produce and respond to enantiospecific pheromones (Birch 1984; Borden, 1985; Byers 1989). Specificity in the enantiomeric composition of pheromones may be an important mechanism in maintaining breeding isolation between sympatric congeners. *Dryocoetes confusus* is sympatric with *D. affaber* and shares the aggregation pheromones (+)-*exo-* and (+)-*endo*-brevicomin. Optimal attraction of *D. affaber* is elicited by a 1:2 ratio of the two compounds; whereas, a 9:1 ratio results in optimal attraction of *D. confusus* (Camacho et al. 1993). Attraction of *D. affaber* was reduced when (+)-*exo*-brevicomin was released with (+)-*endo*-brevicomin at the 9:1 ratio and (-)-*endo*-brevicomin was also found to be inhibitory (Camacho et al. 1994). (+)-*endo*-Brevicomin was inhibitory to *D. confusus* when released with (+)-*exo*-brevicomin at a 1:1 ratio (Stock et al. 1990; Camacho et al. 1993) and (-)-*exo*-brevicomin disrupted attaction to the optimal blend (Camacho et al. 1993).

Olfactory receptor cells specific to enantiomers of aggregation pheromones are present in *I. pini* and *I. paraconfusus* (Mustaparta et al. 1980, 1984), *I. typographus* (Tømmerås et al. 1984) and *Scolytus scolytus* (F.) (Wadhams et al. 1982). Perception of the species-specific enantiomeric blend of (+)-*exo-* and (+)-*endo*-brevicomin by *D. affaber* and *D. confusus* is likely similarly achieved by specific olfactory receptor cells. Because attraction of spruce beetles is reduced by naturally produced (+)-enantiomers of *exo-* and *endo*-brevicomin (Figures 6,7), they may also posess enantiospecific receptor cells. This suggests that spruce beetles and *D. affaber* co-evolved because it would be adaptive for spruce beetles to recognize the enantiospecific pheromones of competing secondary species.

Spruce beetle attraction was also reduced by (±)- and (+)-ipsdienol. *Ips tridens* produces ipsdienol in a 1:4 ratio of (+):(-)-enantiomers (Chapter 2). Ipsdienol is produced and utilized by many scolytid species (Borden 1982). The (+)-enantiomer may be a major pheromone for other secondary species associated with the spruce beetle. Production of some (+)-ipsdienol by *I. tridens* would be adaptive because it reduces spruce beetle attraction and would minimize competitive interactions.

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

Interspecific pheromonal inhibition is also common among lepidopterans. For instance, the bollworm, *Heliothis zea* Boddie, and the tobacco budworm, *Heliothis virescens* F., share four pheromone components (*Z*)-11-, (*Z*)-9-, and (*Z*)-7-hexadecenal and hexadecanal. Three additional components, (*Z*)-9-tetradecenal, tetradecanal, and (*Z*)-11-hexadecen-1-ol, in *H. virescens* are responsible for pheromone specificity and reproductive isolation of the two species. When *H. zea* males become habituated to the critical *H. virescens* pheromone components in a permeated atmosphere, they are unable to discriminate between females of the two species resulting in fatal interspecific matings with *H. virescens* females (Stadelbacher et al. 1983).

My results suggest that recognition by spruce beetles of the pheromones of *I. tridens* and *D. affaber* is an adaptive mechanism that enables them in part to avoid direct competitive interactions. It may, therefore, be possible to exploit the pheromones of secondary species to induce competitive displacement or exclusion of the spruce beetle for management purposes.

4.0 Semiochemical induced competition between the spruce beetle, *I. tridens*, and *D. affaber* in felled spruce trees

4.1 Introduction

Traditionally interspecific competition has been considered to be a major factor in structuring animal and plant communities (Darwin 1859; MacArthur 1958). In two major reviews of field experiments which investigated interspecific competition across a broad range of taxa (Schoener 1983; Connell 1983), evidence for interspecific competition was found in up to 90% of published studies and asymmetry in competitive ability was found to be common across all taxa. Resource exploitation was the most common mechanism of competition among all but marine invertebrates (Schoener 1983). However, the importance of present-day competitive interactions on the distribution, abundance, and resource use of species in natural communities has been questioned because observed evidence, such as differences in species distributions, may be the result of differences in host selection behavior or divergence caused by interspecific competition in the past (Connell 1980). The design of experiments investigating interspecific competition has been criticized for employing phenomenological rather than mechanistic approaches (Tilman 1987). Recent studies on competitive interactions have adopted a more experimental and often field-based approach. A review of the recent literature on interspecific competitive interactions in plant-herbivore systems found indications of interspecific competitive effects in 75% of the interactions (Denno et al. 1995). Similarly, a meta-analysis of 47 recent articles of competition studies involving 217 interspecific comparisons which analyzed the size of competitive effects rather than simply summarizing results by "vote counting" as in the case of reviews, found a large and significant overall effect of competition on the biomass of one or more of the competing species (Gurevitch et al. 1992). Therefore, interspecific competition has been reinstated as an important force in structuring insect herbivore communities (Stewart 1996).

Intraspecific competition occurs if a resource is in limited supply, resulting in reduced fitness of competing individuals of a species. Particular individuals may be favored, for instance if they are established in a habitat earlier than others; however, because roles may easily be reversed, competing individuals of a species are inherently equivalent. The effects of intraspecific competition are density dependent and fall within a continuum of forms with the most extreme described as "scramble" and "contest" (Nicholson 1954). In this model, at densities below some threshold carrying capacity of the resource, there is no competition; all individuals survive and produce the maximum number of offspring. In scramble competition, above a threshold density, all individuals die. In contest competition, at densities above a threshold, individuals fall within two classes; some survive to produce the maximum number of offspring while all others die. Some combination of reduced survivorship and fecundity of individuals that is intermediate between these two extreme forms generally occurs (Begon and Mortimer 1986).

Intraspecific competition has been observed for the spruce beetle. When spruce beetles were artificially introduced into spruce bolts at different densities, egg gallery length, brood production per female, and adult size of brood insects were significantly and inversely related to gallery spacing (Safranyik and Linton 1985).

Interspecific competition occurs when a resource that is shared by members of different species is in limited supply and niche overlap exists (Arthur 1987). It may occur through interference or exploitation. Interference is a direct mechanism whereby organisms affect one another through interactions such as threat behavior, physical attack, or territoriality. Exploitation is indirect and occurs solely through reduction in the available pool of resources (Keddy 1989). The spruce beetle, *I. tridens*, and *D. affaber* attack windthrown or fallen spruce trees. All three species depend on the phloem tissue of the host tree for food and habitat. Their life cycles broadly overlap, with gallery construction and brood development occurring simultaneously for all three species over several months (Bright 1976). As a resource, the phloem is limited because it occupies an essentially two-dimensional space and characteristically exists in suitable trees that are well scattered throughout a forest (Atkins 1966). The phloem in fallen spruce trees is also limited temporally. It can be considered an ephemeral habitat because its suitability for colonization by scolytids deteriorates rapidly over time. Thus, the breeding and feeding activities of the spruce beetle, *I. tridens*, and *D. affaber* clearly overlap, both spatially and temporally, in the highly restricted environment of the phloem resource. Competition for ephemeral and patchy resources is frequently severe (Hanski 1987). Models of competing populations in patchy environments predict that species may survive competition either because of good dispersal or good competitive abilities. Pioneers or colonizing species are generally good dispersers. Spatial heterogeneity of resources influences the relative merits of dispersal and competitive abilities for survival (Hanski and Ranta 1983). The initially most widespread species has an advantage and may exclude its competitor from a patchy environment (Hanski 1983). However, species may coexist if the distribution of sites is heterogenous (Platt and Weis 1985), if intraspecific competition increases faster than interspecific competition and, if species distributions are clumped in habitat patches (Hanski 1987).

A group of species that exploit the same class of environmental resources in a similar way is defined as a guild (Arthur 1987). The competitive exclusion principle states that competing species within a guild cannot co-exist if there is no differentiation between their realized niches. If differentiation of niches is allowed by the habitat, co-existence of potential competitors is possible (Begon and Mortimer 1986). Based on this principle, a species can be excluded or displaced from its niche if a competitor makes identical demands on a limited environmental resource.

The spruce beetle, *I. tridens*, and *D. affaber* may partially differentiate niches within the phloem habitat. Spruce beetles were most numerous on the underside of the boles of fallen trees whereas secondary species were most abundant on the upper surface (Gara et al. 1995). In addition, the proportion of secondary scolytids was higher in the upper stem while both the spruce beetle and secondary species were found at the base of spruce trees.

Competition between members of a guild for a limited resource can reduce the fitness of one or more species as a result of some combination of lowered fecundity and survivorship (Begon and Mortimer 1986). This phenomenon may be exploited by pest managers in a number of ways. Environmental conditions can be altered to promote competition among a guild of pests. For instance, in managed seed orchards of white fir, *Abies concolor* (Gord. and Glend.), elimination of aperiodicity of cone crops may lead to enhanced competition between members of the insect pest complex, thus leading to decreased pest species diversity through competitive exclusion which in turn would simplify the development of integrated pest management programs (Shea 1989).

If a species has an advantage over another competing species, displacement may result. It may be possible to artificially replace an aggressive economically important pest with a secondary or beneficial species (Payne and Richerson 1985). For instance, *Parthenium hysterophorus* L., an obnoxious asteraceous weed which has spread over millions of hectares of land in India, has been competitively displaced through sustained efforts to introduce *Cassia uniflora*, a leguminous undershrub of some economic value (Joshi 1991).

Competitive exclusion could also be used to exclude a pest from a resource and prevent it from becoming established. This technique is used in the management of pathogenic diseases. Inoculation of hosts with protective organisms can be effective in inhibiting or excluding infection by disease-causing organisms. For example, oral inoculation of young chicks with lactose-utilizing cecal bacteria is effective in protecting them from infection by *Salmonella enteritiditis* (Behling and Wong, 1994). Several strains of bacteria and fungi with antimicrobial properties have been used to exclude pathogenic diseases of plants such as purple blotch and botrytis leaf blight of onion (Tyagi et al. 1990; James and Sutton 1996), groundnut root and stem rot diseases (Sreenivasaprasad and Manibhushanrae 1993), bean and banana wilt pathogens (El-Abyad et al. 1996), brown rot of pear (Montesinos 1996), and fusarium wilt of watermelon (Larkin et al. 1996) and tomato (El-Shanshoury et al. 1996).

Neither competitive displacement, nor exclusion have been implemented operationally as pest management tactics for bark beetles or any other insects. However, competitive displacement has been demonstrated experimentally for *I. pini* which is able to outcompete the mountain pine beetle (Rankin and Borden 1991; Safranyik et al. 1995, 1996). Because increased mortality in nature as an apparent result of competition by secondary species has been observed for the spruce beetle (McCambridge and Knight 1972; Whitmore 1983; Gara et al. 1995), there may be considerable potential for developing pest management tactics involving competitive displacement or exclusion of the spruce beetle.

Throughout this thesis the terms competitive displacement and competitive exclusion are used to refer to pest management tactics based on the competitive exclusion principle. With reference to beetles, I define competitive displacement as the elimination of an established species from all or part of the habitat it occupies through replacement by a competitor. Competitive exclusion occurs when competing members of a guild prevent members of another species from occupying their fundamental niche thus preventing them from becoming established in a habitat. Both competitive displacement and exclusion of bark beetles could be induced through the judicious use of semiochemicals (Payne and Richerson 1985; Borden 1989).

The objective of this study was to evaluate the feasibility of using competitive displacement as a management tactic for the spruce beetle. My specific objectives were to investigate the competitive interactions between the spruce beetle, *I. tridens*, and *D. affaber*, to explore the mechanisms of competitive interactions including the potential role of species specific fungal symbionts, and to test the hypothesis that spruce beetle success can be reduced in trees in which co-attack by *I. tridens*, *D. affaber*, or both, is induced by baiting with their respective pheromones following spruce beetle establishment.

4.2 Methods

Experiment 10 consisted of a trap tree baiting experiment conducted from 17 May to 9 August 1994 in a stand of Engelmann spruce, subalpine fir, and lodgepole pine near Princeton, B.C. The area was affected by a large spruce beetle outbreak and contained a very high spruce beetle population and many attacked standing trees. Large diameter, healthy spruce trees were felled individually approximately 50 m apart into the stand along cleared rights-of-way or cutblock margins so that the entire length of the bole was shaded. All trees were within 10 km of each other. Within one week of felling, the trees were baited with spruce beetle tree baits that were subsequently removed and replaced with baits for the secondary species after spruce beetle establishment. The experiment was laid out in randomized complete blocks and comprised 10 replicates of five treatments: 1) unbaited control; 2) spruce beetle bait; 3) spruce beetle bait followed by *I. tridens* bait; 4) spruce beetle bait followed by *D. affaber* bait; and 5) spruce beetle bait followed by baits for both *I. tridens* and *D. affaber*.

Spruce beetle tree baits consisted of α-pinene released at 1.5 mg per 24 h from 1.5 mL Eppendorf tubes and frontalin released at 2.6 mg per 24 h from 400 μL Eppendorf tubes which were sealed in polyethylene bags (Phero Tech, Inc.). *Ips tridens* baits consisted of 3 bubble caps each releasing (±)-ipsdienol at 0.2 mg per 24 h and 3 bubble caps each releasing *cis*-verbenol at a 83:17 ratio of the (-)- and (+)-enantiomers at 0.6 mg per 24 h (Phero Tech, Inc.). *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h from glass capillary tubes (1.0

mm ID) which were sealed at one end and placed in perforated 400 µL Eppendorf tubes. The tubes were enclosed in open-sided waxed carton containers to protect from exposure to rain and ultraviolet light and to enable the baits to be fastened to the trees. (±)-*exo*-Brevicomin (96.1 % pure) was obtained from Phero Tech, Inc.. (+)-*endo*-Brevicomin (98.8 % chemical and 90.2% optical purity) was synthesized by B.D. Johnston (Dept. of Chemistry, S.F.U.) according to procedures developed by Johnston and Oehlschlager (1982).

Each tree was assigned a single treatment and baits were attached at three positions: 2 m from the severed butt of the tree; at the point where the bole measured 30 cm in diam.; and midway between the two. All baits were attached to the North or shaded side of the tree, where the spruce beetle and the secondary species are most likely to interact.

On 9 June 1994, it was noted that spruce beetles had initiated attacks and established galleries in the baited trees. One gallery was sampled per tree and its length measured. The average gallery length (mean ± SE) was 4.7 ± 2.6 cm. All spruce beetle tree baits were removed and replaced with baits for the secondary species, except for trees receiving only the spruce beetle bait treatment.

On 12 July 1994, three rectangular sections of bark, 20 x 25 cm, were removed from each tree using a chisel and hammer. Bark samples were taken from the area immediately below and approximately 40 cm to one side of each bait (or where baits would have been attached on the control trees). Thus, samples were from the region nearest the underside of the bole where spruce beetles prefer to attack. The bark samples were stored in plastic bags at -18 °C until analyzed. A second set of bark samples was collected from the areas immediately below and approximately 40 cm to the other side of each bait position on 9 August 1994.

The sections of bark were analyzed by measuring bark sample area, counting the numbers of galleries and entrance holes and the numbers of eggs, larvae, pupae, and callow adults of each species, and measuring maternal gallery lengths. The density per m^2 for each measured variable was computed by dividing its value by the area of the bark sample. Four replicates of the experiment were destroyed in a forest fire between the two sampling periods; therefore, the final analysis included only six replicates.

Spearman rank correlation coefficients were computed by treatment for the relationships between spruce beetle attack density and attack densities of *I. tridens* and *D. affaber* at the end of the study (second set of bark samples). Correlations were also determined for relationships between spruce beetle and *I. tridens* or *D. affaber* progeny densities. These were compiled, not to describe in detail the relationship between the parameters being compared, but solely to determine if there was a negative association between the spruce beetle and the secondary species and if the association varied with treatment. The frequencies of negative and positive correlations were compared by a log-likelihood ratio chi-square (G^2) test (Zar 1984).

The data for attack density (number of entrance holes per m^2), total length of galleries (cm) per m^2, progeny density per m^2, mean length (cm) per gallery, and mean number of progeny per gallery for each species were transformed by $\log_{10}(x + 1)$ to satisfy assumptions of normality and homoscedasticity (Zar 1984). For each bark sample period, the transformed data were analyzed by a univariate split-plot three factor ANOVA. The main effects in the model were treatment, replicate and the split-plot variable bark sample position. The model also tested for interactions between treatment and replicate and between treatment and position. Means for treatment and position were compared by the REGW test (SAS 1990). The distribution of progeny developmental stage between the different treatments was analyzed by a chi-square contingency analysis.

An analysis of the effect of attack densities of the three species on gallery construction and progeny production by each species was conducted to test for direct interactions between the spruce beetle and the secondary species. Attack densities of each species were classified into low, medium and high density classes based on the ranges of densities observed for each species. For the spruce beetle, the range of attack densities for each class were: low <100 per m^2; medium 100 to 150 per m^2; and high > 150 per m^2. For *I. tridens*, the range of attack densities for each class were: low <20 per m^2; medium 20 to 70 per m^2; and high > 70 per m^2. For *D. affaber*, the range of attack densities for each class were: low < 10 per m^2; medium 10 to 30 per m^2; and high > 30 per m^2. For each species transformed data, $\log_{10}(x + 1)$, for gallery length per m^2, progeny density per m^2, length per gallery, and number of progeny per gallery were analyzed by a split-plot ANOVA with model factors for spruce beetle attack density class, *I. tridens* attack density class, and the interaction between them. A separate split-plot ANOVA was performed with model factors for spruce beetle attack density class, *D. affaber* attack density class, and the interaction between them. In all cases $\alpha = 0.05$.

4.3 Results

Spruce beetle attack density was negatively associated with attack densities of both *I. tridens* and *D. affaber* in most treatments (Table 2). Correlation coefficients were not negative in two cases: the relationship with *D. affaber* attack density after baiting with baits for both secondary species was weakly positive and the relationship with *I. tridens* attack density after baiting with *I. tridens* baits was neutral. The relationships between spruce beetle progeny densities and progeny densities of the two secondary species were similar to those for attack densities (Table 2). While large *P*-values indicate that individual correlations generally were not significant, there was a significantly greater frequency of negative than positive correlations ($G^2 = 4.045$, $P = .0441$). Therefore, the overall relationship between spruce beetle attack and progeny densities and those of the secondary species appeared to be negative.

Results from the first and second bark sample collections were similar except that responses for all variables tended to increase with time. Significant differences occurred only in the results for the second bark sample collection (Figures 10-12). The analysis of

Table 2 Correlation coefficients (r) for the relationships between attack densities and progeny densities of the spruce beetle, *I. tridens*, and *D. affaber* in felled spruce trees that were baited with spruce beetle baits followed by *I. tridens* baits, *D. affaber* baits, or baits for both secondary species after spruce beetle establishment.

