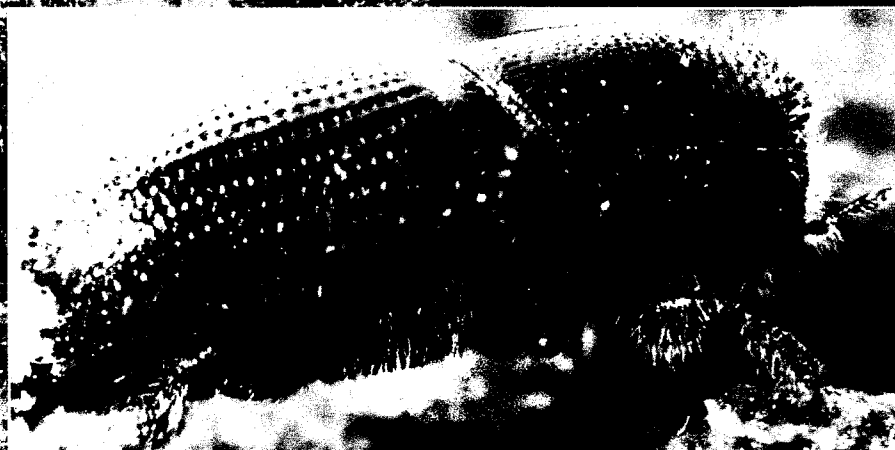# Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis

Edited by
François Lieutier,
Keith R. Day,
Andrea Battisti,
Jean-Claude Grégoire
and Hugh F. Evans

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Chapter 8

CHEMICAL ECOLOGY OF BARK BEETLES IN A COMPLEX OLFACTORY LANDSCAPE

J.A. BYERS

Department of Crop Science, Swedish University of Agricultural Sciences, 230 53 Alnarp, Sweden
Present address: Western Cotton Research Laboratory, Agricultural Research Service, USDA, 4135 E. Broadway Rd., Phoenix, AZ 85040, USA

1. INTRODUCTION

The Scolytidae (bark and ambrosia beetles) comprise a taxonomic group of at least 6000 species that, although appearing similar, may differ widely in their ecology and biochemical adaptations to host trees. Bark beetle species that feed on phloem (a relatively thin layer just under the corky bark) are usually restricted to one or a few host species, whereas ambrosia beetle species that are xylomycetophagous (wood-feeding) and introduce symbiotic fungi for "cultivation" in their galleries generally colonize a larger range of hosts (S.L. Wood 1982). Most biological knowledge on bark and ambrosia beetles derives from studies on relatively few pest species in the genera *Dendroctonus, Ips, Scolytus, Xyleborus, Trypodendron, Tomicus=Blastophagus* (Fig. 1), *Pityogenes, Hypothenemus, Pityophthorus, Hylastes,* and *Gnathotrichus.*

Many of these species are obligate and facultative tree-killing bark beetles that comprise only about 10% of scolytid species in the United States and Canada (Raffa *et al.* 1993). However, these pests that kill trees are the most likely to significantly influence the evolution of the host tree and its chemistry.

The diversity of bark beetle biology, in which each species is adapted to only one or a few host tree species, probably has resulted due to natural selection from the great variety of plant biochemicals. It is also theorized that each species of tree has coevolved various chemicals to defend against the herbivorous selection pressures of the tree-killing bark beetles (Erlich and Raven 1965; Feeny 1975; Cates 1981; Berryman *et al.* 1985; Byers 1995). Semiochemicals (behavior modifying chemicals) from both the tree and the beetle have many functions during the life cycle of a bark beetle (for reviews see D.L. Wood 1982; Borden 1982, 1997; Lanier 1983; Birch 1984; Borden *et al.* 1986; Byers 1989a, b, 1995; Raffa *et al.* 1993; Schlyter and

Birgersson 1999). Host and non-host plant chemicals can be attractive, repellent, toxic, or nutritious to bark beetles. These chemicals may have affects on: (1) finding and accepting the host tree (host selection and suitability), (2) feeding stimulation and deterrence, (3) plant resistance, (4) pheromone/allomone biosynthesis and communication, and (5) attraction of predators, parasites and competitors of bark beetles.

Figure 1. Electron micrograph of male (top) and female Tomicus piniperda from Sweden.