Relationship	Treatment	Attack density		Progeny density	
		r	*P*	r	*P*
Spruce beetle *vs I. tridens*					
	Control	-.42	.08	-.36	.13
	Spruce beetle bait	-.54	.02	-.55	.02
	Spruce beetle bait followed by *I. tridens* bait	.05	.83	.28	.27
	Spruce beetle bait followed by *D. affaber* bait	-.61	.007	-.61	.007
	Spruce beetle bait followed by *I. tridens* *D. affaber* bait	-.55	.02	-.55	.02
Spruce beetle *vs D. affaber*					
	Control	-.42	.08	-.48	.05
	Spruce beetle bait	-.15	.55	-.11	.65
	Spruce beetle bait followed by *I. tridens* bait	-.44	.06	-.63	.005
	Spruce beetle bait followed by *D. affaber* bait	-.35	.15	-.36	.14
	Spruce beetle bait followed by *I. tridens* and *D. affaber* bait	.12	.61	.03	.89

Figure 10 Spruce beetle, *I. tridens*, and *D. affaber* attack densities in Experiment 10 (17 May - 9 August 1994), Arastra Creek, Princeton, B.C. Spruce beetle baits consisted of α-pinene and frontalin released at 1.5 mg and 2.6 mg per 24 h respectively. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h respectively. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. N=6. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

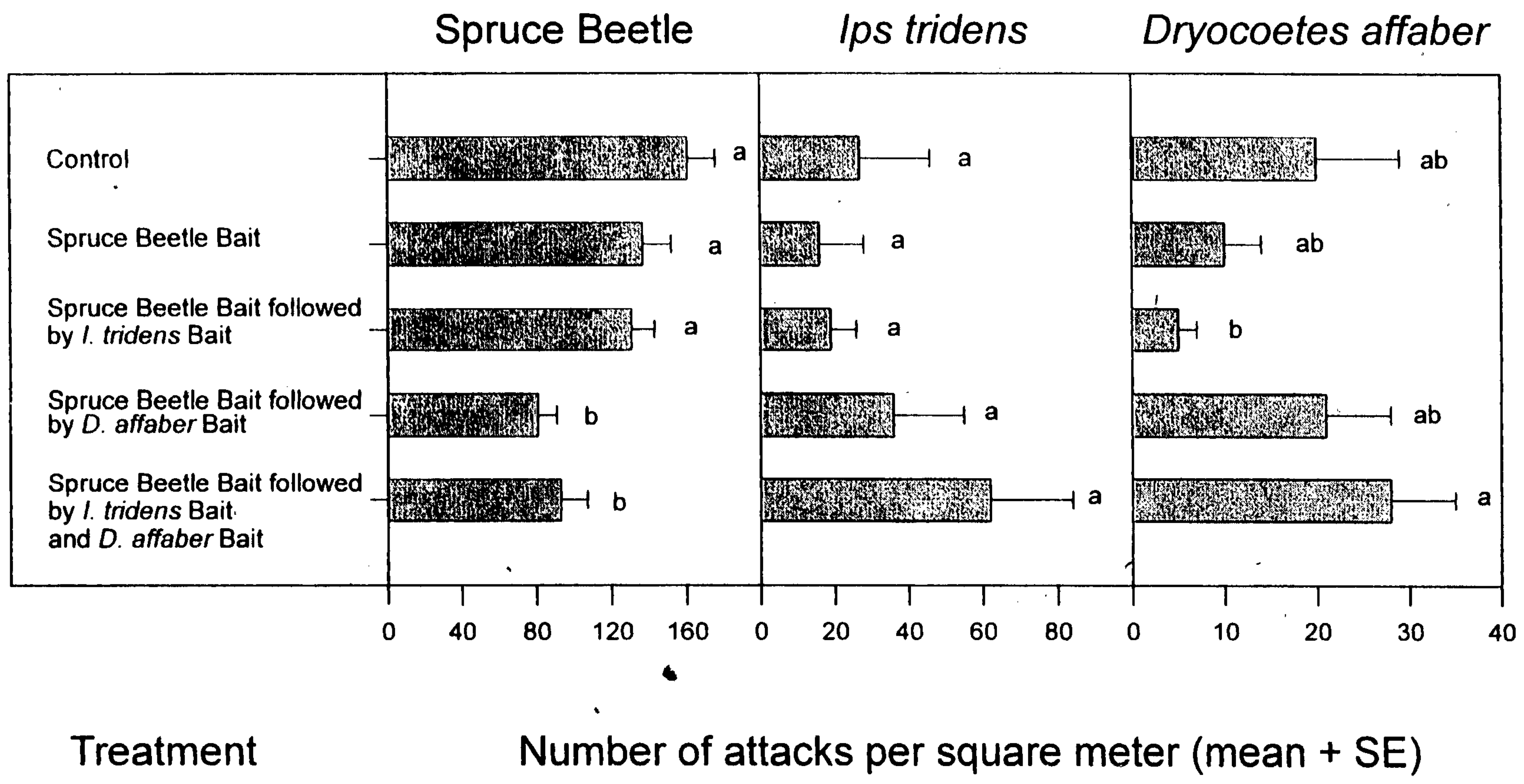

Spruce Beetle
Ips tridens
Dryocoetes affaber
Control
Spruce Beetle Bait
Spruce Beetle Bait followed by *I. tridens* Bait
Spruce Beetle Bait followed by *D. affaber* Bait
Spruce Beetle Bait followed by *I. tridens* Bait and *D. affaber* Bait
a
a
a
b
b
a
a
a
a
a
ab
ab
b
ab
a
0
40
80
120
160
0
20
40
60
80
0
10
20
30
40
Treatment
Number of attacks per square meter (mean + SE)

Figure 11 Spruce beetle, *I. tridens*, and *D. affaber* gallery lengths per m^2 in Experiment 10 (17 May - 9 August 1994), Arastra Creek, Princeton, B.C. Spruce beetle baits consisted of α-pinene and frontalin released at 1.5 mg and 2.6 mg per 24 h respectively. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h respectively. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. N=6. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

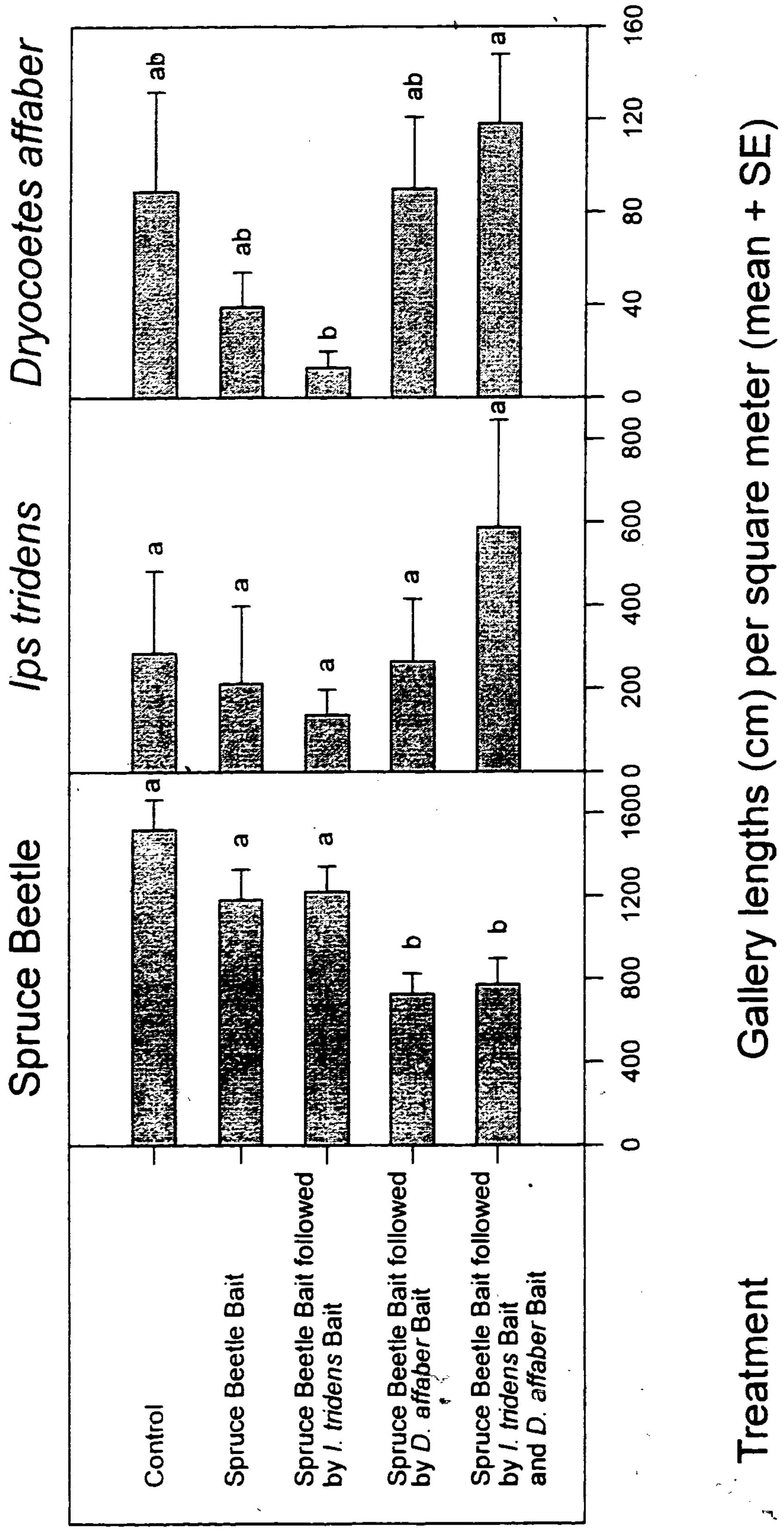
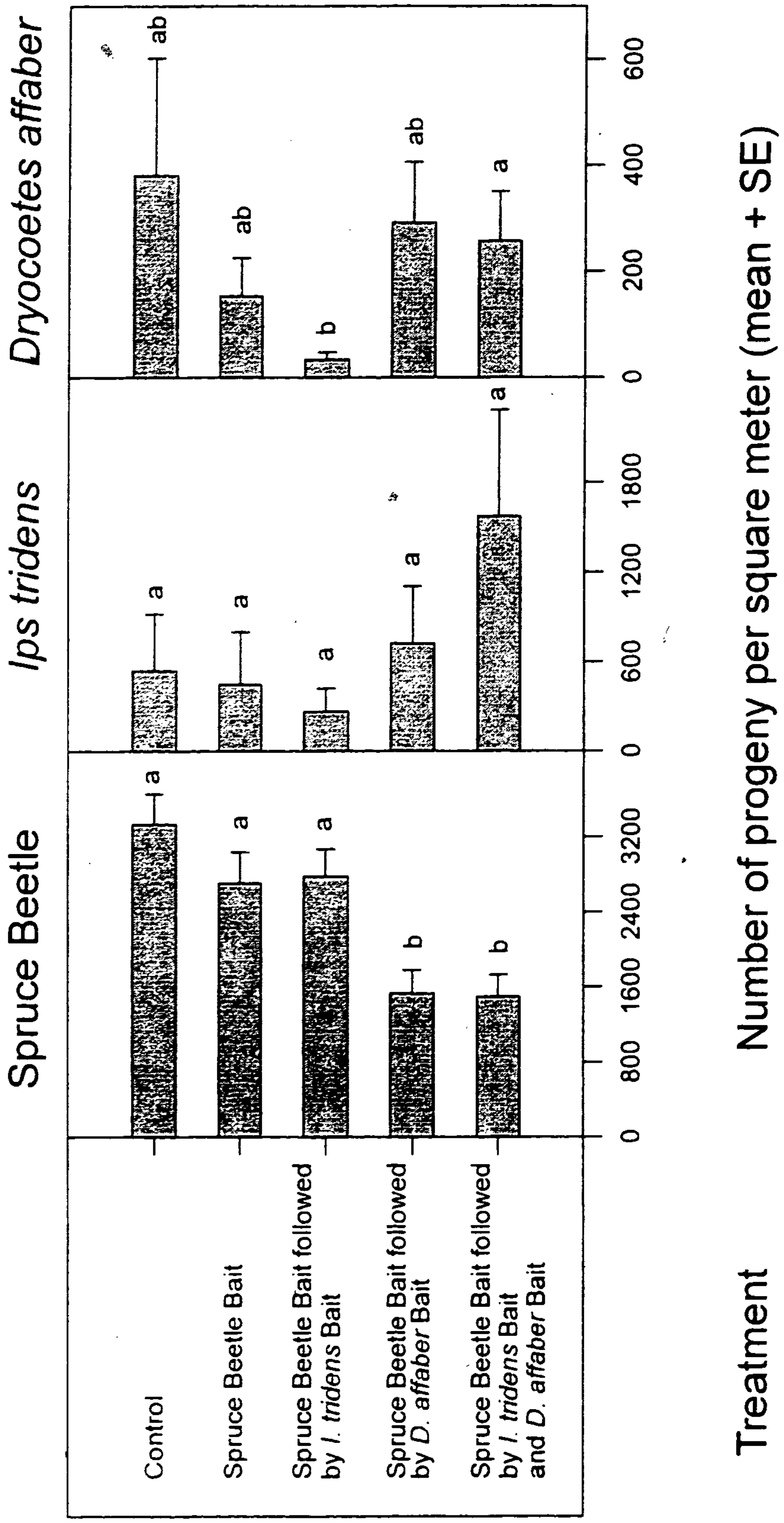

Spruce Beetle
Ips tridens
Dryocoetes affaber
Control
Spruce Beetle Bait
Spruce Beetle Bait followed by I. tridens Bait
Spruce Beetle Bait followed by D. affaber Bait
Spruce Beetle Bait followed by I. tridens Bait and D. affaber Bait
a
a
a
b
b
a
a
a
a
a
ab
ab
b
ab
a
0
400
800
1200
1600
0
200
400
600
800
0
40
80
120
160
Gallery lengths (cm) per square meter (mean + SE)
Treatment

Figure 12 Spruce beetle, *I. tridens*, and *D. affaber* progeny densities in Experiment 10 (17 May - 9 August 1994), Arastra Creek, Princeton, B.C. Spruce beetle baits consisted of α-pinene and frontalin released at 1.5 mg and 2.6 mg per 24 h respectively. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h respectively. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. N=6. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.


Spruce Beetle
Ips tridens
Dryocoetes affaber
Control
Spruce Beetle Bait
Spruce Beetle Bait followed by I. tridens Bait
Spruce Beetle Bait followed by D. affaber Bait
Spruce Beetle Bait followed by I. tridens Bait and D. affaber Bait
Treatment
Number of progeny per square meter (mean + SE)
0
800
1600
2400
3200
0
600
1200
1800
0
200
400
600
a
a
a
b
b
a
a
a
a
a
ab
ab
b
ab
a

variance showed a significant effect for treatment but not for replicate or position or for their interactions with treatment for spruce beetle attack density, gallery length per m^2, and progeny density, and for *D. affaber* attack density and gallery length per m^2.

Spruce beetle attack densities per m^2 were significantly decreased in trees that were baited with *D. affaber* baits or both *D. affaber* and *I. tridens* baits after spruce beetle establishment (Figure 10). *Ips tridens* attack density did not differ between treatments. *Dryocoetes affaber* attack densities were significantly higher on trees that were baited with pheromones of both secondary species than on trees baited with *I. tridens* pheromones, and were intermediate for unbaited control trees, trees baited with spruce beetle baits alone or spruce beetle baits followed by *D. affaber* baits.

Results for gallery length per m^2 for all three species followed the same trend as for attack densities (Figure11). Similarly, spruce beetle progeny density per m^2 was significantly reduced in trees on which spruce beetle baits were followed by *D. affaber* baits or baits for both secondary species (Figure 12). However, *I. tridens* and *D. affaber* progeny densities did not differ significantly between treatments.

Mean gallery lengths did not differ between treatments for the spruce beetle (range 8.3 - 9.4 cm, F=1.21, *P*=.505), *I. tridens* (range 6.8 - 11.0 cm, F=.50, *P*=.7313), or *D. affaber* (range 2.7 - 4.3 cm, F=0.71, *P*=.7313). Likewise, the number of progeny per gallery did not differ between treatments for the spruce beetle (range 16.3 - 20.6, F=1.49, *P*=.4197), *I. tridens* (range 11.9 - 27.5, F=1.04, *P*=.4860), or *D. affaber* (range 7.0 - 15.1, F=1.83, *P*=.3438).

At the end of the study all *D. affaber* progeny were at the larval stage of development whereas both late instar larvae and pupae were present for the spruce beetle and *I. tridens*. The frequency distributions of larvae and pupae did not differ significantly between treatments for either species (X^2 test, min $P > 0.08$) and ranged from 4.8 % to 10.3 % pupae for the spruce beetle and 6.5% to 12.9% pupae for *I. tridens*.

For each species, gallery length per m^2 and progeny density per m^2 differed significantly between its attack density classes but not between attack density classes of the other species. In no case was there a significant effect for the interactions between attack density classes. Therefore, high attack densities per m^2 for one species was not associated with low values for gallery length per m^2 or progeny density per m^2 for another species (max F=2.13 , min *P*=.1263).

4.4 Discussion

The results of this experiment demonstrate that there was a significant proportion of negative correlations between spruce beetle attack and progeny densities and those of *I. tridens* and *D. affaber* suggesting that the secondary species are negatively associated with and may interact competitively with the spruce beetle (Table 2). Baiting trees with *D. affaber* baits or *I. tridens* and *D. affaber* baits together following spruce beetle establishment reduced subsequent attacks, total gallery construction, and total progeny production by the spruce beetle (Figures 10-12). However, there was no effect of treatment on mean spruce beetle length per gallery, or number of progeny per gallery, nor was there an effect for any species on progeny developmental stage. In addition, within the range of densities achieved, high attack density for any one species was not associated with low gallery lengths per m^2 or progeny density for any other. In general, however, the attack densities for the two secondary species (Figure 10) were probably low because the trees were already heavily attacked by the spruce beetle before baits for the secondary species were attached. Therefore, very limited resources were available for colonization by the secondary species.

Resource exploitation was found to be the main factor in competitive interactions between the pine engraver and the mountain pine beetle (Rankin and Borden 1991). Secondary bark beetles may have a competitive advantage over primary tree killing species because they have shorter life cycles and thus develop and exploit the limited resources more rapidly (McCambridge and Knight 1972; Rankin and Borden 1991). The rapid development of secondary species may also cause the phloem resource to desiccate and deteriorate more quickly than when colonized by the spruce beetle alone. However, in this experiment spruce beetles were allowed to colonize and exploit the resource prior to attack by the secondary species, and warm, dry weather resulted in as rapid development of the spruce beetle as for the secondary species. By the time of the second bark sample collection, most spruce beetle progeny had reached a late instar larval stage and numerous pupae were observed. Therefore, spruce beetles may have had an advantage over the secondary species in resource exploitation. Colonization by the secondary species was limited and the negative effects of competition on the spruce beetle were not strong (Table 2, Figures 10-12).

Timing of secondary species bait placement may have a significant effect on colonization and success by the interacting species of beetles. Safranyik et al. (1995) found that co-baiting trees with mountain pine beetle and pine engraver baits prior to the mountain beetle flight period significantly reduced mountain pine beetle attack density, gallery lengths per m^2, and progeny density compared to control trees baited with mountain pine beetle baits alone. Co-baiting with pine engraver baits one week or three weeks after commencement of mountain pine beetle flight did not significantly reduce attack density or total progeny density of the mountain pine beetle. Pine engraver attacks did not differ significantly between treatments but were numerically highest on trees that were baited prior to mountain pine beetle flight. On trees that were baited with pine engraver baits alone, pine engraver attacks were highest when the timing of bait placement was after attack by the mountain pine beetle. The time lag in maximum pine engraver attack was probably related to host resistance and inhibitory effects of the pheromones of the mountain pine beetle (Safranyik et al. 1996).

My results for the spruce beetle are very similar to those of Safranyik et al. (1995), and suggest that early baiting for the secondary species would have been more effective. The mean spruce beetle gallery length at the time the secondary species baits were affixed to the trees was almost 5.0 cm, indicating that spruce beetle attacks had probably commenced approximately one week previously. It appears that for competitive displacement to be successful, inducing attack by secondary species as soon as possible after spruce beetle attack is necessary to minimize the advantage of spruce beetles in resource exploitation. In this experiment, the window of opportunity had already partially closed only one week after spruce beetle attack. Timing of operational treatment within this window would be virtually impossible.

Interference has also been implicated as a mechanism of competition for bark beetles. It could occur through direct or indirect interactions. Beetles in competing species can cause damage to one another directly through aggressive encounters or cannibalism. Intraspecific cannibalism is a significant mortality factor for several species of bark beetles, with large larvae eating straight through the small ones as they elongate their galleries (Beaver 1974). Spruce beetles are much larger than *I. tridens* or *D. affaber* and might have an advantage in direct aggressive encounters. However, if secondary species were allowed to attack simultaneously with or shortly after the spruce beetle and developed more rapidly, their larvae could be larger than recently hatched spruce beetle larvae. Direct interference was unlikely to be a factor in this experiment since gallery lengths, numbers of progeny per gallery and progeny developmental stages within a species did not differ significantly between treatments and there was no effect of attack density class of any species on total gallery lengths per m^2 or progeny density per m^2 of any other species.

Indirect interference occurs when members of one species interfere with access to a shared resource by destroying it or blocking it from another species. Inoculation with specific fungi associated with beetles of one species may render the phloem unacceptable to beetles of a competing species (Fox et al. 1992). However, no evidence has been found for fungal incompatibilities between the spruce beetle, *I. tridens*, and *D. affaber*. From beetles and from phloem adjacent to their galleries, I isolated *Ophiostoma piceae*

(Munch) H. & P. Sydow, *O. piliferum* (Fries) H. & P. Sydow, and *O. olivaceum* Mathiesen from the spruce beetle, *O. picea* from *I. tridens*, and *O. picea* and *O. olivaceum* from *D. affaber*. Previous studies have also found *O. piceaperda* (Rumb.) von Arx. and *O. coerulescens* (Munch) Nannf. associated with the spruce beetle (Safranyik et al. 1993). No species of fungi has been isolated that is unique to either of the secondary species. In addition, I have found no antagonism between *O. picea*, *O. piliferum*, and *O. olivaceum* when they were grown on malt agar. Growth of *O. piceae* appeared to be somewhat enhanced in the presence of *O. olivaceum* and growth of *O. olivaceum* appeared somewhat inhibited in the presence of *O. piceae*. However, there was no zone of inhibition between colonies of the latter two species and their hyphae readily intermingled.

Bark beetles could also interfere with access to the phloem resource by competitors through semiochemical inhibition. The pheromones of both *D. affaber* and *I. tridens* disrupted attraction of the spruce beetle to spruce beetle lures, whereas spruce beetle lures enhanced attraction of *D. affaber* to its pheromone (Chapter 3, Figures 4,9) After spruce beetles were established and secondary species baits were attached to the trees, inhibition of subsequent spruce beetle attack was probably the most important factor in reducing overall spruce beetle gallery length per m^2 and progeny density, because attacks by the secondary species were not significantly enhanced and no evidence of direct interference was found. Similarly, reduction in mountain pine beetle attack and total brood production was mainly due to the adverse effect of the pine engraver bait on the establishment of attacks by the mountain pine beetle (Safranyik et al. 1995).

There is increasing evidence that synomonal interference with access to a resource by competitors through reciprocal semiochemical inhibition is an adaptive mechanism for bark beetles to avoid competitive encounters (Borden 1975; Byers 1989). After host colonization, bark beetles are completely confined within the limited two-dimensional phloem where intra- and interspecific competition can be severe. Therefore, individuals that can avoid competition by means of genetically controlled behavioral mechanisms would be naturally selected for. Other mechanisms for avoidance of detrimental competition may involve gustatory and auditory detection to avoid intersecting nearby galleries while tunneling, and re-emergence if the probability of finding a more suitable host is high (Byers 1989). Olfactory mechanisms for avoiding competition would be mutually advantageous to competing species because energetic and time costs are low compared to other avoidance mechanisms employed after initiating attack. Mutual olfactory interference would allow the first colonizing species to reserve scarce host material and the perceiving species to avoid direct competition with an already established species (Birch 1978; Light et al. 1983; Rankin and Borden 1991; Borden et al. 1992; Paine and Hanlon 1992, Bertram 1994).