Knowledge of bark beetle chemical ecology and insect-tree relationships is important to devising better ways of managing bark beetle populations and their damage to trees. The strategies that bark beetles use to avoid competition within and between species, to avoid unsuitable host and nonhost trees, to find their host trees and mates, and to maximize their reproductive success can be investigated with the purpose of eventually manipulating these processes to the detriment of the beetles. Most of the following presentation involves species in the genera *Dendroctonus*, *Tomicus*, *Ips*, and *Pityogenes*. Before presenting theories on possible strategies bark beetles use for locating suitable hosts and avoiding competition, it is useful to consider an overview of the life cycle and behavior of bark beetles in relation to semiochemicals.

2. BEHAVIORAL ECOLOGY AND PHYSIOLOGY IN THE LIFE CYCLE OF BARK BEETLES

In general, adults of bark beetles in the above genera overwinter in either forest litter (e.g., *Ips*, *Pityogenes*) or the brood tree (e.g., *Dendroctonus*, *Ips*, *Pityogenes*). In species that have several generations during the summer, emergence is from the brood

Figure 2. Storm-damaged Scots pine, Pinus sylvestris, releases monoterpenes attractive to both sexes of Tomicus piniperda in the early spring.

tree. *Tomicus piniperda* has a more complex life cycle in which adults over-winter in living, nonbrood trees (Salonen 1973; Långström 1983). After emergence, the adults of all species attempt to locate a host tree (termed the dispersal flight), either by orienting to pheromone or plant volatiles. Host suitability may be determined in flight or after landing on the tree. In the monogamous genera *Tomicus* and *Dendroctonus* (subfamily: Hylesininae), the females select the host tree and an entrance hole (attack) to begin construction of oviposition galleries in the phloem. In contrast, males of the polygynous genera *Ips* and *Pityogenes* (subfamily: Scolytinae) begin the entrance hole and later accept several females. In most cases, individuals of only one sex begin the attack, releasing a species-specific blend of chemicals comprising an aggregation pheromone (Byers 1989a). However, in *D. brevicomis,* the female and the joining male each produce a unique synergistic pheromone component that when combined elicit maximal attraction response (Silverstein *et al.* 1968; Kinzer *et al.* 1969). In *T. piniperda,* there is no evidence of an aggregation pheromone (Byers *et al.* 1985; Löyttyniemi *et al.* 1988); instead, host-tree chemicals induce aggregation (Fig. 2).

Species of bark beetles feed only on one or a few host tree species, which are perceived and located by means of the beetle's various sensory receptors that are located on their antennae and mouthparts. Except for morphological studies on *D. ponderosae* and *I. typographus*, little is known about the sensilla on the maxillary and labial palpi mouthparts of bark beetles (Whitehead 1981; Hallberg 1982). In these species there is clearly a large number of chemosensilla (Fig. 3), which appear to be important for host selection and food discrimination.

In other insects, the tarsi and ovipositor have chemosensilla that are involved in host acceptance (Städler 1984), but these structures have not been studied in bark
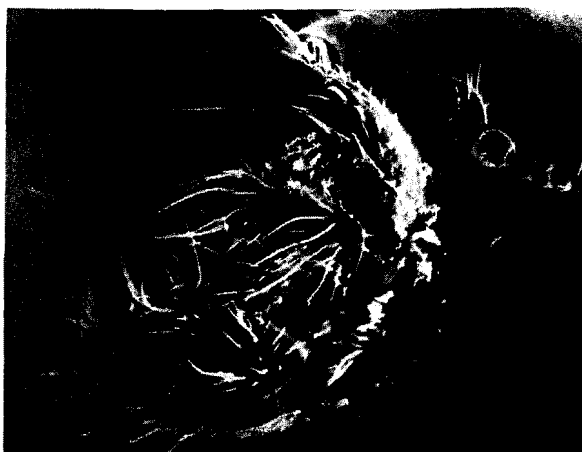
Figure 3. Electron micrograph of mouthparts of Tomicus piniperda.

Figure 4. Electron micrograph of antenna and eye of Tomicus piniperda.

beetles. Most work with bark beetles has focused on the antennae (Fig. 4), which are known to have sensilla responsive to volatile pheromone and host components, as well as other air-borne chemostimulants (Borden and Wood 1966; Payne *et al.* 1973; Payne 1979; Mustaparta 1984; Faucheux 1989).

The electrophysiological response of an insect to semiochemicals can be studied with an electroantennogram (EAG) of the whole antenna or by the single-cell technique that measures responses of specific receptor cells (Payne 1979). Each antennal receptor cell contains multiple acceptor sites that interact with the chemicals.

Bark beetle olfactory cells on the antennae have been shown to be of several functional types, which probably are found in all species. These types include: (1) a highly specific cell such as the ipsdienol-sensitive ones in *I. paraconfusus* and *I. pini* that are responsive only to one of two possible enantiomers (identical atomic structures but not superimposable, e.g., α-pinene in Fig. 5), (2) a pheromone-sensitive one that is also responsive to other synergists or inhibitors such as the frontalin cells of *D. frontalis*, which have at least two acceptor types each specific for one enantiomer of frontalin, and (3) a "generalist" type that responds to host monoterpenes as well as pheromones (Mustaparta *et al.* 1980; Payne *et al.* 1982; Dickens *et al.* 1985; Dickens 1986).

Vision plays a vital role during orientation flights of bark beetles, and in conjunction with antennae enable bark beetles to locate semiochemical sources. The eyes of many bark beetles (e.g., *Ips*, *Scolytus*, and *Pityogenes*) consistently have only about 100-240 ommatidia (Fig. 4), which is less than many insects (Chapman 1972; Byers *et al.* 1989a). Based on electrophysiological recordings, two color receptor types have been identified in the eyes with a maximum absorbance at 450 nm (blue) and 520 nm (green) (Groberman and Borden 1982).

Observations of *I. paraconfusus*, *I. typographus*, *D. brevicomis*, *P. chalcographus*, and *T. piniperda* in flight chambers under dim red light or in complete darkness using an electronic vibration detector indicate they will not fly after dark (Lanne *et al.* 1987; Byers and Löfqvist 1989; Byers unpublished). Bark beetles are attracted in greater numbers to traps baited with host odor or pheromone that are placed next to "tree trunk silhouettes" than to traps without such visual stimuli, indicating that beetles orient to the tree trunk during landing (Moser and Browne 1978; Borden *et al.* 1982; Tilden *et al.* 1983; Lindgren *et al.* 1983; Bombosch *et al.* 1985; Ramisch 1986; Chénier and Philogène 1989). Beetles of some species prefer to land on horizontal silhouettes rather than on vertical ones of the same size (Pitman and Vité 1969). Another indication that bark beetles have relatively poor visual acuity is that *T. piniperda* males must walk within 1 cm of a female beginning her entrance hole before they appear to detect her and initiate guarding behavior (Byers 1991). Both *T. piniperda* and *D. brevicomis* individuals can be induced to drop off a tree by movements of the human body about 2 m away (about the same angle of resolution and relative size, my observations).

Primary attraction to host tree volatiles can be considered to occur over a "long-" or "short-range." The concept of range differs between authors and depends on the insect considered. Here I consider long-range attraction for bark beetles to be flight orientation over a meter or more to a semiochemical source. In reality the division is arbitrary, since bark beetles may orient over practically any distance depending on the release rate of the semiochemical. At very high release rates the insect may not closely approach the source due to adaptation (Baker *et al.* 1988). However, the concept of range is valid at natural release rates. Attraction to pheromone is certainly long-range. For example, three parallel lines spaced 4.6 m apart and hung with sticky screens spaced every 1.5 m intercepted *I. paraconfusus* in a "V"-shaped pattern narrowing to a pheromone source of 50 males boring in a pine log (Byers 1983a). In this experiment, beetles appeared to orient over a distance of at least 17 m. *S. quadrispinosus* beetles
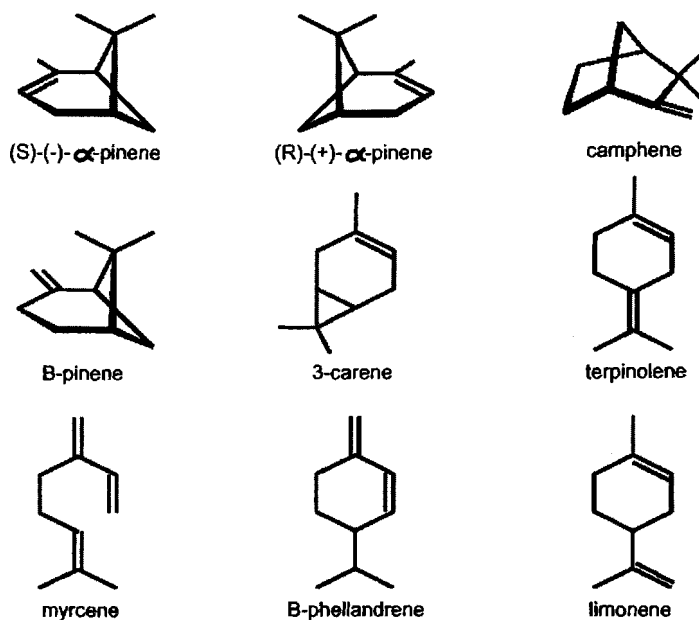
(S)-(-)-α-pinene   (R)-(+)-α-pinene   camphene