My results provide further evidence for the occurrence of interspecific competition in natural insect communities. Such evidence may be inferred if manipulation of the abundance of one species results in a change in density, fecundity or mortality, or niche realization of another species (Schoener 1983; Connell 1983). The results of Experiment 10 showed that manipulations that resulted in numerically enhanced abundance of secondary species through semiochemical-induced attack resulted in reduced attack density, gallery length per m^2, and progeny density of the spruce beetle (Figures 10-12). While there were no significant differences in *I. tridens* attack densities between treatments, they were numerically highest and *D. affaber* attacks were significantly highest in trees that were co-baited with pheromones of both secondary species after spruce beetle attack. As a result spruce beetle attack density was negatively associated with attack densities of both secondary species (Table 2). The most common mechanism of competition reported in published studies was consumptive exploitation (Schoener 1983). Similarly, my results demonstrate that resource exploitation is a primary means of competition between the spruce beetle and associated secondary species. My results also fit the general pattern whereby competitive effects are most likely in patchy ephemeral habitats (Hanski 1987) and among species that are closely related, introduced, less mobile, aggregated, or feed on distinct common resources such as phloem (Denno et al. 1995). Because pioneer species tend to be good dispersers, the spruce beetle may be a better disperser than the secondary species. Therefore, the spruce beetle may be able to locate and colonize breeding material with a patchy distribution throughout a stand and successfully exploit available resources before secondary species attack. Later colonizing species may be superior competitors. Baiting susceptible hosts with secondary species pheromones may interfere with colonization and resource exploitation by the spruce beetle and favor competition by the secondary species thus altering the relative merits of dispersal and competition and the outcome of interactions between the spruce beetle and the secondary species.

Resource exploitation and indirect interference through inhibition of access to the resource appear to be the most important mechanisms of competition between the spruce beetle, *I. tridens*, and *D. affaber*. Therefore, management tactics which aim to displace the spruce beetle by inducing attacks by secondary species after the spruce beetle has already become established in trees has limited utility. The impact of the secondary species would probably not be sufficient to retard the development of an outbreak, let alone to reduce an outbreak to a manageable level in a timely fashion.

5.0 Semiochemical-mediated competitive exclusion of spruce beetles from felled spruce trees using pheromones of *I. tridens* and *D. affaber*

5.1 Introduction

Because exploitation and indirect interference through synomonal interruption of spruce beetle attraction by secondary species are important mechanisms of competition, the tactic of competitive exclusion may be more promising than competitive displacement for management of the spruce beetle. Competitive exclusion would be used to prevent population buildup in areas with sub-outbreak populations and where abundant breeding material is available. This would be particularly effective if the pheromones of secondary species had a dual role in inhibiting spruce beetle attack while at the same time inducing secondary species to exploit available resources. Both interference and exploitation competition (Begon and Mortimer 1986) would be invoked.

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

5.2 Exclusion of spruce beetles from individual felled spruce trees

5.2.1 Methods

Three trap tree baiting experiments were conducted in forests of "interior"[1] spruce and subalpine fir near Mackenzie, B.C. For all three experiments trap trees (healthy, large diameter spruce trees) were felled individually approximately 30 m apart into the margins of the stand along rights-of-way. Trees were baited within one week of felling at three positions: 2 m from the severed butt; at the point where the bole measured 30 cm in diam.; and midway between the two. All baits were attached on the North or shaded side of the tree. At the end of each experiment rectangular bark sections (approximately 20 x 25 cm) were removed with a chisel and hammer and stored in plastic bags at -18 °C. The bark samples were analyzed by measuring the area of the bark sample, counting the number of galleries, entrance holes, eggs, larvae, pupae and callow adults of each species and measuring maternal gallery lengths. The identities of the attacking species were determined based on the characteristic shape and size of the galleries. In many instances parental beetles were present in the egg galleries and were used to confirm species identifications. A significant number of galleries formed by *P. rufipennis* were found and it was not possible to distinguish them from galleries formed by *D. affaber* unless adult beetles were present. Therefore, only galleries with adults present were tallied and measured which would tend to slightly underestimate attack density of *D. affaber*. A few *I. perturbatus* were also found. They were distinguished from *I. tridens* based on their larger body size, greater width to length ratio, and the conical and acute shape of the third declivital spine (Bright 1976). Their egg galleries tended to be significantly wider than those of *I. tridens*. In addition, *I. tridens* galleries generally appeared as contiguous pairs with only a thin septum of phloem between them. Therefore, based on gallery pattern and

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[1] White and Engelmann spruce are sympatric over large areas in British Columbia. Natural introgressive hybridization between the two species occurs resulting in a swarm of hybrids especially at mid elevations (Daubenmire 1974). Operationally, these hybrids are collectively referred to as "interior" spruce.

the presence of adult beetles, only those galleries formed by *I. tridens* were tallied and measured. Densities of each of the measured variables was computed by dividing their values by the area of the bark sample.

Experiment 11, conducted from 10 May to 4 August 1994, examined competitive interactions between the spruce beetle, *I. tridens*, and *D. affaber* and tested whether spruce beetle attack and success is reduced in logs that are baited with secondary species pheromones prior to spruce beetle flight. The experiment comprised eight replicates of four treatments: 1) unbaited control; 2) *I. tridens* pheromone; 3) *D. affaber* pheromone; and 4) *I. tridens* pheromone plus *D. affaber* pheromone. Trap trees were felled in five locations within 30 km of each other. All replicates were laid out within one location. *Ips tridens* and *D. affaber* pheromone baits were identical to those used in Experiment 10 (Chapter 4). On 7 July 1994 and 4 August 1994 three bark samples were removed from the areas immediately below each bait (or analogous positions on control trees). The first bark samples were taken approximately 40 cm to one side of the bait positions and the second bark samples approximately 40 cm to the other side of each bait position. Two replicates were eliminated from the experiment because baits had been removed and destroyed by animals (probably bears) prior to bark sample collection. A third replicate was removed from the analysis because no spruce beetle galleries were observed in any of the bark samples from any of the treatments including control trees.

Experiments 12 and 13, conducted from 16 May to 6 August 1995, tested whether simplified or racemic pheromone components were as effective as the enantiospecific pheromones of *I. tridens* and *D. affaber* in reducing spruce beetle attack and success on felled spruce trees. Experiment 12 comprised seven replicates of three treatments: 1) unbaited control; 2) *D. affaber* bait; and 3) (±)-*endo*-brevicomin. Experiment 13 comprised seven replicates of four treatments: 1) unbaited control; 2) *I. tridens* bait; 3) (±)-ipsdienol; and 4) (±)-ipsdienol plus amitinol. *Dryocoetes affaber* baits were identical to those used in Experiment 11 except that the Eppendorf tubes were placed in polyethylene bags (Phero Tech Inc.) instead of waxed carton containers. (±)-*endo*-Brevicomin baits were prepared in the same way as the *D. affaber* baits but contained only (±)-*endo*-brevicomin (95.6% pure, Phero Tech, Inc.) released at 0.2 mg per 24 h rather than the 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin. *Ips tridens* baits were identical to those used in Experiment 11. (±)-Ipsdienol baits consisted of 3 bubble caps each releasing (±)-ipsdienol at 0.2 mg per 24 h (Phero Tech, Inc.). Amitinol was synthesized by H.D. Pierce, Jr. (Dept. of Biological Sciences, S.F.U.) as described in Chapter 2 and was released from bubble caps at 0.02 mg per 24 h (Phero Tech, Inc.).

On 11 July 1995 two bark samples (approximately 20 x 25 cm) were removed from each tree in Experiments 12 and 13. One bark sample was taken from the location immediately below and approximately 40 cm to one side of the bait at the base of the tree and the second sample was taken equidistant from the bait at the butt and the bait at the midpoint of the bole (or the analogous position on control trees). A second set of four bark samples was collected from each tree in both experiments on 7-10 August 1995. Bark sections were removed from the positions immediately below and approximately 40 cm to the other side of each bait position, and from the point equidistant from the bait at the butt and the bait at the midpoint of the bole (or the analogous positions on control trees). Only two samples were collected from each tree during the first sampling period to provide an indication of early attack levels. The full set of four bark samples per tree was removed at the end of the experiment when complete information about gallery establishment and progeny production could be obtained for all species. Samples from the locations intermediate between baits were included to determine the range of efficacy of the baits on the large diameter section of the tree where spruce beetles may prefer to attack.

For Experiment 11, Spearman rank correlation coefficients were calculated by treatment for relationships between spruce beetle attack density and *I. tridens* and *D. affaber* attack densities for the second bark sample collection. Correlations were also determined for the relationships between spruce beetle progeny density and *I. tridens* and *D. affaber* progeny densities by treatment. These were compiled, not to describe in detail the relationship between the parameters being compared, but solely to determine if there was a negative association between the spruce beetle and the secondary species and if the relationships varied between treatments. The frequency of negative and positive correlations were compared by a log-likelihood ratio chi-square (G^2) test (Zar 1984).

For all three experiments, the data for the density of each of the measured variables was transformed by $\log_{10}(x + 1)$ to satisfy assumptions of normality and homoscedasticity (Zar 1984). For each bark sample collection period, the transformed data were analyzed by a univariate split-plot three factor ANOVA. The main effects in the model were treatment, replicate and the split-plot variable bark sample position. The model also tested for interactions between treatment and replicate and between treatment and position. Means for treatment and for position were compared by the REGW test (SAS 1990).

An analysis of the effect of attack densities of the three species on gallery construction and progeny production by each species was conducted to test for direct interactions between the spruce beetle and the secondary species. Attack densities of each species were classified into low, medium and high density classes based on the ranges of densities observed for each species. For the spruce beetle, the range of attack densities for each class were: low <15 per m^2; medium 15 to 30 per m^2; and high > 30 per m^2. For *I. tridens*, the range of attack densities for each class were: low <20 per m^2; medium 20 to 70 per m^2; and high > 70 per m^2. For *D. affaber*, the range of attack densities for each class were: low < 10 per m^2; medium 10 to 20 per m^2; and high > 20 per m^2. For each species transformed data, $\log_{10}(x + 1)$, for gallery length per m^2, progeny density per m^2, length per gallery, and number of progeny per gallery were analyzed by a split-plot ANOVA with model factors for spruce beetle attack density class, the split-plot variable *I. tridens* attack density class, and the interaction between them. A separate split-plot ANOVA was performed with model factors for spruce beetle attack density class, the split-plot variable *D. affaber* attack density class, and the interaction between them. In all cases $\alpha = 0.05$.

5.2.2 Results

In all three experiments the results for the two bark sampling periods were similar, but by the second sampling period responses for measured variables increased and showed increasing differences between treatments. Therefore, only results from the second bark sample collection are reported.

In Experiment 11, spruce beetle attack density was negatively associated with *I. tridens* attack density in all baited trees, most strongly so in trees baited with *I. tridens* baits or baits for both secondary species (Figure 13). Very similar relationships were seen between spruce beetle and *I. tridens* progeny densities (Figure 14). Spruce beetle attack density was negatively associated with *D. affaber* attack density in trees baited with *D. affaber* or *I. tridens* baits (Figure 15). Relationships between spruce beetle and *D. affaber* progeny densities were very similar (Figure 16). Unbaited control trees tended to have the highest spruce beetle attack and progeny densities and the lowest corresponding secondary beetle densities. Conversely, where attack densities by the secondary species were high, spruce beetle attack densities were low (Figures 13-16). While *P*-values for individual correlations tended to be large indicating that relationships were not significant, the frequency of negative correlations was signficantly greater than that of positive correlations ($G^2 = 3.56$, $P = .05$). Therefore, overall relationships between spruce beetle attack and progeny densities and those of the secondary species appeared to be negative.

ANOVA revealed a significant effect for treatment but not for replicate, position, or their interactions with treatment for attack density, gallery length per m^2, and progeny density per m^2 for all three species. Spruce beetle attack densities were significantly

Figure 13 Relationships between attack densities of the spruce beetle and *I. tridens* in felled spruce trees that were baited with *I. tridens* baits, *D. affaber* baits, or baits for both secondary species prior to spruce beetle flight.

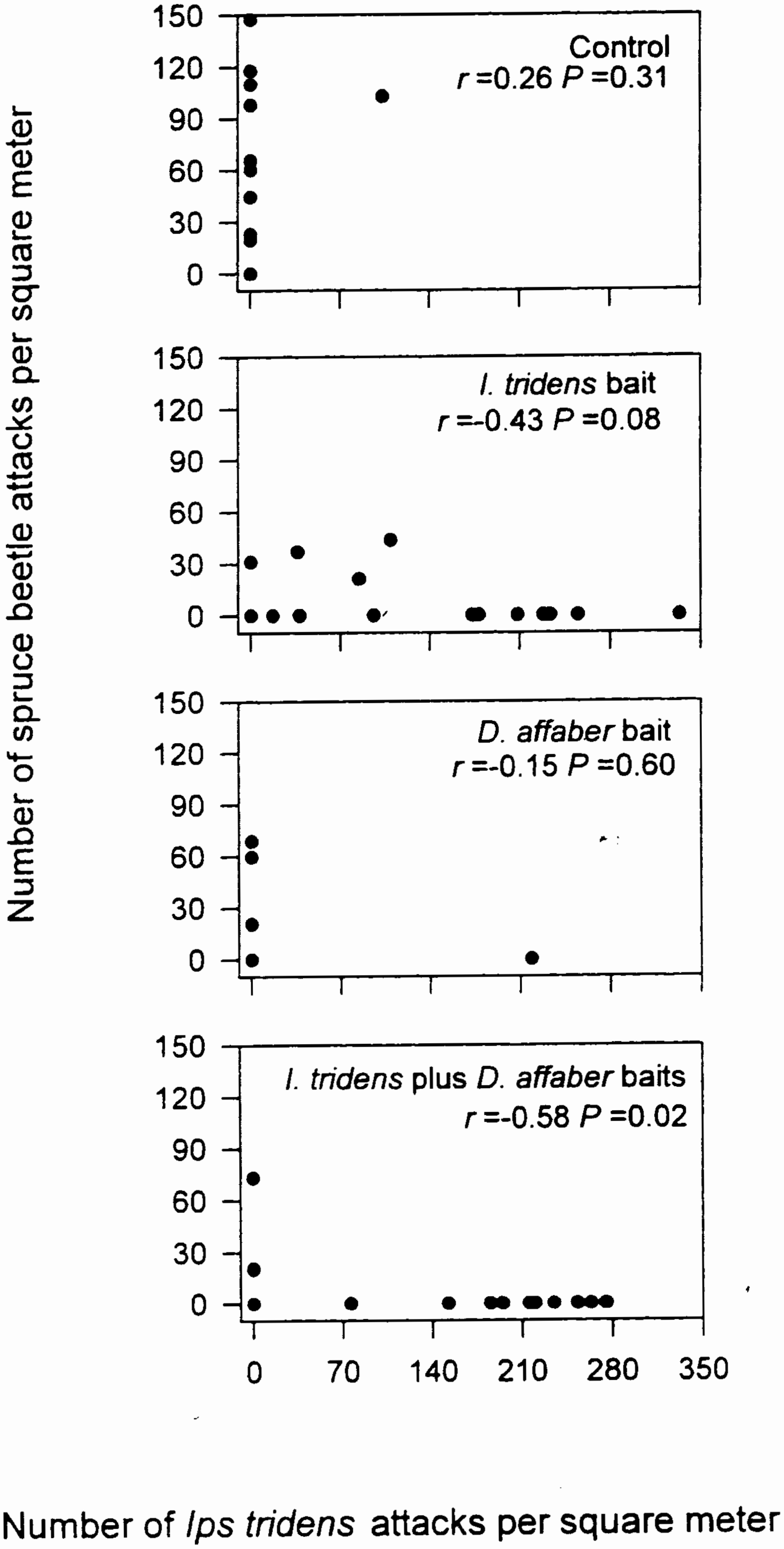

Number of spruce beetle attacks per square meter
150
120
90
60
30
0
Control
r =0.26 P =0.31
I. tridens bait
r =-0.43 P =0.08
D. affaber bait
r =-0.15 P =0.60
I. tridens plus *D. affaber* baits
r =-0.58 P =0.02
0
70
140
210
280
350
Number of *Ips tridens* attacks per square meter

Figure 14 Relationships between progeny densities of the spruce beetle and *I. tridens* in felled spruce trees that were baited with *I. tridens* baits, *D. affaber* baits, or baits for both secondary species prior to spruce beetle flight.

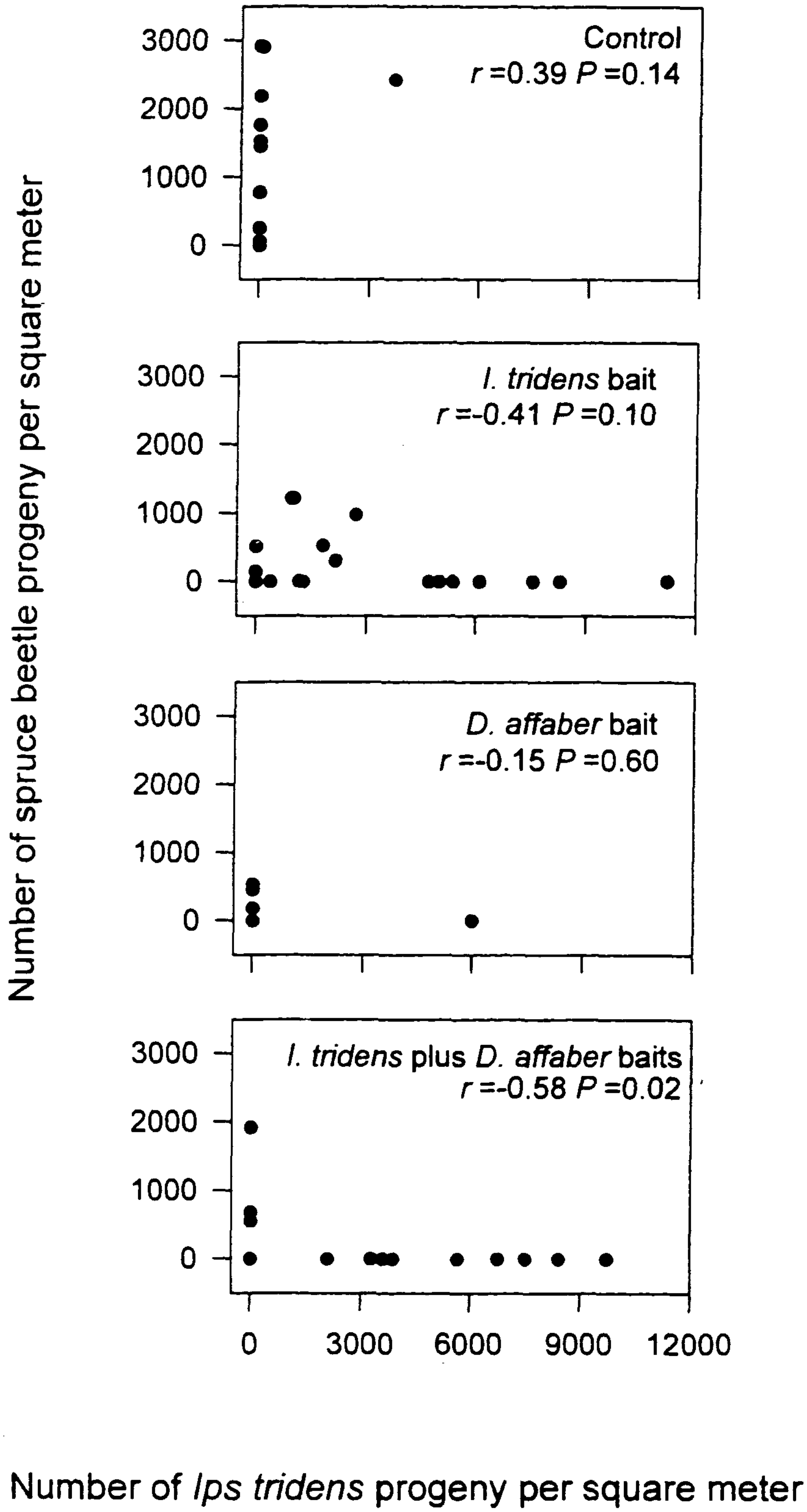

Control
r =0.39 P =0.14
I. tridens bait
r =-0.41 P =0.10
D. affaber bait
r =-0.15 P =0.60
I. tridens plus D. affaber baits
r =-0.58 P =0.02
3000
2000
1000
0
0
3000
6000
9000
12000
Number of spruce beetle progeny per square meter
Number of Ips tridens progeny per square meter

Figure 15 Relationships between attack densities of the spruce beetle and *D. affaber* in felled spruce trees that were baited with *I. tridens* baits, *D. affaber* baits, or baits for both secondary species prior to spruce beetle flight.

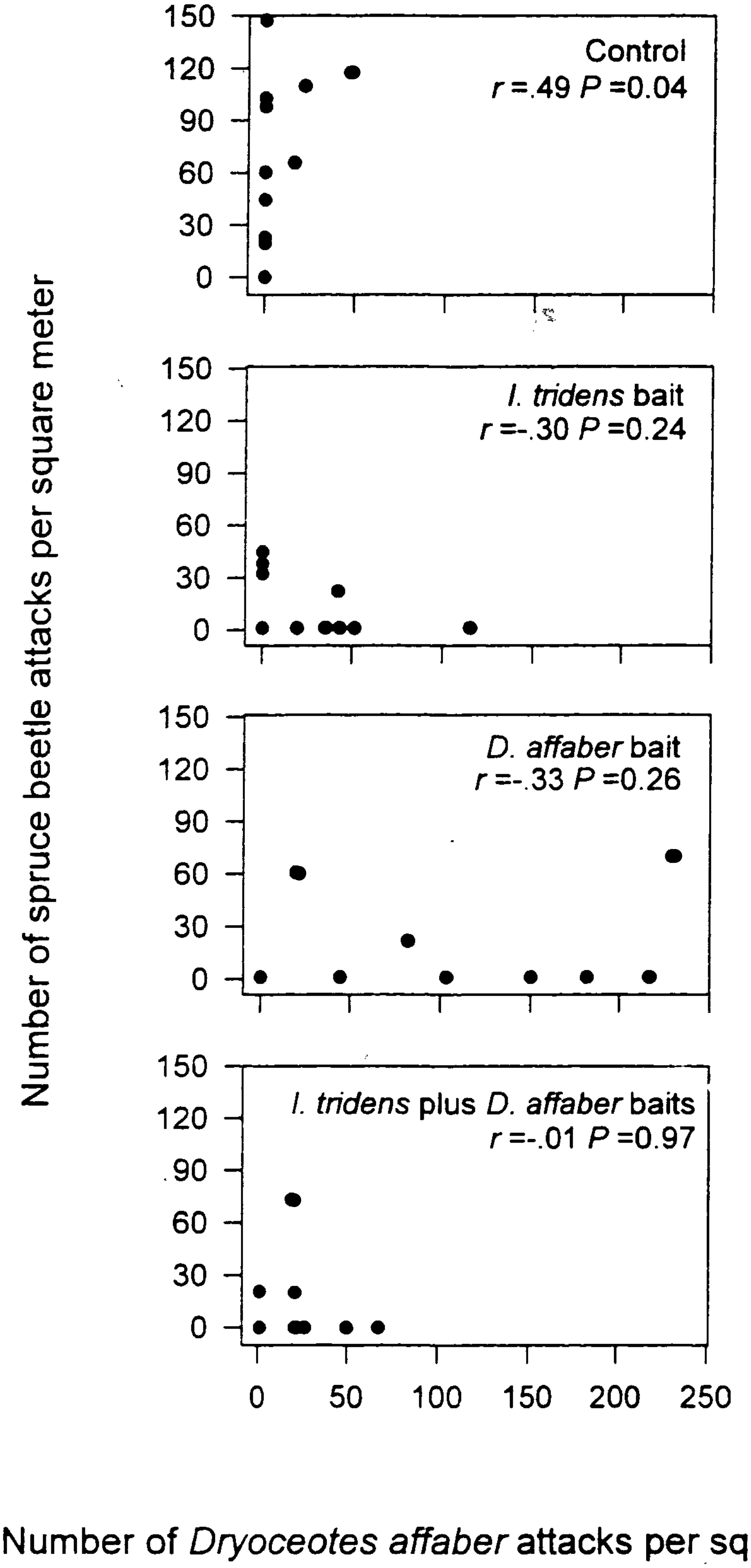
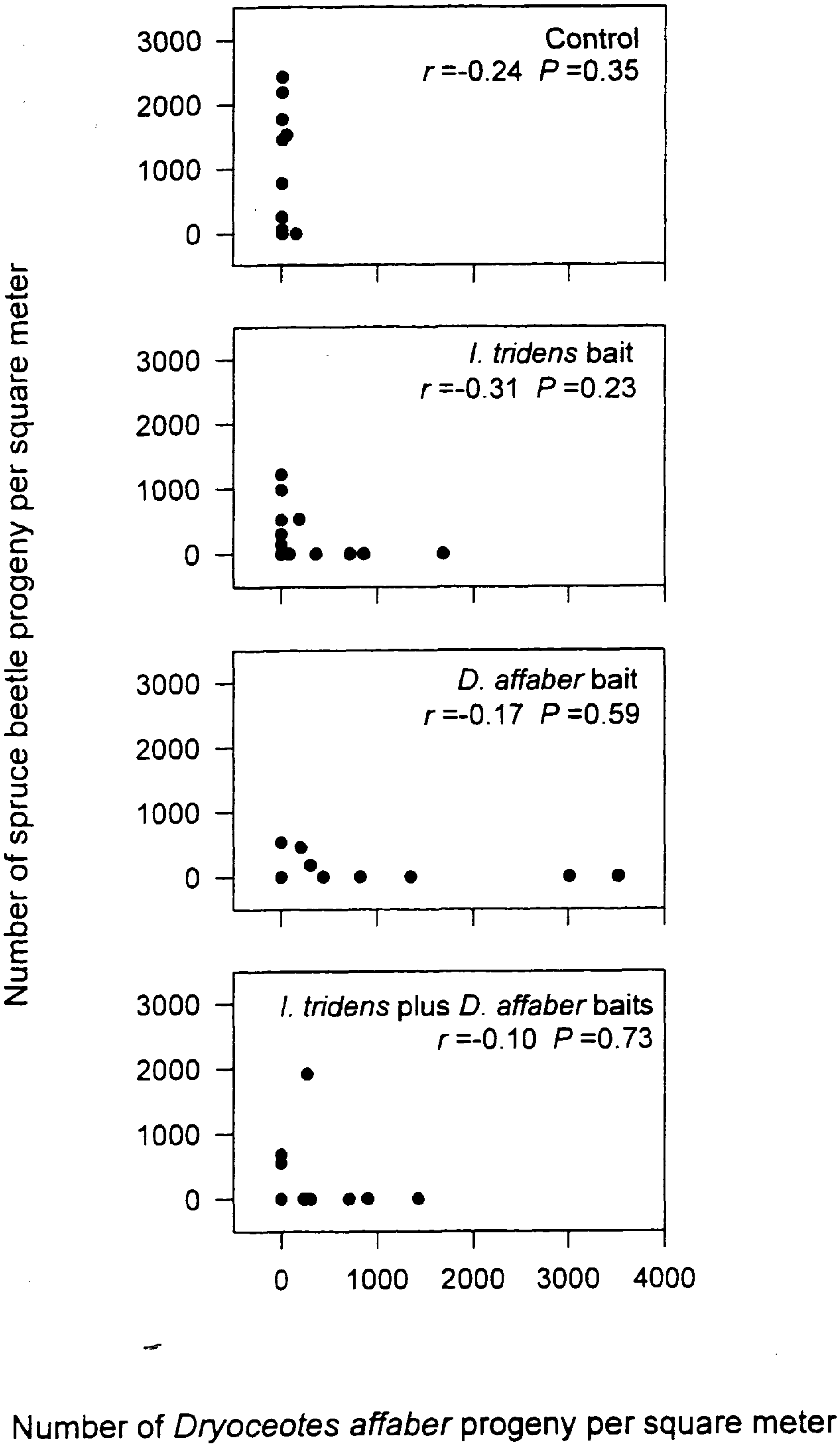

Control
r =.49 P =0.04
I. tridens bait
r =-.30 P =0.24
D. affaber bait
r =-.33 P =0.26
I. tridens plus D. affaber baits
r =-.01 P =0.97
150
120
90
60
30
0
0
50
100
150
200
250
Number of spruce beetle attacks per square meter
Number of Dryoceotes affaber attacks per square meter

Figure 16 Relationships between progeny densities of the spruce beetle and *D. affaber* in felled spruce trees that were baited with *I. tridens* baits, *D. affaber* baits, or baits for both secondary species prior to spruce beetle flight.


Control
r =-0.24 *P* =0.35
I. tridens bait
r =-0.31 *P* =0.23
D. affaber bait
r =-0.17 *P* =0.59
I. tridens plus *D. affaber* baits
r =-0.10 *P* =0.73
3000
2000
1000
0
0
1000
2000
3000
4000
Number of spruce beetle progeny per square meter
Number of *Dryoceotes affaber* progeny per square meter

reduced in trees that were baited with *I. tridens* baits, *D. affaber* baits, or baits for both secondary species compared to unbaited control trees (Figure 17). On the other hand, *I. tridens* attack density was significantly increased on trap trees baited with *I. tridens* baits alone or combined with *D. affaber* baits. Attacks by *D. affaber* were significantly increased on trees baited with *D. affaber* baits alone. Very similar patterns of responses were seen for gallery length per m^2 (Figure 18) and progeny density per m^2 (Figure 19) for all three species.

Mean length per gallery did not differ between treatments for the spruce beetle (range 5.7 - 10.4 cm, F= 1.28, *P*=.2115), *I. tridens* (range 8.8 - 10.5 cm, F=11.09, *P*=0.0859), or *D. affaber* (range 2.4 - 5.4 cm, F=1.00, *P*=.5634). Similarly, the mean number of progeny per gallery did not differ between treatments for the spruce beetle (range 8.2 - 29.1, F=1.41, *P*=.1274), *I. tridens* (range 26.2 - 28.5, F=1.89, *P*=.402), or *D. affaber* (range 8.0 - 19.0, F=1.90, *P*=.2464). All spruce beetle, *I. tridens*, and *D. affaber* progeny were at the larval stage at the time of the second bark sample. There were significant effects of attack density class within each species, but not between species on gallery length per m^2 and progeny density per m^2 (max F=2.16, min *P*=.1278).

In Experiments 12 and 13, ANOVA again showed that for attack density, gallery length per m^2, and progeny density per m^2, within each species the only significant effect was for treatment . The lack of significant effect for position indicates that the baits were as effective at inducing attack between baits as they were at each bait position.

In Experiment 12, spruce beetle attack densities were significantly reduced in trees that were baited with ($\pm$)-*endo*-brevicomin, but in contrast to Experiment 11 (Figure 17), not in trees that were baited with *D. affaber* baits (Figure 20). Both *I. tridens* and *D. affaber* attack densities were significantly increased in trees baited with ($\pm$)-*endo*-brevicomin compared to densities in unbaited control trees. Statistically identical patterns occurred for gallery length per m^2 (Figure 21) and progeny density per m^2 (Figure 22) for the spruce beetle and *I. tridens*. For *D. affaber*, gallery length per m^2 was highest in trees

Figure 17 Spruce beetle, *I. tridens*, and *D. affaber* attack densities in Experiment 11 (10 May - 4 August 1994), Mackenzie, B.C. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h respectively. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. N=5. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

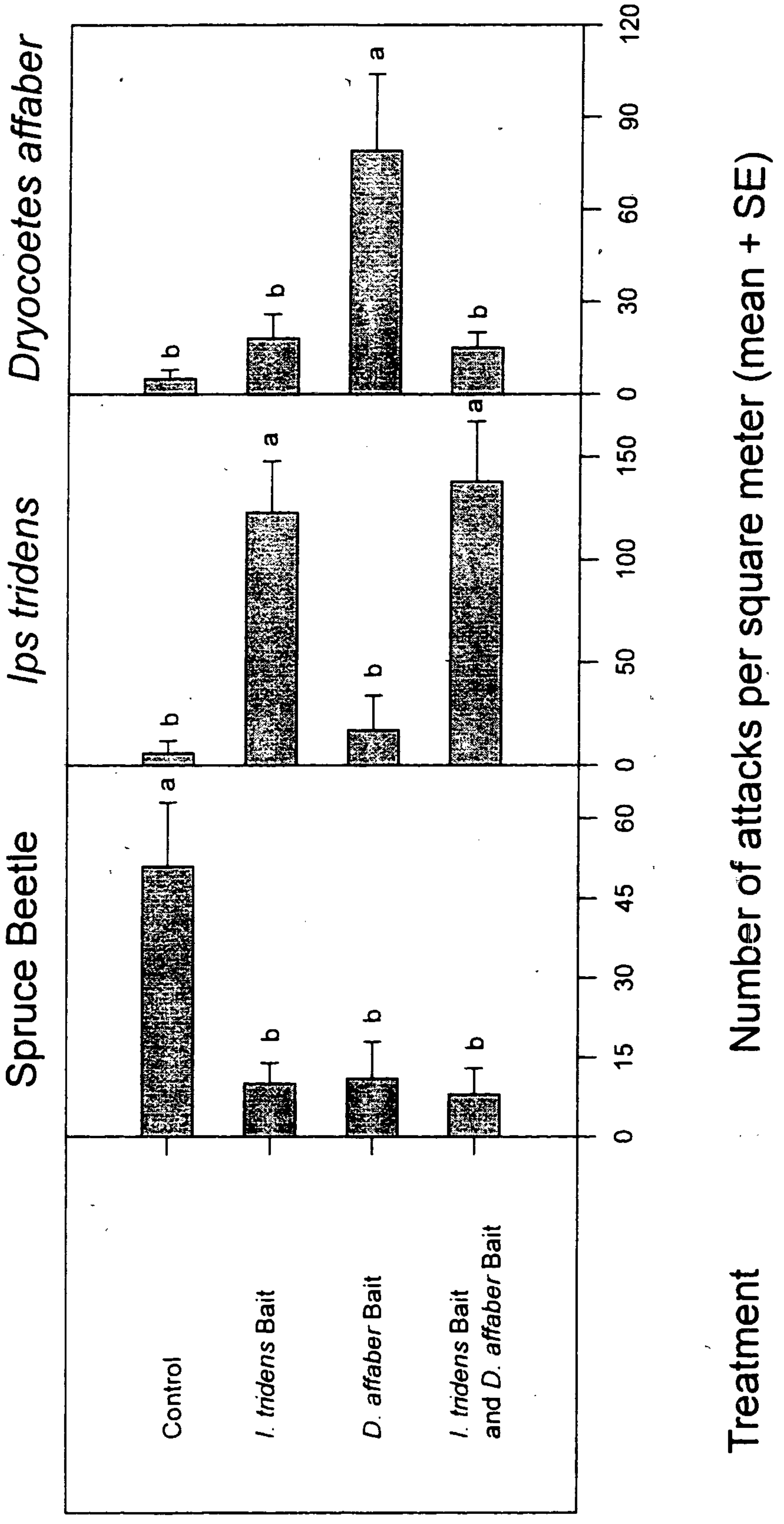

Spruce Beetle
Ips tridens
Dryocoetes affaber
Control
I. tridens Bait
D. affaber Bait
I. tridens Bait and D. affaber Bait
Treatment
Number of attacks per square meter (mean + SE)
0
15
30
45
60
0
50
100
150
0
30
60
90
120
a
b
b
b
b
a
b
a
b
b
a
b

Figure 18 Spruce beetle, *I. tridens*, and *D. affaber* gallery lengths per m^2 in Experiment 11 (10 May - 4 August 1994), Mackenzie, B.C. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h respectively. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. N=5. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

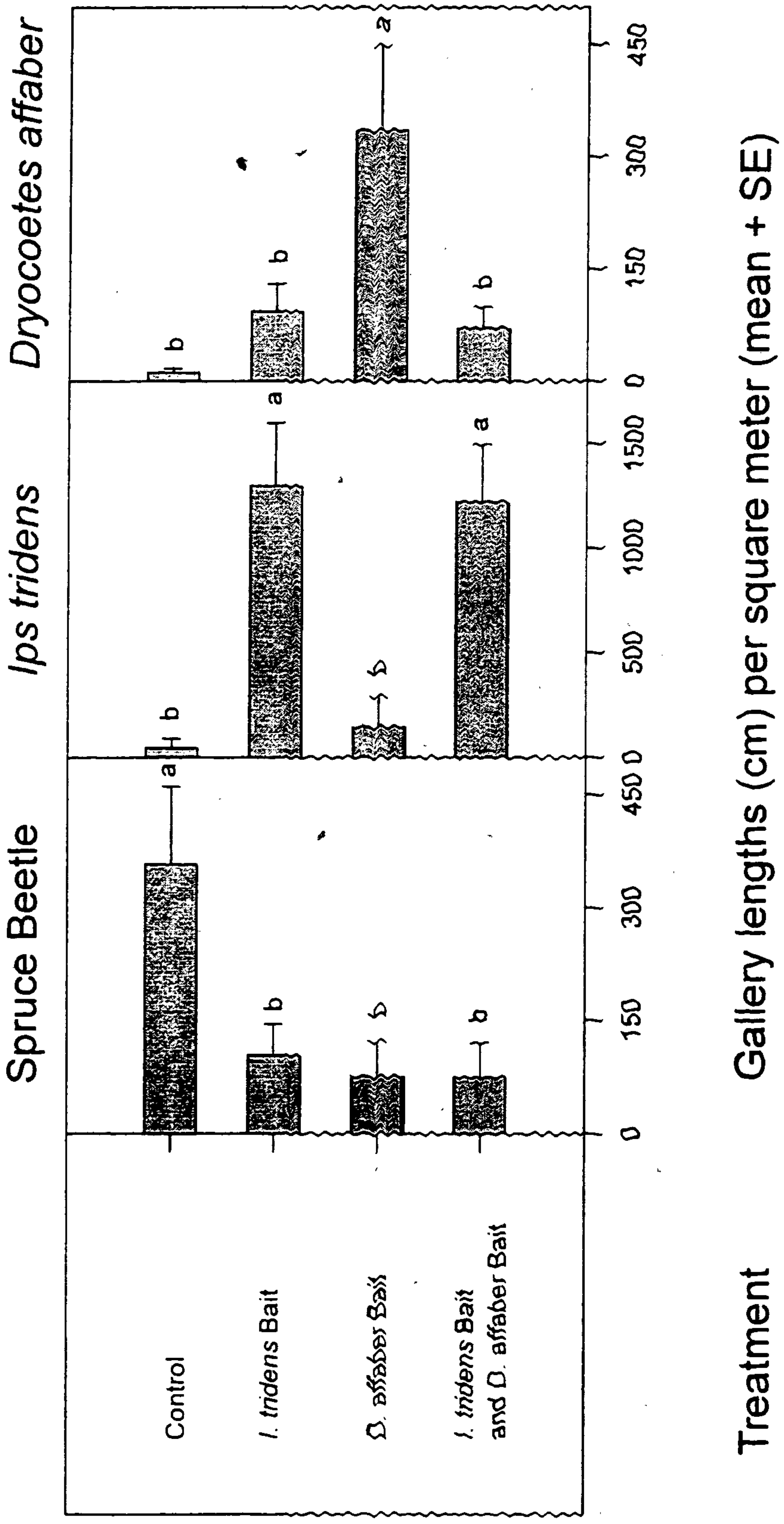

Spruce Beetle
Ips tridens
Dryocoetes affaber
Treatment
Control
I. tridens Bait
D. affaber Bait
I. tridens Bait and D. affaber Bait
Gallery lengths (cm) per square meter (mean + SE)
0
150
300
450
0
500
1000
1500
0
150
300
450
a
b
b
b
b
a
b
a
b
b
a
b

Figure 19 Spruce beetle, *I. tridens*, and *D. affaber* progeny densities in Experiment 11, (10 May - 4 August 1994), Mackenzie, B.C. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h respectively. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. N=5. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

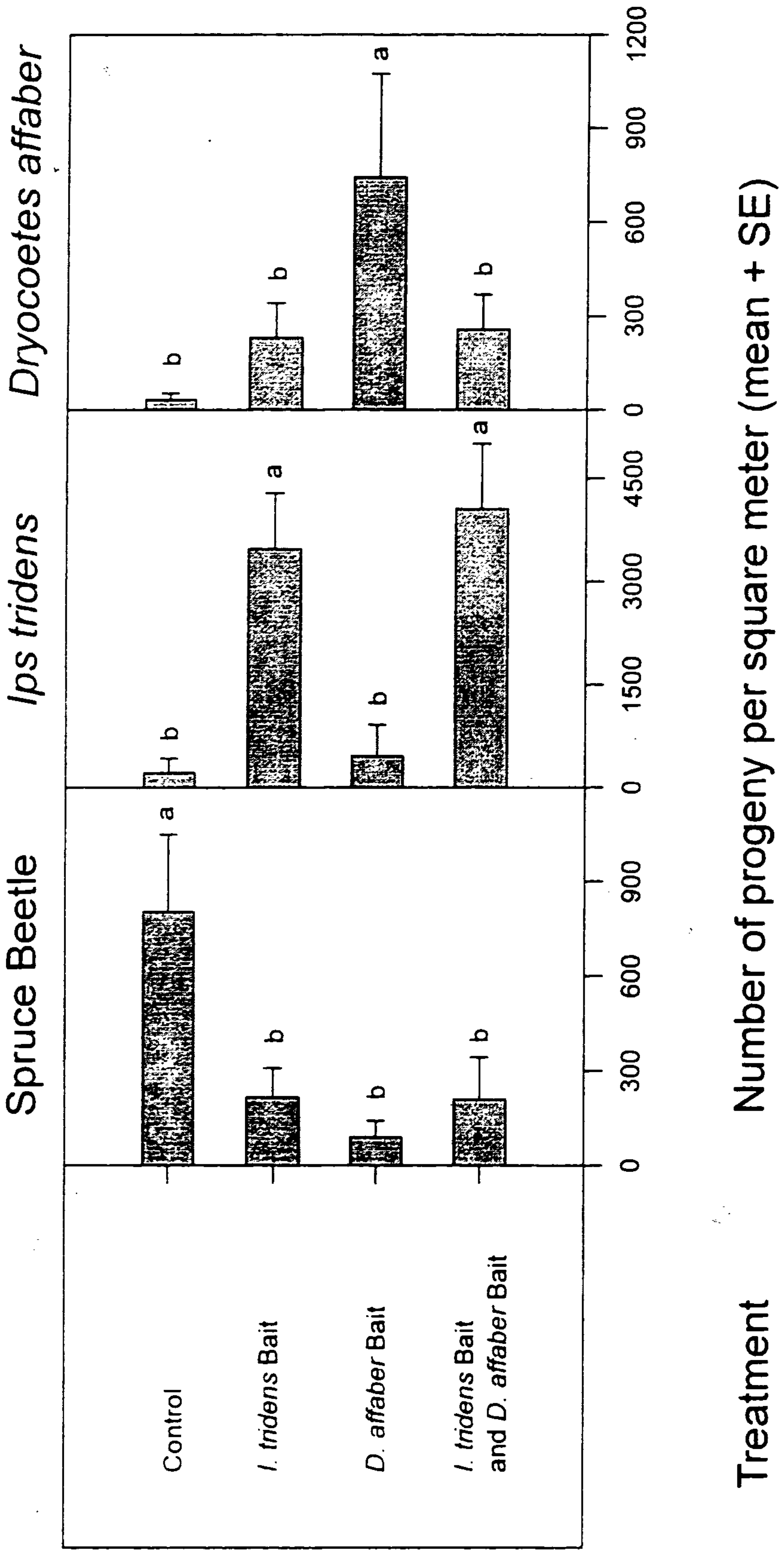

Spruce Beetle
Ips tridens
Dryocoetes affaber
Treatment
Number of progeny per square meter (mean + SE)
Control
I. tridens Bait
D. affaber Bait
I. tridens Bait and D. affaber Bait
0
300
600
900
0
1500
3000
4500
0
300
600
900
1200
a
b
b
b
b
a
b
a
b
b
a
b

Figure 20 Spruce beetle, *I. tridens*, and *D. affaber* attack densities in Experiment 12 (16 May - 6 August 1994), Mackenzie, B.C. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. (±)-*endo*-Brevicomin was released at 0.2 mg per 24 h. N=7. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

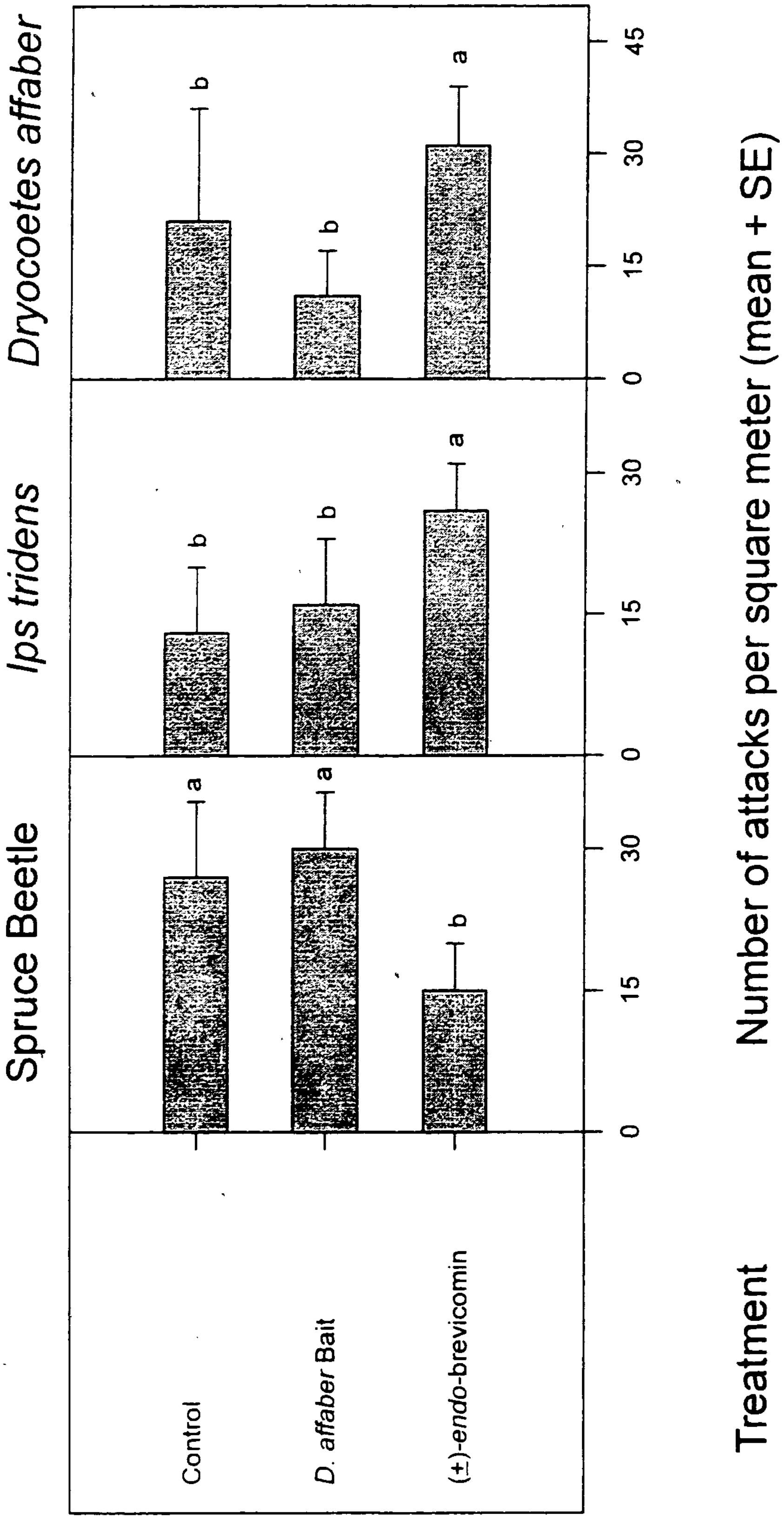

Spruce Beetle
Ips tridens
Dryocoetes affaber
Control
D. affaber Bait
(±)-endo-brevicomin
Treatment
Number of attacks per square meter (mean + SE)
0
15
30
45
a
a
b
b
b
a
b
b
a

Figure 21 Spruce beetle, *I. tridens*, and *D. affaber* gallery lengths per m^2 in Experiment 12 (16 May - 6 August 1994), Mackenzie, B.C. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. (±)-*endo*-Brevicomin was released at 0.2 mg per 24 h. N=7. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

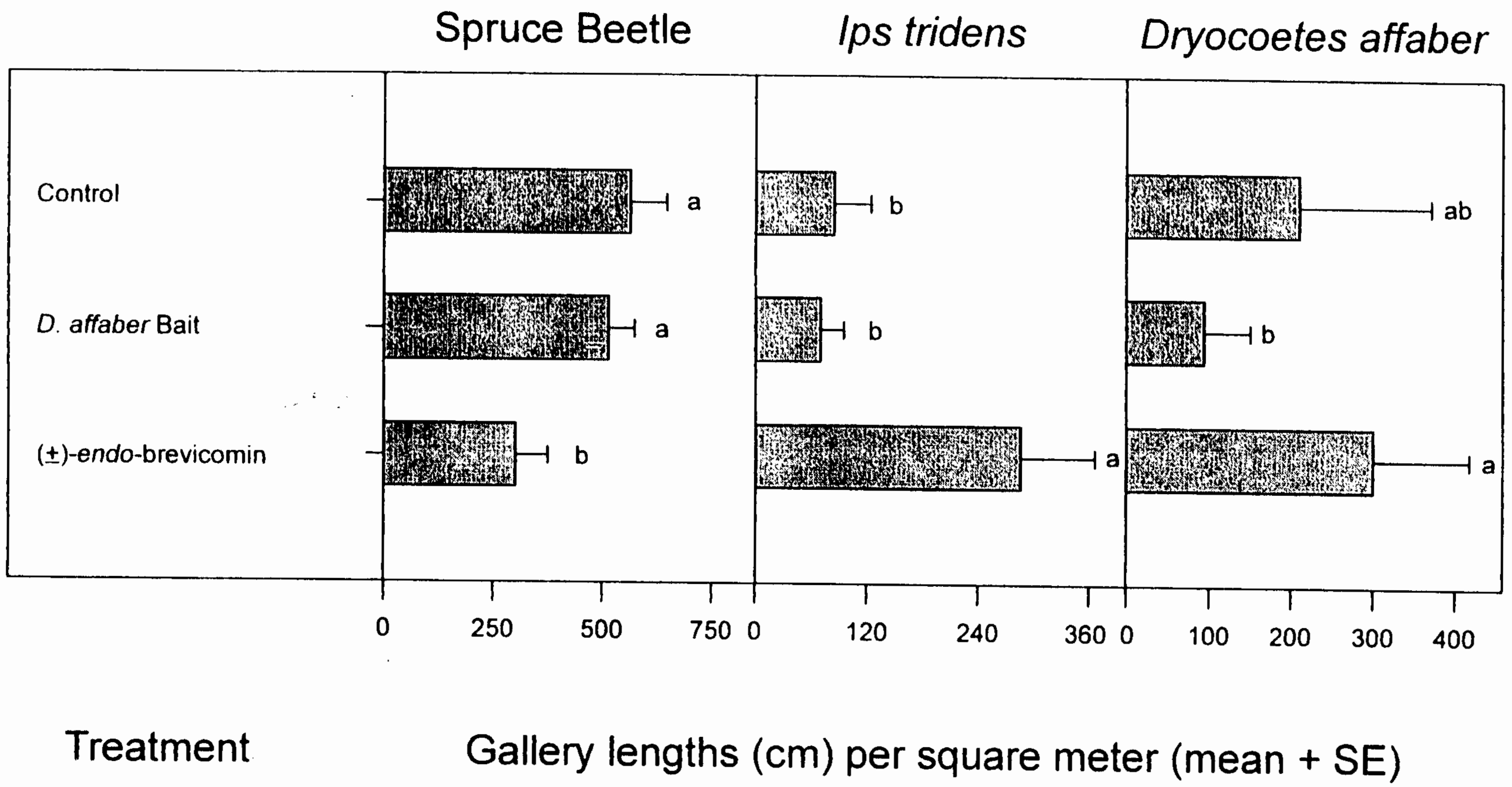
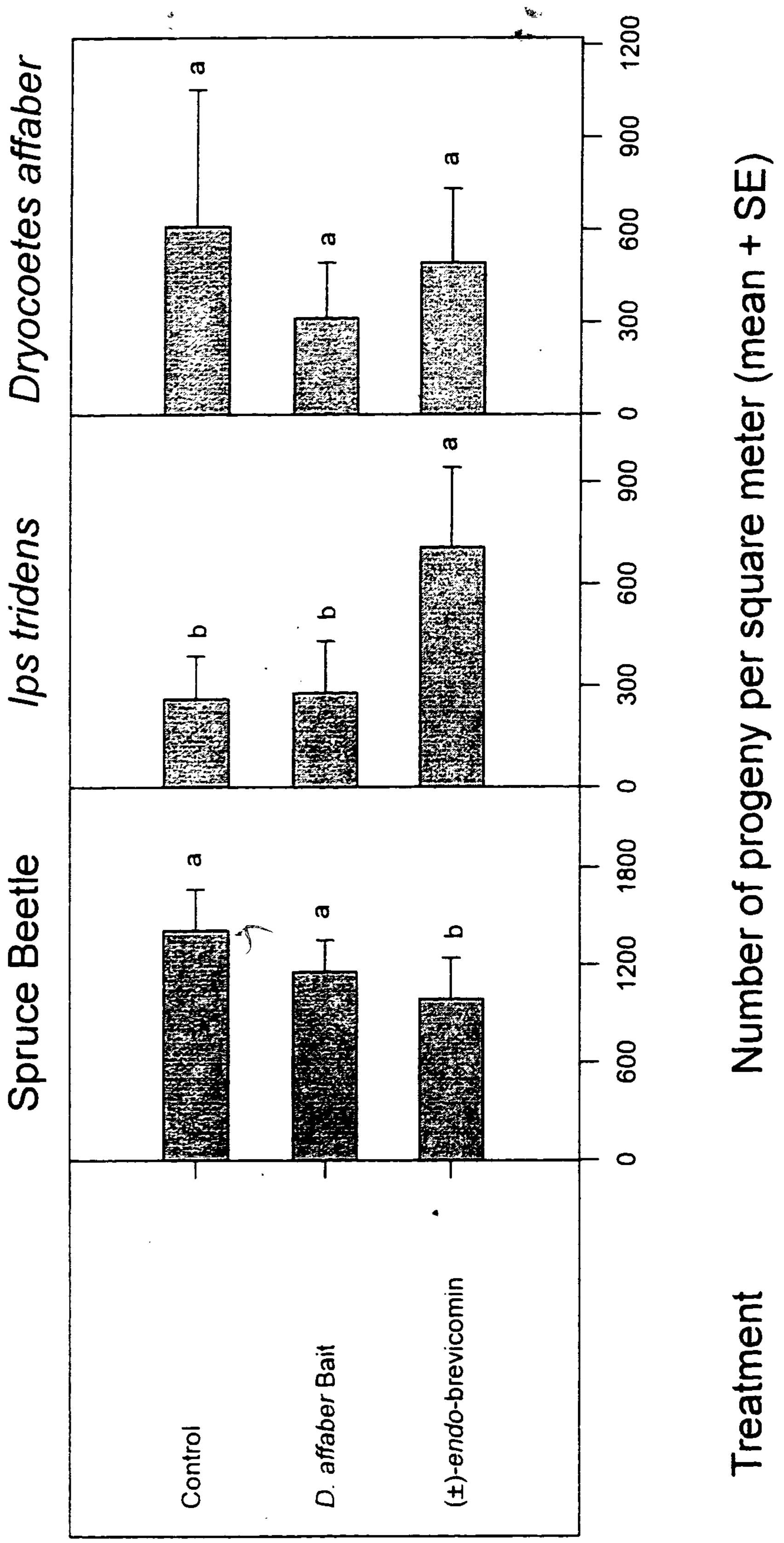

Spruce Beetle
Ips tridens
Dryocoetes affaber
Control
D. affaber Bait
(±)-endo-brevicomin
a
a
b
b
b
a
ab
b
a
0
250
500
750
0
120
240
360
0
100
200
300
400
Treatment
Gallery lengths (cm) per square meter (mean + SE)

Figure 22 Spruce beetle, *I. tridens*, and *D. affaber* progeny densities in Experiment 12 (16 May - 6 August 1994), Mackenzie, B.C. *Dryocoetes affaber* baits consisted of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin released at 0.2 mg per 24 h. (±)-*endo*-Brevicomin was released at 0.2 mg per 24 h. N=7. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.


Treatment
Control
D. affaber Bait
(±)-endo-brevicomin
Spruce Beetle
a
a
b
0
600
1200
1800
Ips tridens
b
b
a
0
300
600
900
Dryocoetes affaber
a
a
a
0
300
600
900
1200
Number of progeny per square meter (mean + SE)

baited with (±)-*endo*-brevicomin and lowest in trees baited with *D. affaber* baits (Figure 21) and progeny densities did not differ significantly between treatments (Figure 22).

In Experiment 13, spruce beetle attack density was significantly reduced only in trees that were baited with the *I. tridens* bait which consisted of (±)-ipsdienol plus *cis*-verbenol (Figure 23). Attack densities were not reduced in trees that were baited with (±)-ipsdienol alone or (±)-ipsdienol plus amitinol. Conversely, *I. tridens* attack densities were significantly increased in trees baited with *I. tridens* baits. There were no significant differences in *D. affaber* attack densities between the different treatments. Again, the patterns for gallery length per m^2 (Figure 24) and progeny density per m^2 (Figure 25) were statistically the same as those for attack density.

5.2.3 Discussion

The results of all three experiments show that when trees are baited with secondary species baits prior to spruce beetle flight, spruce beetle attack is inhibited and the secondary species are able to attack successfully and exploit the resource. There was a significant proportion of negative correlations between spruce beetle attack and progeny densities and attack and progeny densities of both secondary species in Experiment 11 (Figures 13-16). In unbaited control trees, spruce beetles were able to exploit the resource at the expense of the secondary species (Figures 17-19). Success of the secondary species was enhanced on trees baited with their respective pheromones allowing them to exploit the resource at the expense of spruce beetles (Figures 17-19). These results support the conclusion in Chapter 4 that resource exploitation and indirect interference in accessing the resource are important mechanisms of competitive interactions between the spruce beetle, *I. tridens*, and *D. affaber*. Differences in host preference by spruce beetles, *I. tridens*, and *D. affaber* are unlikely to account for differential degrees of success, because all trees in the study were similar

Figure 23 Spruce beetle, *I. tridens*, and *D. affaber* attack densities in Experiment 13 (16 May - 6 August 1994), Mackenzie, B.C. *Ips tridens* baits consisted of ($\pm$)-ipsdienol and *cis*-verbenol released at 0.6 and 1.8 mg per 24 h, respectively. ($\pm$)-Ipsdienol and amitinol were released at 0.6 and 0.02 mg per 24 h, respectively. N=7. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

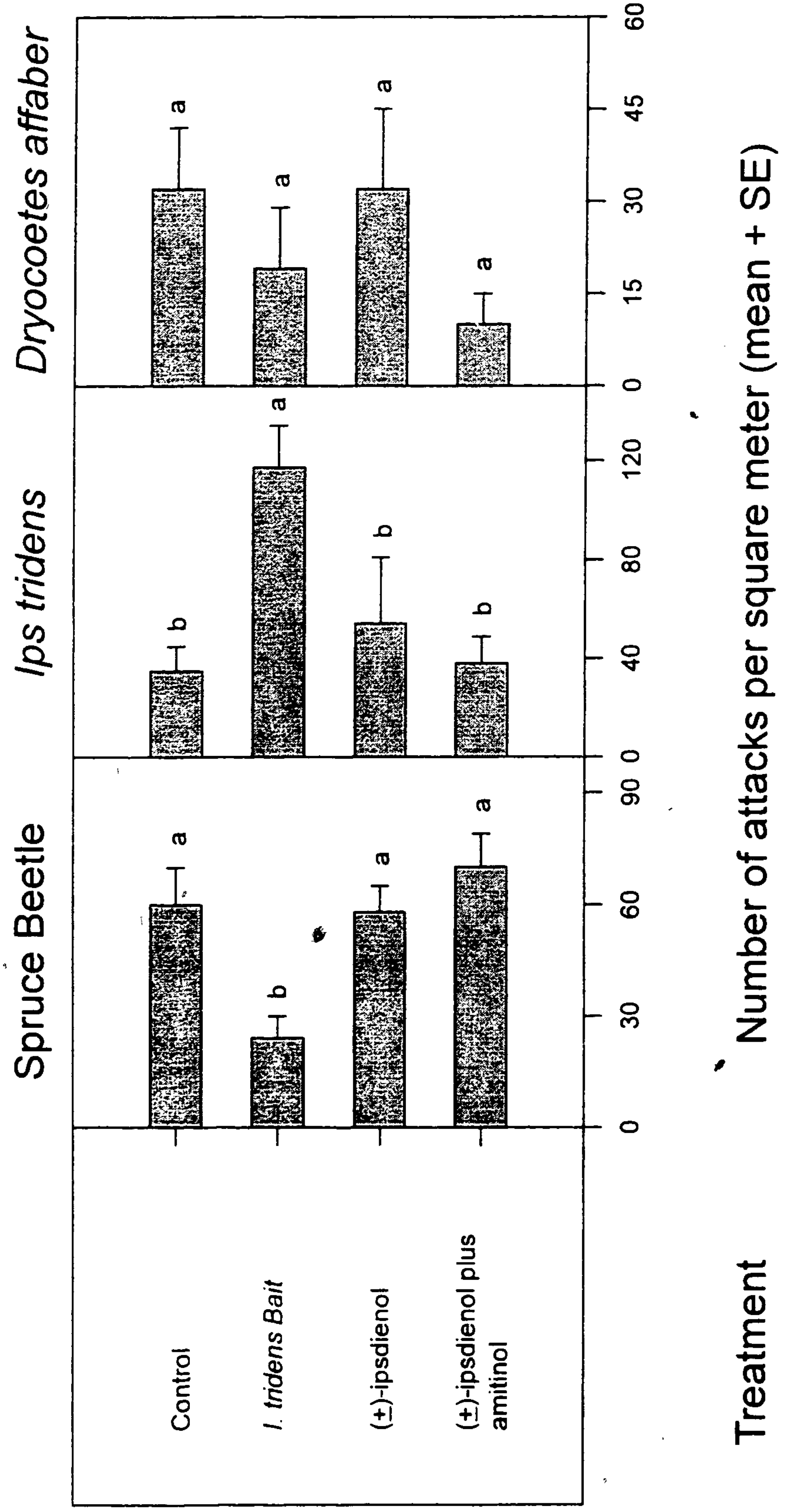

Spruce Beetle
Ips tridens
Dryocoetes affaber
Treatment
Control
I. tridens Bait
(±)-ipsdienol
(±)-ipsdienol plus amitinol
Number of attacks per square meter (mean + SE)
0
30
60
90
0
40
80
120
0
15
30
45
60
a
b
a
a
b
a
b
b
a
a
a
a

Figure 24 Spruce beetle, *I. tridens*, and *D. affaber* gallery lengths per m^2 in Experiment 13 (16 May - 6 August 1994), Mackenzie, B.C. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h, respectively. (±)-Ipsdienol and amitinol were released at 0.6 and 0.02 mg per 24 h, respectively. N=7. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

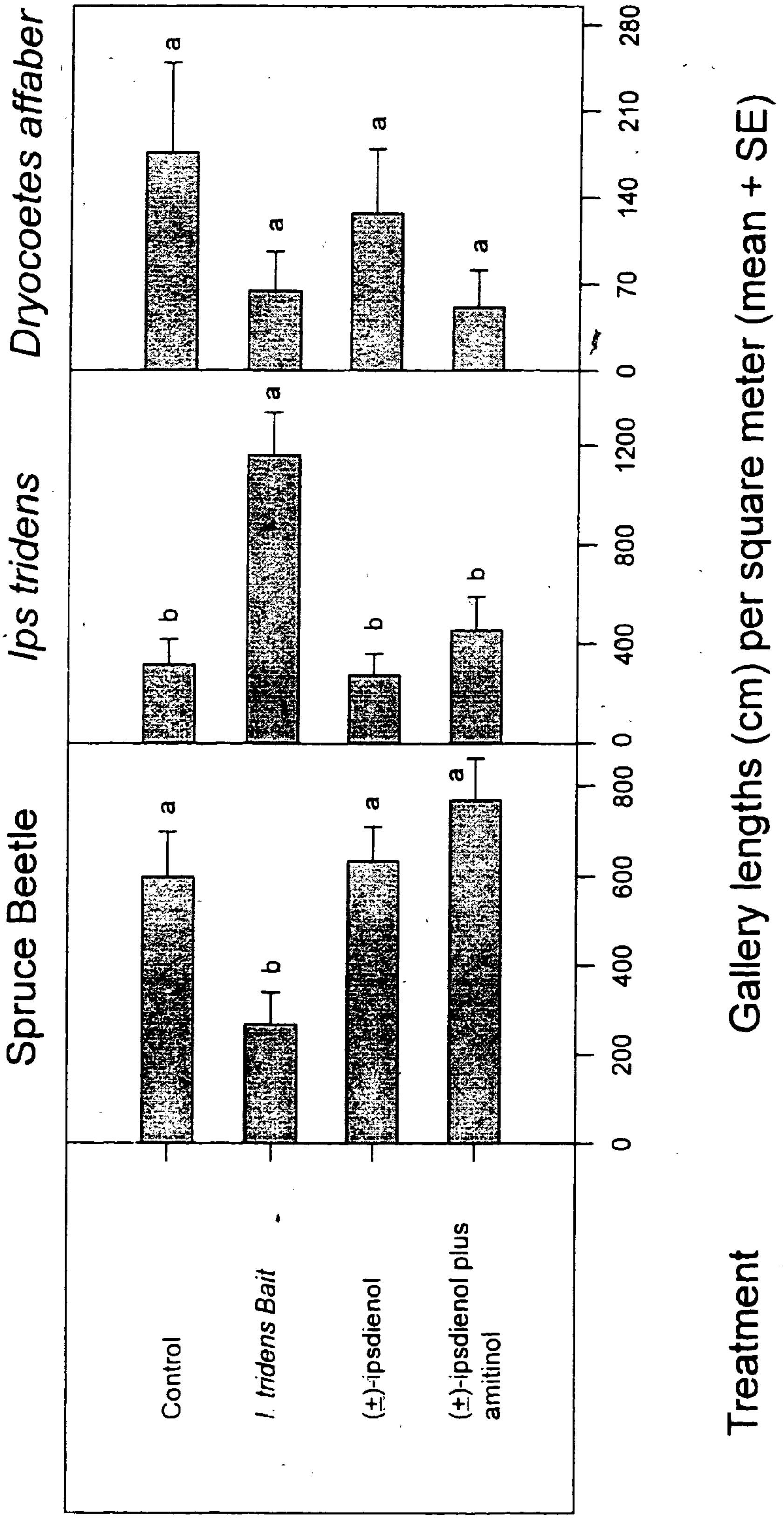
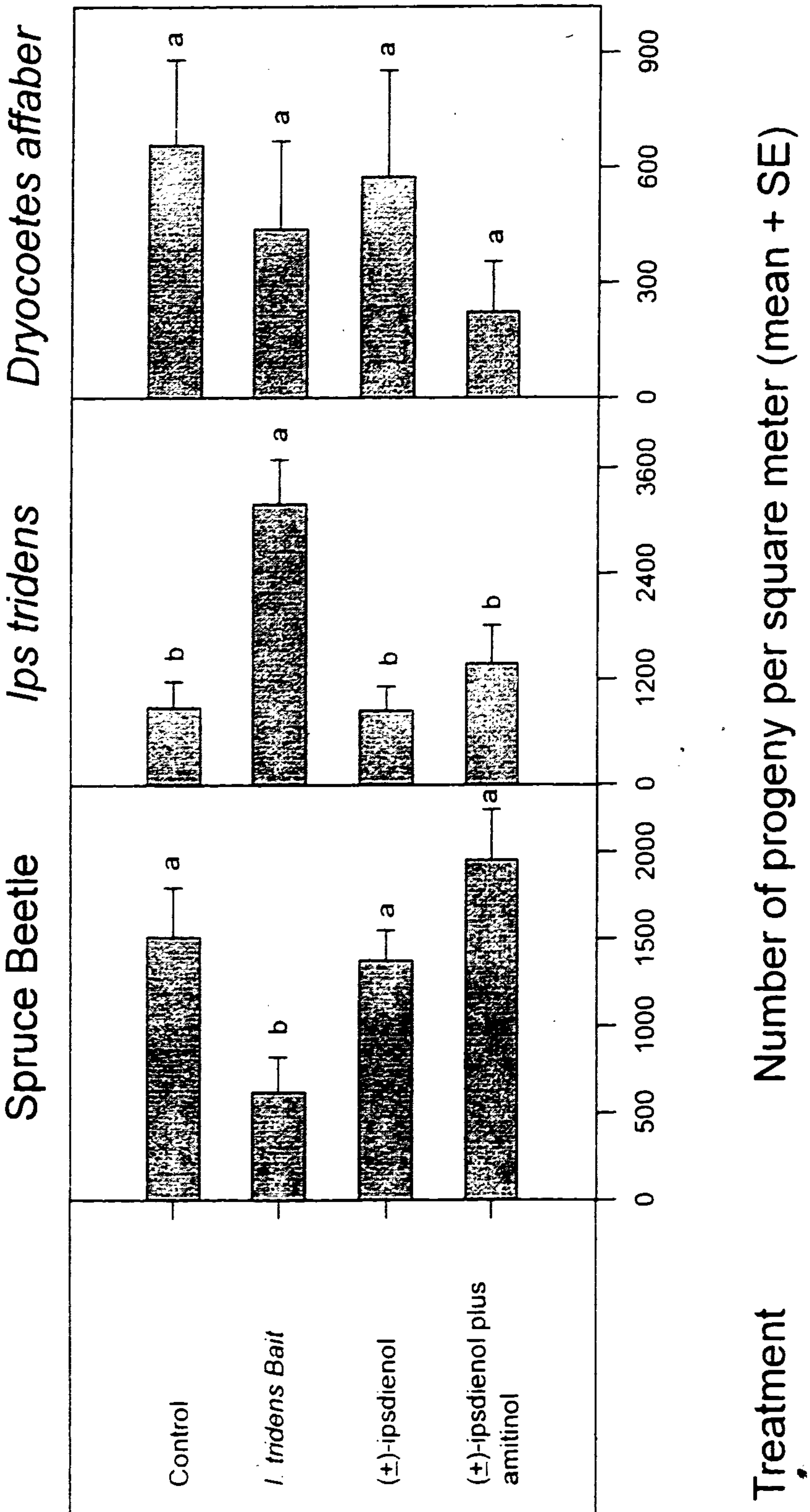

Spruce Beetle
Ips tridens
Dryocoetes affaber
Treatment
Control
I. tridens Bait
(±)-ipsdienol
(±)-ipsdienol plus amitinol
a
b
a
a
b
a
b
b
a
a
a
a
0
200
400
600
800
0
400
800
1200
0
70
140
210
280
Gallery lengths (cm) per square meter (mean + SE)

Figure 25 Spruce beetle, *I. tridens*, and *D. affaber* progeny densities in Experiment 13 (10 May - 4 August 1994), Mackenzie, B.C. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h, respectively. (±)-Ipsdienol and amitinol were released at 0.6 and 0.02 mg per 24 h, respectively. N=7. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.


Spruce Beetle
Ips tridens
Dryocoetes affaber
Treatment
Control
I. tridens Bait
(±)-ipsdienol
(±)-ipsdienol plus amitinol
Number of progeny per square meter (mean + SE)
0
500
1000
1500
2000
0
1200
2400
3600
0
300
600
900
a
b
a
a
b
a
b
b
a
a
a
a

diameter, vigor, and placement in the stand. In addition, randomization and replication of treatments would have removed any potential bias due to host differences.

Attack densities, gallery lengths per m^2, and progeny densities for both secondary species were much higher in experiment 11 (Figures 17-19) than they were for competitive displacement in Experiment 10 (Chapter 4, Figures 10-12). In further contrast to the results of Experiment 10 all three parameters of attack success were greatly increased in trees with the respective secondary species baits (Figures 17-19). On the other hand, attack densities, gallery lengths per m^2, and progeny densities for the spruce beetle were much lower in Experiment 11 (Figures 17-19) than for competitive displacement in experiment 10 (Chapter 4, Figures10-12). These differences may be due in part to a somewhat lower spruce beetle population level in the area of the study for Experiment 11. However, the main effect undoubtedly stems from placement of the secondary species pheromones on the trees prior to spruce beetle flight, thus interfering with spruce beetle attack from the outset.

Attack by *I. tridens* was not inhibited by the pheromone for *D. affaber* (Figure 17) and was enhanced by baits consisting only of (±)-*endo*-brevicomin (Figure 20). The bait for *D. affaber* contained (±)-*exo*-brevicomin, a compound that was identified in volatiles produced by *I. tridens* males boring in Engelmann spruce logs and which elicited antennal responses by *I. tridens* females (Chapter 2, Figure 1). *exo*-Brevicomin may be an aggregation pheromone for *I. tridens*, and it is possible that it is cross-attracted to the pheromone of *D. affaber*, which contains both *exo*- and *endo*-brevicomin. On the other hand, *D. affaber* attack density was significantly enhanced only on trees baited with *D. affaber* baits alone, and was strongly inhibited when baits for both secondary species were combined (Figure 17). It would be adaptive for weaker competitors to avoid colonizing hosts that are already occupied, whereas stronger competitors or species that are able to co-exist successfully in the same host need not avoid each other. Small secondary scolytids may be able to co-exist successfully in the same host tree by partitioning the resource and by colonizing areas of the phloem throughout the tree that are not exploited by other species. Therefore, mutual pheromonal inhibition would not be necessary. Moreover, species that are able to co-exist successfully may be cross-attracted. Two secondary species, *P. knechteli* and *I. pini* are able to co-exist successfully in lodgepole pine and avoid direct competition by partitioning the resource (Poland and Borden 1994a). *Pityogenes knechteli*, the smaller beetle, is able to colonize portions of the phloem not occupied by *I. pini* and is cross-attracted to bolts infested with *I. pini* males (Poland and Borden 1994b) and to synthetic pheromones of *I. pini* (Savoie 1996). Neither species is found colonizing the same host tree as *I. latidens* or *I. mexicanus* which also attack lodgepole pine. Therefore, the former two species are apparently unable to co-exist in the same host as the latter two and both *P. knechteli* and *I. pini* are mutually inhibited by pheromones of *I. latidens* and *I. mexicanus*. Southern pines are commonly co-infested by *Dendroctonus frontalis* Zimmerman, *Ips grandicollis* Eichhoff, *Ips calligraphus* Germar, and *Ips avulsus* Eichhoff. Interspecific semiochemical communication is very important in delineating breeding areas within the tree and influencing the sequence of colonization. The secondary species, *I. avulsus*, is so small that it may exploit the phloem tissue throughout the tree that remains unexploited by the other species. Attraction of *I. avulsus* is enhanced in the presence of *I. grandicollis* which may ensure rapid colonization of the tree by two species that can co-exist and avoid direct competition (Birch et al. 1980).

The lack of differences in mean lengths per gallery and numbers of progeny per gallery for the spruce beetle between treatments may be a result of combined intra- and interspecific effects. Because trees with low secondary species attack densities tended to have high spruce beetle attack densities (Figures 13,15), reductions in interspecific encounters would be offset by increased intraspecific encounters. The reverse situation would exist in trees with low spruce beetle attack densities and high secondary species attack densities. Safranyik and Linton (1985) found that increased intraspecific competition resulted in reduced gallery lengths and number of progeny per female. The mean lengths per gallery and numbers of progeny per gallery in Experiment 11 were very similar to those found in the highest spruce beetle density treatments tested by Safranyik and Linton (1985). Therefore, intra- and interspecific effects may offset each other in reducing gallery lengths and progeny production in the different treatments.

The lack of significant differences in mean lengths per gallery and mean number of progeny per gallery for the three species between treatments and the lack of effect of attack density class of any species on total gallery length or progeny densities of the other species supports the conclusion of Chapter 4 that direct interference is unlikely to be an important mechanism of competitive interaction.

While spruce beetle attack densities were significantly reduced in trees baited with secondary species pheromones (Figure 17), attack by the spruce beetle was not completely prevented. Therefore, the resources were not fully utilized by the secondary species and the spruce beetle was not completely eliminated or excluded. More complete resource exploitation might be achieved if the entire guild of competitor species were present. It is probable that pheromones of other secondary species such as *P. rufipennis*, *S. annectans*, *I. perturbatus*, *I. borealis*, and *D. autographus* also disrupt spruce beetle attraction, and could be judiciously included in a cost-effective treatment.

The pronounced reduction in spruce beetle attack densities, gallery lengths and progeny per m^2 in trees baited with secondary species baits (Figures 17-19) indicate that competitive exclusion may have considerable potential for use in spruce beetle management. The implementation of such a management tactic could be challenging. For instance, one must consider the relative abundance of *I. tridens* and *D. affaber*. To maintain or enhance *D. affaber* populations and encourage the presence of both secondary species, some trees must be baited with *D. affaber* baits alone. Another consideration is the use of less costly substitutes for the two-component *I. tridens* bait and the expensive enantiospecific *D. affaber* bait.

The results of Experiment 12 show that (±)-*endo*-brevicomin was effective in reducing spruce beetle attack density and in increasing attack densities by both *I. tridens* and *D. affaber* (Figure 20), while in contrast to Experiment 11 (Figure 17), the *D. affaber* bait was not. This suggests that (±)-*endo*-brevicomin could be a cost-effective substitute for the expensive *D. affaber* bait. On the other hand, in Experiment 13 only the *I. tridens* bait was effective in reducing spruce beetle attack density and in increasing *I. tridens* attack density (Figure 23). Therefore, (±)-ipsdienol in combination with *cis*-verbenol appears to be the only effective *I. tridens* bait available at present for managing spruce beetle populations through competitive exclusion. These results agree with those of Chapter 2 (Figures 2,3) which suggested that (±)-ipsdienol and *cis*-verbenol are important pheromones for *I. tridens* and that amitinol contributes only marginally to *I. tridens* attraction in the field. Attacks by *D. affaber* were not increased by the presence of (±)-ipsdienol, (±)-ipsdienol plus amitinol, or (±)-ipsdienol plus *cis*-verbenol (Figure 23). This result agrees with the results of Experiment 11 showing that *I. tridens* baits were not attractive to *D. affaber* and in fact reduced attacks of *D. affaber* on trees baited for both secondary species (Figure 17).

The results of Experiments 11-13 indicate that interspecific responses of the spruce beetle, *I. tridens*, and *D. affaber* to pheromone baits of *I. tridens* and *D. affaber* were similar in tree baiting experiments near Mackenzie and in trapping experiments conducted near Princeton. In particular, pheromones found to be attractive to the secondary species in southern B.C. were effective in inducing attacks by the secondary species in northern B.C. In addition, secondary species pheromones which interrupted spruce beetle attraction in southern B.C. also reduced spruce beetle attacks in northern B.C. Therefore, despite possible regionally specific differences in semiochemical responses, the pheromones used for competition exclusion of the spruce beetle appear to be effective over a wide geographic range. Once attack by the secondary species is established, natural production of pheromones by the secondary species in the regionally-specific enantiomeric blend would further ensure deterrence of attack by the spruce beetle.

5.3 Exclusion of spruce beetles from groups of felled trap trees

5.3.1 Methods

Experiment 14 was conducted from 26 May to 10 August 1995 in the McGregor Model Forest (Northwood Pulp and Timber Tree Farm License #30) near Prince George, B.C. The purpose of this experiment was to determine whether competitive exclusion would be feasible for preventing spruce beetle attacks and population buildup in simulated patches of windthrown trees. The experiment tested the hypothesis that spruce beetle attack and success can be reduced in trees that are felled in groups (patches) of four that are baited with pheromones of either or both secondary species prior to spruce beetle flight. The experiment comprised six replicates of four treatments laid out in randomized complete blocks. For each patch four healthy, large-diameter spruce trees within 5 m of each other were felled in a group on 26 May 1995. Patches were separated by at least 50 m. Each patch was assigned a single treatment: 1) unbaited control; 2) all four trees baited with *I. tridens* bait; 3) all four trees baited with *D. affaber* bait; or 4) two trees baited with *I. tridens* bait and two trees baited with *D. affaber* bait. *Dryocoetes affaber* and *I. tridens* baits were placed on separate trees to minimize interference with attack by *D. affaber* in the presence of the *I. tridens* bait as was seen in Experiment 11 (Figure 17).

Baiting of the trees was done within three days of felling and followed the same protocol as for experiments 11-13. *Ips tridens* baits were identical to those used in Experiment 11. *Dryocoetes affaber* baits were similar to those used in Experiment 11 except that a 1:2 mixture of (±)-*exo*- and (±)-*endo*-brevicomin was used instead of a 1:1 mixture of (±)-*exo*- and (+)-*endo*-brevicomin. (±)-*endo*-Brevicomin was used because insufficient quantities of (+)-*endo*-brevicomin were available. The (-)-enantiomer in (±)-*endo*-brevicomin partially inhibited attraction of *D. affaber* in trapping experiments

(Camacho et al. 1994) but (±)-*endo*-brevicomin has the offsetting advantage of inhibiting spruce beetle attraction (Chapter 3, Figure 6), and inducing competitive exclusion of spruce beetles in individually felled trees (Figure 20). Bark samples were collected in the same manner as for Experiments 12 and 13. The first set of two bark samples per tree was collected on 13-14 July 1995 and the second set of 4 bark samples per tree was collected on 7-10 August 1995. Data collection and statistical analyses were identical to those for Experiments 12 and 13.

5.3.2 Results

The results from the two bark sampling collection periods were similar. Therefore, results from the second bark sample period are reported. ANOVA showed a significant effect for treatment but not for replicate, position, or their interactions with treatment for attack density, gallery length per m^2, and progeny density per m^2 of all three species. The lack of effect for position agrees with the results from Experiments 12 and 13 that showed that the baits were effective in inducing attack evenly along the entire bole.

In Experiment 14, spruce beetle attack densities and gallery lengths per m^2 were significantly reduced by all treatments but *D. affaber* baits alone (Figures 26, 27). Progeny density was reduced only in trees baited with *I. tridens* baits either in patches baited with *I. tridens* pheromones or the pheromones of both secondary species (Figure 28). *Ips tridens* attack densities, gallery lengths per m^2, and progeny densities were lowest in trees from patches in which all trees were baited with *D. affaber* baits and highest in patches baited with *I. tridens* baits, or in trees baited with its own pheromone in co-baited patches (Figures 26-28). *Dryocoetes affaber* attack densities, gallery lengths per m^2, and progeny densities were low in patches baited with *I. tridens* baits, and high in patches baited with *D. affaber* baits or trees baited with its own pheromone in co-baited patches (Figures 26-28).

Figure 26 Spruce beetle, *I. tridens*, and *D. affaber* attack densities in Experiment 14, (26 May - 10 August 1994) Prince George, B.C. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h, respectively. *Dryocoetes affaber* baits consisted of a 1:2 mixture of (±)-*exo*- and (±)-*endo*-brevicomin released at 0.2 mg per 24 h. N=6. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

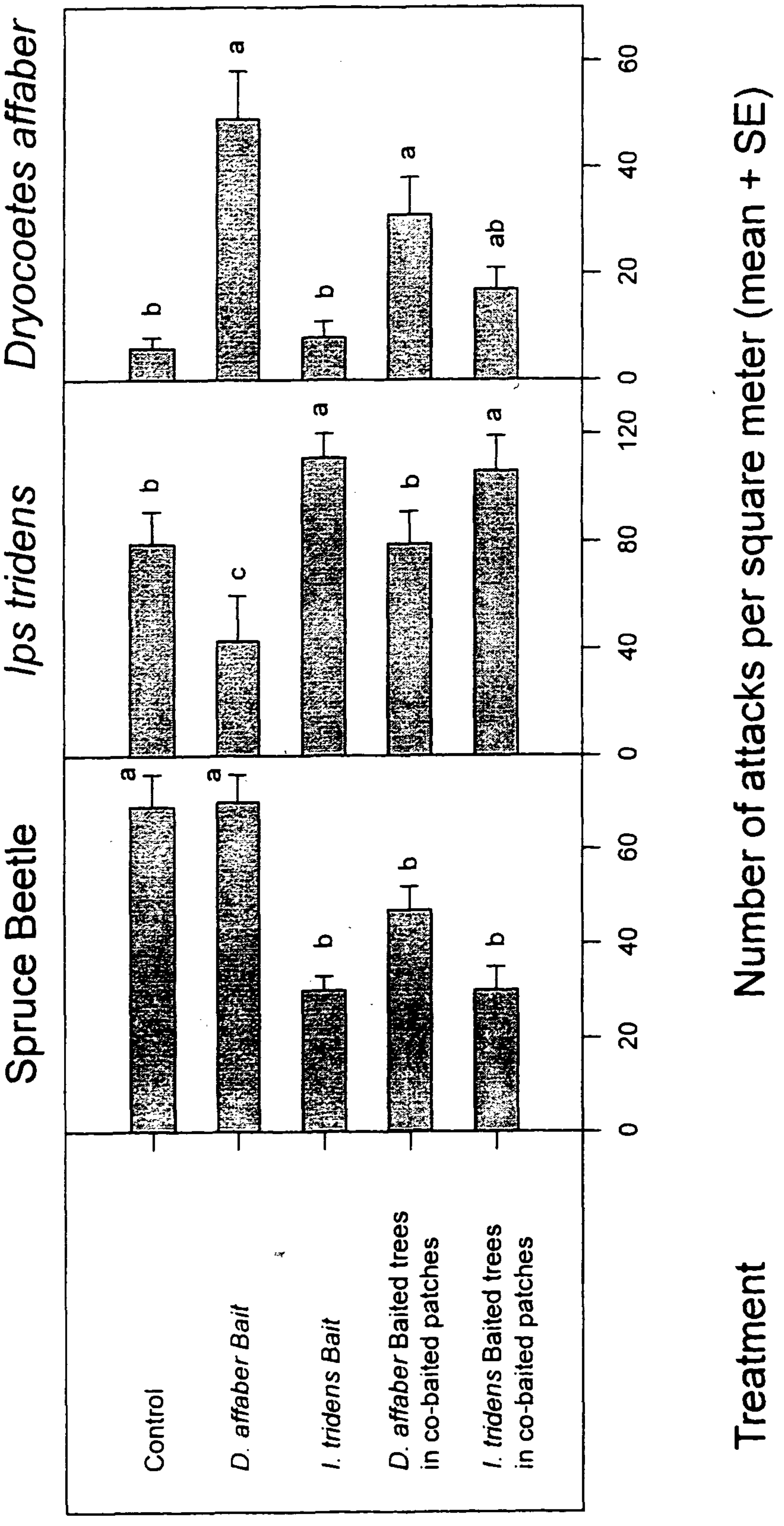

Spruce Beetle
Ips tridens
Dryocoetes affaber
Control
D. affaber Bait
I. tridens Bait
D. affaber Baited trees in co-baited patches
I. tridens Baited trees in co-baited patches
a
a
b
b
b
b
c
b
a
b
a
b
a
b
a
ab
0
20
40
60
0
40
80
120
0
20
40
60
Number of attacks per square meter (mean + SE)
Treatment

Figure 27 Spruce beetle, *I. tridens*, and *D. affaber* gallery lengths per m^2 in Experiment 14 (26 May - 10 August 1994), Prince George, B.C. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h, respectively. *Dryocoetes affaber* baits consisted of a 1:2 mixture of (±)-*exo*- and (±)-*endo*-brevicomin released at 0.2 mg per 24 h. N=6. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.

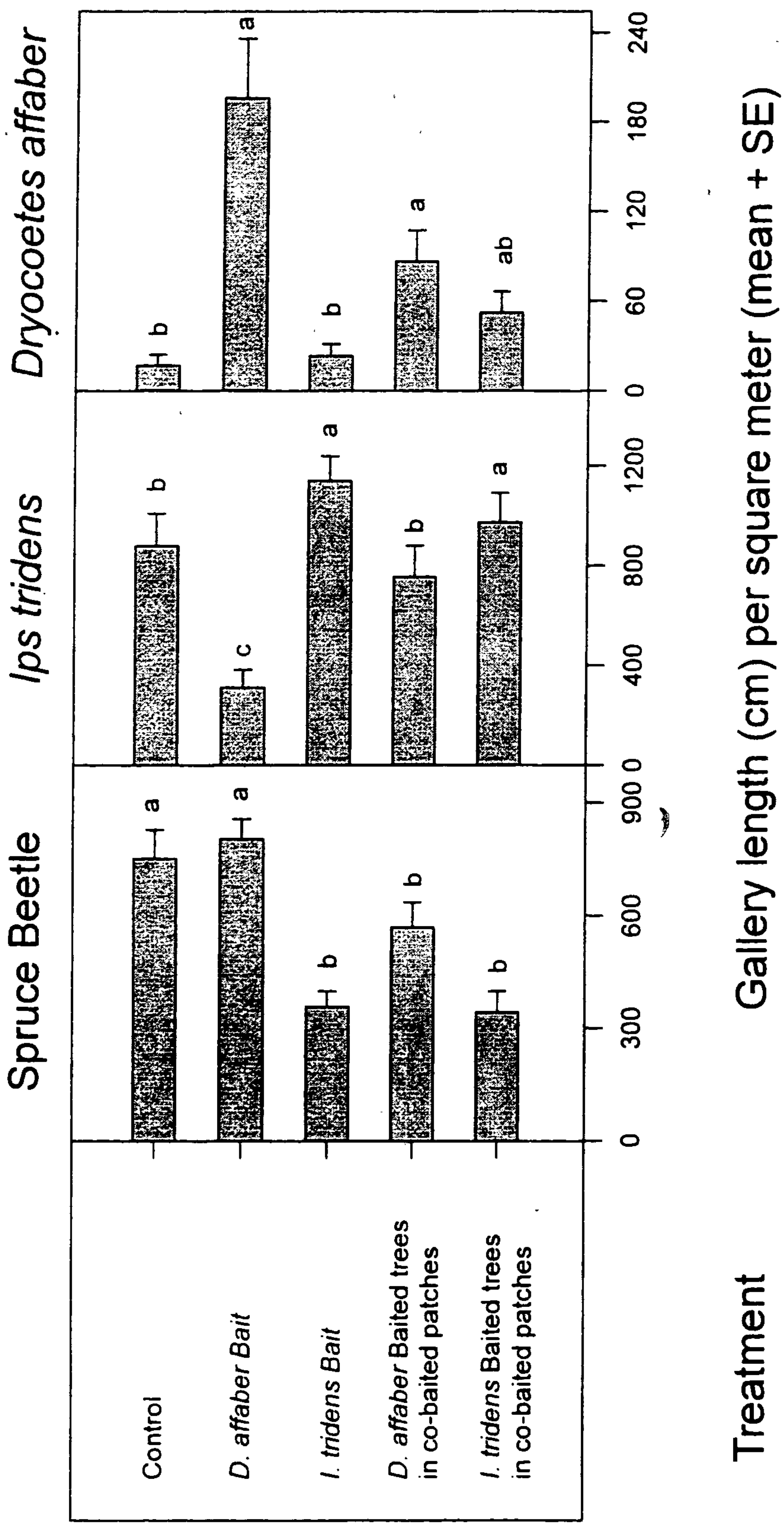
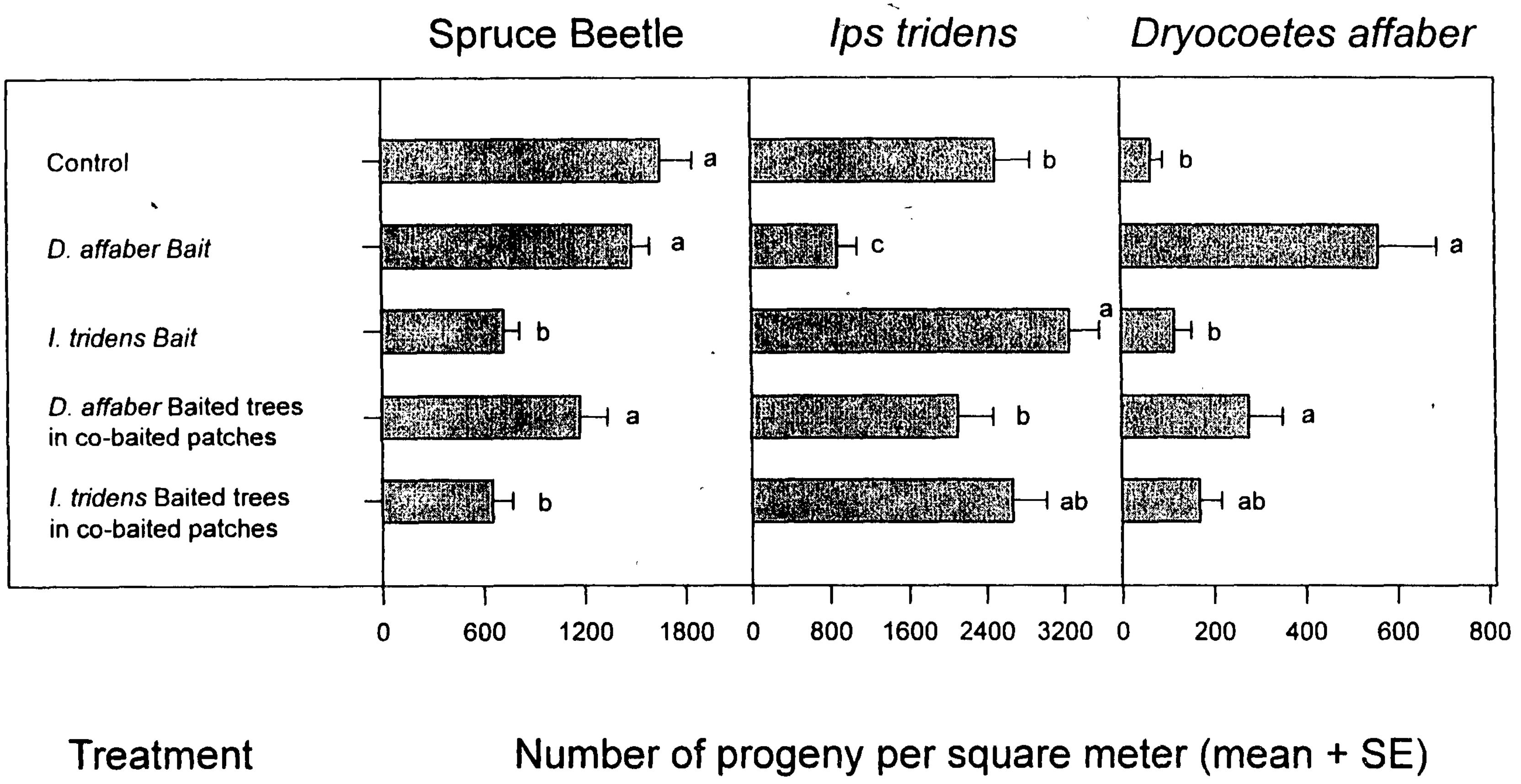

Spruce Beetle
Ips tridens
Dryocoetes affaber
Treatment
Control
D. affaber Bait
I. tridens Bait
D. affaber Baited trees in co-baited patches
I. tridens Baited trees in co-baited patches
Gallery length (cm) per square meter (mean + SE)
0
300
600
900
0
400
800
1200
0
60
120
180
240
a
a
b
b
b
b
c
a
b
a
b
a
b
a
ab

Figure 28 Spruce beetle, *I. tridens*, and *D. affaber* progeny densities in Experiment 14 (26 May - 10 August 1994), Prince George, B.C. *Ips tridens* baits consisted of (±)-ipsdienol and (-)-*cis*-verbenol released at 0.6 and 1.8 mg per 24 h, respectively. *Dryocoetes affaber* baits consisted of a 1:2 mixture of (±)-*exo*- and (±)-*endo*-brevicomin released at 0.2 mg per 24 h. N=6. Bars topped by the same letter are not significantly different, REGW test, $P < 0.05$.


Spruce Beetle
Ips tridens
Dryocoetes affaber
Control
D. affaber Bait
I. tridens Bait
D. affaber Baited trees in co-baited patches
I. tridens Baited trees in co-baited patches
a
a
b
a
b
b
c
a
b
ab
b
a
b
a
ab
0
600
1200
1800
0
800
1600
2400
3200
0
200
400
600
800
Treatment
Number of progeny per square meter (mean + SE)

5.3.3 Discussion

The results of Experiment 14 show that baiting patches of felled trees with *I. tridens* baits, regardless of whether the trees were all baited with *I. tridens* baits or were adjacent to trees baited with *D. affaber* baits, was effective in reducing spruce beetle attack density, resource exploitation, and progeny production. In turn, *I. tridens* attack density, gallery length per m^2, and progeny density were increased (Figures 26-28). Although *D. affaber* attack density and success was significantly increased in trees baited with *D. affaber* baits, regardless of patch treatment, spruce beetle attack density and success was not correspondingly reduced.

These results lead to a tentative conclusion that competitive exclusion of the spruce beetle would be feasible in patches of trees, but they illustrate the complexity of implementing it as a management tactic. As in Experiment 11, the results suggest that *I. tridens* may be a stronger competitor than *D. affaber*. However, a similar result could have been obtained if *I. tridens* were more abundant than *D. affaber* at the study site. *Dryocoetes affaber* attack densities did not appear to be as high as they were on *D. affaber* baited trees in Experiment 11 (Figures 17-19) in which inhibition of spruce beetle attack by *D. affaber* baits was effective, and were only slightly higher than those in Experiment 12 in which inhibition of spruce beetle attack was ineffective (Figures 20-22). The fact that (±)-*endo*-brevicomin was substituted for (+)-*endo*-brevicomin in Experiment 14 was probably not significant because in Experiment 12 spruce beetle attack density was significantly reduced in trees baited with (±)-*endo*-brevicomin (Figure 20).

Another possible explanation for the lack of competitive exclusion of the spruce beetle by *D. affaber* in Experiment 14 is that environmental conditions can influence the outcome of competitive interactions (Begon and Mortimer 1986). Therefore, while *D. affaber* may be a strong competitor under some conditions (McCambridge and Knight 1972), its competitive ability may be reduced under different conditions. Its peak flight period occurs approximately one month later than that for the spruce beetle and *I. tridens* (Bright 1976; Camacho-Vera 1993). If early season environmental conditions are favorable for spruce beetle development in the absence of *I. tridens*, it may gain a competitive advantage over *D. affaber* through rapid exploitation of the phloem resource.

Ips tridens attack densities were significantly higher on trees baited with *I. tridens* baits than on trees baited with *D. affaber* baits regardless of patch treatment (Fig 26). Therefore, *I. tridens* was not cross-attracted to the *D. affaber* bait on its own. *Ips tridens* attack densities were actually significantly reduced when all trees in a patch were baited with *D. affaber* baits. However, it is not possible to conclude from this experiment that *D. affaber* baits probably would not disrupt the attraction of *I. tridens* because no disruptive effect occurred in Experiment 11 when trees were co-baited for both secondary species (Figures 17-19).

Dryocoetes affaber attack densities were significantly increased only in trees that were baited with *D. affaber* baits regardless of patch treatment (Figure 26). This result agrees with the results from Experiment 11, which showed that *D. affaber* was not cross-attracted to trees baited with *Ips tridens* baits (Figure 17).

Overall, Experiment 14 shows that baiting patches of felled trees with *I. tridens* baits prior to spruce beetle flight was effective in reducing spruce beetle colonization and increasing colonization by *I. tridens*. This evidence coupled with the results of Experiments 11-13 indicates that baiting trees with secondary species baits prior to spruce beetle flight consistently results in reduced spruce beetle attack density, gallery length per m^2, and progeny density. If implemented operationally, baiting of susceptible hosts for secondary species would have two positive effects: 1) inducing attack by the secondary species; and 2) partially repelling spruce beetles. Thus spruce beetle attack could be reduced and the probability of population buildup to outbreak levels would be minimized.

5.3.4 Implications for spruce beetle management

To implement biologically-based management programs successfully, a thorough understanding of the biology and ecological interactions among the organisms being manipulated is required. Numerous environmental factors can influence these interactions. Therefore, the implementation of biologically-based control programs is complex and the outcome cannot always be predicted. Another feature of biologically-based pest management is that pest species are generally not eliminated, but rather their populations are kept at tolerable levels below the threshold for economic injury (Pedigo 1989).

The potential use of competitive exclusion for spruce beetle management is no exception to these rules. Its success in preventing spruce beetle population buildup would be dependent on interactions between populations of the spruce beetle and the secondary species, the distribution and availability of suitable hosts, environmental conditions, and other pest management tactics with which it might be integrated. It is most likely to succeed where endemic beetle populations are at sub-outbreak levels, populations of secondary species are abundant, host resources such as fresh windthrown trees are available, the stand is relatively healthy, and climatic conditions are relatively cool and moist. These conditions are often found in riparian zones which are often protected from intrusions such as harvesting but which can be sources of outbreaks if spruce beetle populations build up in the blowdown in these areas. Therefore, competitive exclusion could be of great value in managing the spruce beetle in these sensitive sites where alternative management approaches are not feasible.

Combinations of different inhibitory semiochemicals may enhance the competitive exclusion effect. For instance, attraction of western pine beetle to its pheromones, *exo*-brevicomin and frontalin, plus kairomonal myrcene is inhibited by ipsdienol, a pheromone for the sympatric species, *I. paraconfusus* (Byers and Wood 1980, 1981). Addition of verbenone, the antiaggregation pheromone for the western pine beetle synergized the inhibitory effect of ipsdienol (Paine and Hanlon 1991). 3,2-Methylcyclohexenone (MCH) is a known antiaggregation pheromone for the spruce beetle, that has proven to be moderately effective in reducing spruce beetle attacks on treated host material (Kline et al. 1974; Furniss et al. 1976). If MCH proved not to be inhibitory to *I. tridens* and *D. affaber* and if synergism occurred between the inhibitory effects of MCH and synomones for competing secondary species on the spruce beetle, a more effective competitive exclusion tactic might be developed.

Interspecific pheromonal inhibition is not necessarily restricted to sympatric bark beetles that attack the same host species. Congeners that attack different host species may employ specific synomones to aid in breeding isolation. For instance, *trans*-verbenol acts as an aggregation pheromone for the mountain pine beetle (Pitman 1971) but as an antiaggregant for the related western pine beetle (Wood 1972). Therefore, aggregation and antiaggregation pheromones, such as *trans*-verbenol and verbenone for the mountain pine beetle, may also be inhibitory to the spruce beetle and should be explored.

Host and non-host compounds may also act as inhibitors for scolytids. Limonene was shown to be repellent to the fir engraver in laboratory bioassays (Bordasch and Berryman 1977). The phenylpropanoid, 4-allylanisole, is an important volatile constituent of healthy pines. It was shown to be as repellent to the southern pine beetle as the antiaggregation pheromone, verbenone, in field trials (Hayes et al. 1994), albeit at very high release rates. Foliar and resin levels of 4-allylanisole were significantly reduced in injured or stressed trees which were also the most susceptible to beetle attack (Cobb et al. 1972). Repellency of 4-allylanisole to the spruce beetle has also been reported (Werner 1994). Non-host, green leaf volatiles have been found to inhibit the aggregation responses of bark beetles. Hexanal and hexanol interrupted attraction of the southern pine beetle to its pheromone (Dickens 1992) and a (*E*)-(2)- and (*Z*)-(3)-hexenol were particularly repellent to the mountain pine beetle when combined with attractive semiochemicals (Wilson et al. 1996). Combinations of green leaf alcohols and aldehydes disrupted attraction of the spruce beetle to spruce beetle lures (unpublished results). Even if such compounds were repellent to the secondary species used in competitive exclusion treatments, they could still be integrated into a management strategy that employed a number of tactics.

Other pheromone-based management tactics such as containment and concentration with aggregation pheromones could be employed with and complement competitive exclusion. Shore et al. (1990) found that α-pinene plus frontalin was effective in containing and concentrating a spruce beetle infestation in a grid-baited stand prior to sanitation harvesting. The use of attractive felled trap trees where their removal is possible, and grid-baiting infested areas that can subsequently be harvested could be used as the "pull" component in a "push-pull" management strategy (Lindgren and Borden 1993), in which the "push" component involved competitive exclusion in adjacent riparian or sensitive leave areas, as well as the use of antiaggregation pheromones and non-host volatiles in reserve stands of commercial timber. In such an integrated management program, competitive exclusion could reduce or replace the use of arsenical-treated lethal trap trees (Hodgkinson 1985).

6.0 Responses of a bark beetle predator, *Thanasimus undatulus* Say (Coleoptera: Cleridae), to pheromones of the spruce beetle and two sympatric species (Coleoptera: Scolytidae)

6.1 Introduction

In addition to scolytid competitors there are an astonishing number of arthropod species associated with the subcortical galleries of bark beetles (Dahlsten 1982). Interactions among the co-existing organisms may greatly influence their dynamics and population distributions (Begon and Mortimer 1986). Mortality from arthropod predators and parasites may play an important role in keeping endemic bark beetle populations at low levels, thus minimizing the likelihood of large infestations (Hopping 1947, Reid 1957, Ryan and Rudinsky 1962, Kline and Rudinsky 1964, Johnsey et al. 1965, Berisford 1968, Overgaard 1968, Moore 1972, Nagel and Fitzgerald 1975).

Members of the family Cleridae are among the principal predators of several bark beetles (Dahlsten 1982). However, clerid predators may play only a small role in regulating spruce beetle populations. More significant mortality factors include envelopment by resin, interspecific competition by other scolytids, and consumption by dipteran predators (McCambridge and Knight 1972; Whitmore 1983; Gara et al. 1995).

Entomophagous insects, including numerous species of clerids, commonly use scolytid pheromones as kairomones in host recognition (Dixon and Payne 1980, Bakke and Kvamme 1981, Wood 1982, Billings and Cameron 1984). *Thanasimus undatulus* Say is a generalist predator that has been reportedly attracted to ipsdienol (Miller and Borden 1990), *cis*-verbenol plus ipsenol (Miller et al. 1991), and frontalin (Ross and Daterman 1995).

Thanasimus undatulus is a predator of the spruce beetle. It was attracted to traps baited with frontalin as a spruce beetle lure (Kline et al. 1974), and aggregated in large numbers on frontalin-baited spruce trees (Dyer 1973). Addition of seudenol to frontalin did not significantly enhance attraction of *T. undatulus* (Dyer and Hall 1980). There is evidence that it exhibits enantiospecificity in recognition of pheromones of its prey. *Thanasimus undatulus* was attracted preferentially to *S*-(-)-frontalin in a Douglas-fir stand, while both enantiomers were equally attractive in a spruce stand, a finding consistent with the observation that the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, preferred *S*-(-)- or (±)-frontalin over the *R*-(+)- enantiomer, while the spruce beetle appeared to be equally attracted to both *S*-(-)-, *R*-(+)-, and (±)-frontalin (Lindgren 1992). Such specificity in response suggests that the importance of *T. undatulus* as a predator of spruce beetles may have been underestimated. For example, its larvae may not be very effective as subcortical predators of spruce beetle larvae (McCambridge and Knight 1972; Whitmore 1983), but adults may prey largely unnoticed on adult spruce beetles that are in the act of colonizing new hosts, a hypothesis that is consistent with Dyer's (1973) observations.

In order to maximize the efficacy of pheromone-based management of bark beetle pests, negative effects on natural enemies must be minimized and positive effects encouraged. Accordingly, I collected and enumerated *T. undatulus* adults whenever they responded to pheromone-baited traps. Herein I report the responses of this clerid predator to combinations of pheromones for the spruce beetle and two competing secondary species, *I. tridens* and *D. affaber*.

6.2 Materials and Methods

Various combinations of pheromone components were tested in multiple-funnel traps (Lindgren 1983) laid out in randomized complete blocks in the margins of spruce stands (Chapters 2,3). Significant numbers of *T. undatulus* were captured in three experiments: Experiment 2 (Chapter 2), and Experiments 6 and 8 (Chapter 3). Experiment 6, conducted from 29 June to 11 August 1994, compared spruce beetle and *D. affaber* responses to combinations of spruce beetle lures and racemic mixtures of the two components of the *D. affaber* pheromone, *exo*- and *endo*-brevicomin. It comprised

20 replicates of five treatments: 1) unbaited control; 2) spruce beetle lure; 3) spruce beetle lure with (±)-*exo*-brevicomin; 4) spruce beetle lure with (±)-*endo*-brevicomin; and 5) spruce beetle lure with (±)-*exo*-brevicomin and (±)-*endo*-brevicomin. Experiment 8, conducted from 14 July to 17 August 1994, compared spruce beetle and *I. tridens* responses to combinations of spruce beetle lures and the different enantiomers of ipsdienol, a component of the *I. tridens* pheromone. It comprised 20 replicates of five treatments: 1) unbaited control; 2) spruce beetle lure; 3) spruce beetle lure with (+)-ipsdienol; 4) spruce beetle lure with (-)-ipsdienol; and 5) spruce beetle lure with (±)-ipsdienol. Experiment 2, conducted from 3 to 11 July 1996, compared responses of the spruce beetle and *I. tridens* to spruce beetle lures and three *I. tridens* pheromone components, (±)-ipsdienol, (-)-*cis*-verbenol, and amitinol. It comprised 10 replicates of six treatments: 1) unbaited control; 2) spruce beetle lure; 3) (±)-ipsdienol and (-)-*cis*-verbenol; 4) (±)-ipsdienol, (-)-*cis*-verbenol, and amitinol; 5) spruce beetle lure with (±)-ipsdienol and (-)-*cis*-verbenol; and 5) spruce beetle lure with (±)-ipsdienol, (-)-*cis*-verbenol, and amitinol.

Spruce beetle lures consisted of α-pinene released at 1.5 mg per 24 h from 1.5 mL Eppendorf tubes and frontalin released at 2.6 mg per 24 h from 400μL Eppendorf tubes (Phero Tech Inc.). Racemic and chirally pure (97%) ipsdienol were released at 0.2 mg per 24 h from bubble caps (Phero Tech Inc.). *cis*-Verbenol was released at 0.6 mg per 24 h from bubble caps (Phero Tech Inc.). Amitinol was synthesized by H.D. Pierce (Dept. of Biological Sciences, S.F.U.) according to procedures described in Chapter 2 and was released from bubble caps at 0.02 mg per 24 h (Phero Tech, Inc.).

Captured *T. undatulus* were collected and stored in plastic bags at -18 °C for up to 6 months until counted. The numbers captured were transformed by $\log_{10}(x + 1)$ to satisfy assumptions of normality and homoscedasticity (Zar 1984) and then subjected to ANOVA for randomized complete block design treating replicates as blocks. The means were compared by the REGW test (SAS 1990).

6.3 Results and Discussion

In Experiment 6, *T. undatulus* was attracted to spruce beetle lures alone and combined with (±)-*exo*-, (±)-*endo*-, or both (±)-*exo*- and (±)-*endo*-brevicomin (Figure 29). The brevicomins did not alter the response of *T. undatulus* to the spruce beetle lure. This indicates that *T. undatulus* either does not respond to (±)-*exo*- or (±)-*endo*-brevicomin or that responses to the brevicomins alone (not tested) are not enhanced by the presence of frontalin. Since clerids apparently exhibit preferences for enantiospecific pheromones (Lindgren 1992, Herms 1991), a lack of response to (±)-*exo*- or (±)-*endo*-brevicomin by *T. undatulus* would not rule out kairomonal recognition of *D. affaber* as prey. For example, *T. undatulus* may require the enantiospecific pheromone of *D. affaber* consisting of a 1:2 ratio of the (+)-enantiomers of *exo*- and *endo*-brevicomin to elicit a response. However, *T. undatulus* was not captured in sufficient numbers in experiments that tested spruce beetle and *D. affaber* responses to enantiospecific pheromone components for *D. affaber* to allow for data analysis.

Spruce beetle lures were also attractive to *T. undatulus* in Experiment 8. (±)-Ipsdienol and particularly (+)-ipsdienol significantly enhanced attraction of *T. undatulus* to spruce beetle lures (Figure 30). Responses of the related species, *T. dubius* (F.), to different blends of (+)- and (-)-ipsdienol were all positive but preferences differed at different sites in Wisconsin and Michigan and in different years (Herms et al. 1991). Both frontalin and ipsdienol are known to attract *T. undatulus*. My results suggest that *T. undatulus* recognizes and responds to the (+)-enantiomer of ipsdienol and that there is a synergistic effect of combining the two host kairomones. Because *I. tridens* produces mainly (-)-ipsdienol (Chapter 3), *T. undatulus* may be better adapted to respond to pine engravers, *I. pini* (Say) that produce predominantly (+)-ipsdienol in B.C. (Miller et al. 1996).

Figure 29. Numbers of *Thanasimus undatulus* captured in multiple funnel traps in Experiment 6 (29 June - 17 Aug. 1994), Arastra Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. (±)-*exo*- and (±)-*endo*-Brevicomin were released at 0.2 mg per 24 h. N=20. Bars with the same letter within each species and sex are not significantly different, REGW test, *P*<0.05.

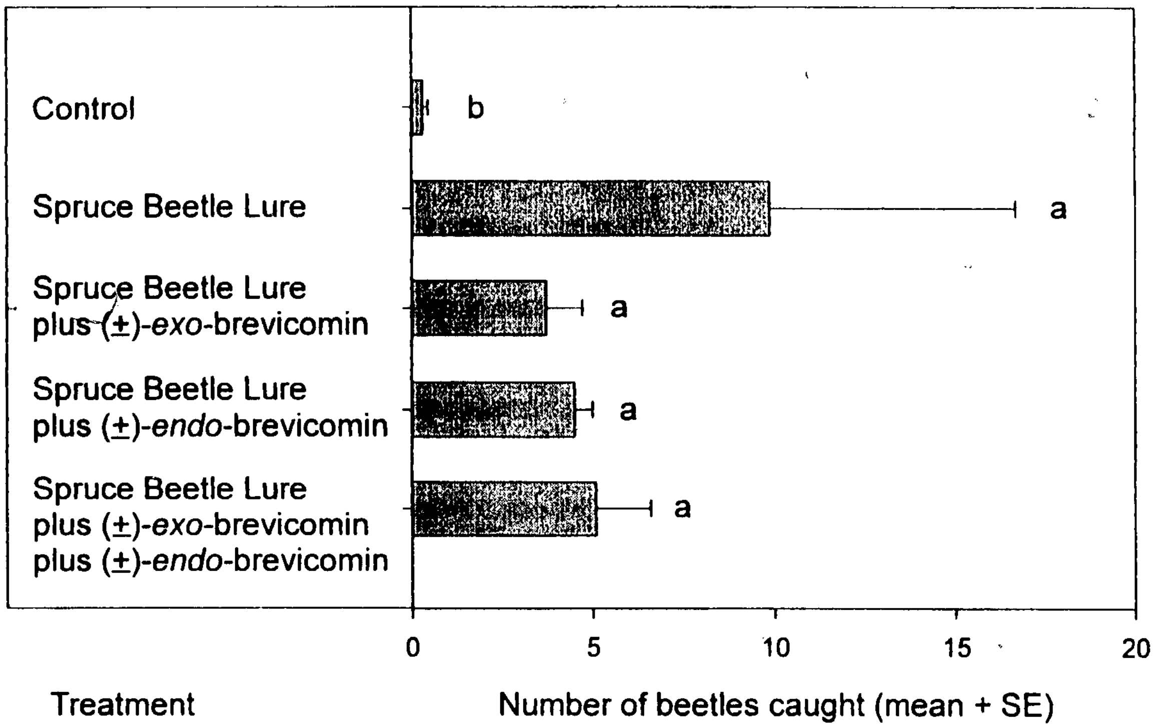
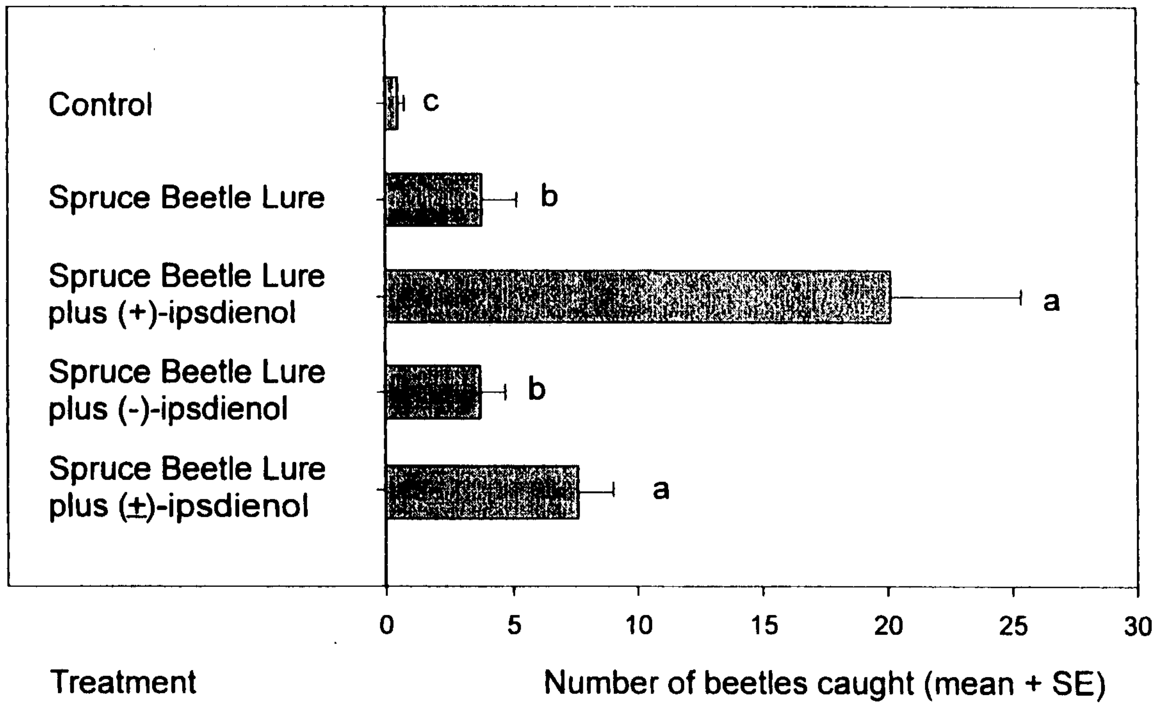

Control
Spruce Beetle Lure
Spruce Beetle Lure plus (±)-*exo*-brevicomin
Spruce Beetle Lure plus (±)-*endo*-brevicomin
Spruce Beetle Lure plus (±)-*exo*-brevicomin plus (±)-*endo*-brevicomin
b
a
a
a
a
0
5
10
15
20
Treatment
Number of beetles caught (mean + SE)

Figure 30. Numbers of *Thanasimus undatulus* captured in multiple funnel traps in Experiment 8 (14 July - 17 August 1994), Arastra Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. Enantiomers of ipsdienol were released at 0.2 mg per 24 h. N=20. Bars for each sex with the same letter are not significantly different, REGW test, $P<0.05$.

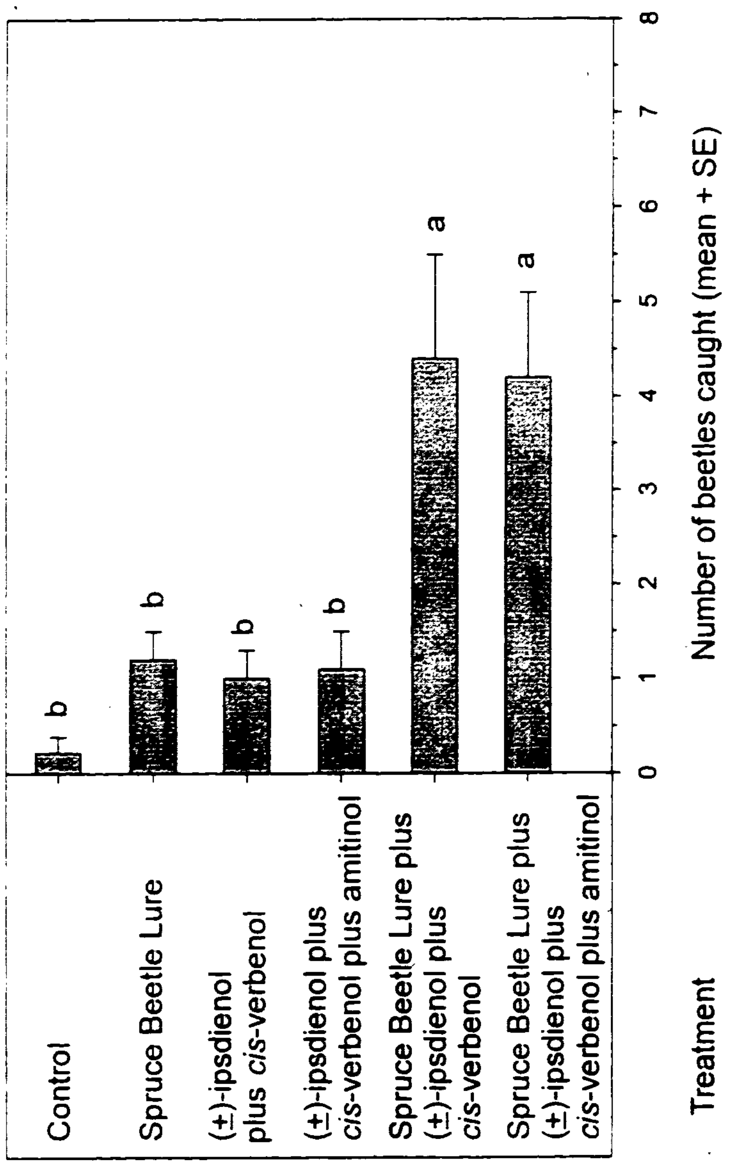

Control
Spruce Beetle Lure
Spruce Beetle Lure plus (+)-ipsdienol
Spruce Beetle Lure plus (-)-ipsdienol
Spruce Beetle Lure plus (±)-ipsdienol
c
b
a
b
a
0
5
10
15
20
25
30
Treatment
Number of beetles caught (mean + SE)

Alternatively, since *I. tridens* does produce small amounts of (+)-ipsdienol, spruce beetles and *T. undatulus* may exploit a minor semiochemical product of *I. tridens* for competitor avoidance and prey location, respectively.

The results of Experiment 2 showed that traps baited with combinations of spruce beetle lures and (±)-ipsdienol and (-)-*cis*-verbenol or (±)-ipsdienol, (-)-*cis*-verbenol, and amitinol, caught significantly more *T. undatulus* than traps baited with spruce beetle lures alone, *I. tridens* pheromones alone, or the unbaited control traps (Figure 31). While the addition of *cis*-verbenol or amitinol had no positive effect on catches of *T. undatulus*, they also had no negative effect. *Thanasimus undatulus* may respond to key pheromone components that are commonly produced by many species, regardless of certain additional components that may be part of the pheromone blend of particular species.

Attraction of *T. undatulus* to *I. tridens* pheromones indicates that baiting susceptible hosts with *I. tridens* pheromones to induce competitive exclusion of the spruce [illegible]tle may also lead to increased densities of the natural enemy, *T. undatulus*. If *T. undatulus* were to prey preferentially on the spruce beetle, the negative impact on spruce beetle populations due to competitive displacement or exclusion by *I. tridens* would be augmented. On the other hand, preferences for small scolytids like *I. tridens* (Kline and Rudinsky 1964; Schmitz 1978) by *T. undatulus* may partially offset the effects of competition on the spruce beetle. Non-preference by *T. undatulus* may simply reduce the level of interspecific competition by reducing population densities of both scolytid species.

Figure 31. Numbers of *Thanasimus undatulus* caught in multiple funnel traps in Experiment 2 (3-11 July 1996), Granite Creek, Princeton, B.C. Spruce beetle lures consisted of frontalin released at 2.6 mg per 24 h and α-pinene released at 1.5 mg per 24 h. (±)-Ipsdienol, (-)-*cis*-verbenol, and amitinol released from bubble caps at 0.2, 0.6, and 0.02 mg per 24 h, respectively. N=10. Bars for each sex with the same letter are not significantly different, REGW test, $P < 0.05$.


Control
Spruce Beetle Lure
(±)-ipsdienol plus *cis*-verbenol
(±)-ipsdienol plus *cis*-verbenol plus amitinol
Spruce Beetle Lure plus (±)-ipsdienol plus *cis*-verbenol
Spruce Beetle Lure plus (±)-ipsdienol plus *cis*-verbenol plus amitinol
Treatment
b
b
b
b
a
a
0
1
2
3
4
5
6
7
8
Number of beetles caught (mean + SE)

7.0

Summary and Conclusions

The most significant result of my research is the demonstration of the potential for development of competitive exclusion as an operational management tactic for the spruce beetle. Several other important results have emerged from my work which contribute to the understanding of interspecific competition and its mechanisms in bark beetles and the role of interspecific semiochemical communication in interspecific interactions.

1) Ipsdienol and *cis*-verbenol were confirmed to be important pheromones for *I. tridens*. Consistent and strong behavioral responses by *I. tridens* to ipsdienol and *cis*-verbenol in the field indicate that they should be sufficient for use in attracting *I. tridens* with the intention of inducing competitive displacement of the spruce beetle.

2) *exo*-Brevicomin produced by *I. tridens* was found for the first time to be produced by a member of the genus *Ips*. Antennal responses to *exo*-brevicomin and increased attack densities by *I. tridens* on trap trees baited with (±)-*endo*-brevicomin or a combination of ipsdienol, *cis*-verbenol, (±)-*exo*- and (+)-*endo*-brevicomin hint at a potential role of *exo*-brevicomin as a pheromone in *I. tridens* and support the need for further research.

3) Spruce beetle attraction to multiple funnel traps baited with spruce beetle lures was reduced in the presence of *I. tridens* pheromones, (±)-ipsdienol and *cis*-verbenol, and of *D. affaber* pheromones, (±)-*exo*- and (+)-*endo*-brevicomin, suggesting that the spruce beetle recognizes pheromones of secondary species to avoid already colonized unsuitable hosts, direct interspecific encounters, and detrimental competition.

4) (±)-*endo*-Brevicomin consistently disrupted spruce beetle attraction to traps. Therefore, it could be a cost-effective substitute for the enantiospecific pheromone

of *D. affaber* for use in disrupting spruce beetle attack and inducing competitive exclusion.

5) Attraction of *D. affaber* to its pheromone was enhanced by spruce beetle lures suggesting that secondary species exploit the pheromones of primary tree killers to aid in host location. Inducing attack by secondary species should not be disrupted after spruce beetle attack.

6) Spruce beetle attack density, gallery lengths per m^2, and progeny density were significantly reduced in trees that were baited with spruce beetle baits followed by *D. affaber* pheromones, (±)-*exo*- and (+)-*endo*-brevicomin, or *D. affaber* pheromones plus *I. tridens* pheromones, (±)-ipsdienol and (-)-*cis*-verbenol, after spruce beetle establishment.

7) In general, negative associations between spruce beetle attack and progeny densities and attack and progeny densities of the secondary species indicate that the two species interact competitively.

8) The primary mechanism of competition was found to be indirect interference by synomonal inhibition of subsequent spruce beetle attacks and reduction in overall resource exploitation because attack densities and success of the secondary species were not significantly increased in co-baited trees and direct interference by the secondary species with individual spruce beetle gallery construction, progeny production, and progeny development was not significant.

9) The impact of the secondary species on spruce beetles that are already established would probably not be sufficient to be of practical use in retarding the development of outbreaks or reducing infestations. Therefore, competitive displacement has limited utility for spruce beetle management.

10) Spruce beetle attack density, gallery lengths per m^2, and progeny density were significantly reduced in individual felled spruce trees baited with *D. affaber* pheromones, (±)-*exo*- and (+)-*endo*-brevicomin, *I. tridens* pheromones, (±)-

ipsdienol and (-)-*cis*-verbenol, pheromones for both secondary species, and the individual *D. affaber* pheromone component (±)-*endo*-brevicomin, prior to spruce beetle attack.

11) *Ips tridens* pheromones, (±)-ipsdienol and (-)-*cis*-verbenol, were effective in reducing spruce beetle attack and success in simulated patches of windthrown trees.

12) Baiting trees with pheromones of secondary species prior to spruce beetle attack would have two positive effects: increasing attacks by the secondary species which could then exploit the phloem resource, and partially repelling the spruce beetle. Therefore, competitive exclusion may have considerable potential for spruce beetle management.

Competitive exclusion of the spruce beetle may provide an alternative tactic for management of the spruce beetle where traditional methods based on tree removal, widespread harvesting, and the use of insecticides are not feasible. Several important factors must be considered in developing and implementing competitive exclusion for operational management of the spruce beetle. The efficacy of competitive exclusion may depend on the relative abundance of secondary species and the abundance and distribution of suitable host material. Reduction in spruce beetle attack and resource exploitation may be enhanced by additional semiochemicals, including pheromones of other potential competitors, pheromones that impart specificity and breeding isolation from congeners that attack other host species, antiaggregation pheromones, and inhibitory host- and non-host volatiles. With further development, competitive exclusion could be incorporated into an integrated pest management program for the spruce beetle for use in isolated or sensitive areas in conjunction with other traditional methods in adjacent areas where feasible.

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Personal Communications:

Setter, R.R., Department of Biological Sciences, Simon Fraser University, Burnaby, B.C.