B-pinene   3-carene   terpinolene

myrcene   B-phellandrene   limonene

Figure 5. Major monoterpenes of conifers. Note that the enantiomers of α-pinene are identical except that they are non-superimposable (mirror images). Camphene, β-pinene, 3-carene, β-phellandrene, and limonene also have two enantiomers, although only (-)-β-pinene and (+)-3-carene are found in trees (Mirov 1961). Myrcene and terpinolene are achiral.

were intercepted by passive traps 12 m from a girdled hickory tree that was attracting these beetles (Goeden and Norris 1964). The distance over which beetles respond anemotactically depends primarily on the release rate of the volatile (under mild wind conditions). In Denmark, I once observed *I. typographus* flying slowly upwind (0 to 0.5 m/s ground speed) in 3 m/s gusty winds to a large fallen spruce tree under massive attack. During their orientation to this pheromone source, beetles were flying at 3-6 m in height from at least as far away as 50 m downwind. Jactel (1991) estimated that the maximum attraction distance of *I. sexdentatus* to pheromone-baited traps was 80 m.

An index of attraction strength for a particular semiochemical release rate is known as the "effective attraction radius" (*EAR*), which is proportional, but considerably smaller, than the maximum attraction distance (Byers *et al.* 1989a). The *EAR* is the radius that a trap would need to be enlarged, as a spherical "passive" trap, in order to intercept as many dispersing insects as were actually caught on the trap when baited. For example, the *EAR* of *T. piniperda* to a blend of three host monoterpenes, released at rates equivalent to a cut log of Scots pine from each of 10 traps along a 12-m high pole, was largest at the lowest trap (*EAR* = 1.3 m). The same design found an *EAR* of 3.2 m for *I. typographus* response to a blend of its pheromone components (Fig. 5). These comparisons indicate that the EAR can be larger for a pheromone than for host

volatiles. However, both these values would be greater at higher chemical release rates. Schlyter (1992) discusses several additional concepts of attraction distance, including the attraction range (the maximum distance over which insects can be shown to be attracted) and the sampling range (the distance over which insects reach a source in a given time period).

The optomotor anemotaxis mechanism for orientating to pheromone sources proposed for insects, especially moths (David et al. 1982; Baker 1989), also appears to function in bark beetles (Choudhury and Kennedy 1980). In this theory, a bark beetle attempts to fly directly upwind when in contact with a packet of pheromone-laden air of the plume, but casts (flies from side to side with respect to the source) when contact is lost. The beetle senses the wind direction while flying by observing the ground below: in no wind, or head-on wind, the ground moves directly underneath during flight. However, if the visual ground field also moves from right to left somewhat, for example, then wind is coming from the left, and the beetle turns to the left to minimize the transverse ground shift and keep the ground moving directly underneath, in this manner the insect heads upwind and toward the pheromone source.

Short-range attraction could be considered to occur within one meter of the source such as when flying along the trunk as I have observed for *T. piniperda*; however, after landing the beetle must use a mechanism other than optomotor anemotaxis. While walking, the ground does not move under the beetle due to wind, but the beetle probably can still sense wind direction by mechanoreceptors, and use "casting" or circling movements to locate the odor source. Beetles walking in an arena with laminar airflow respond to a point source of synthetic pheromone (or air from an attacked log) by walking directly upwind within the odor plume. If they walk outside the plume, they would experience a concentration gradient decline as they walked. By turning slightly with respect to the upwind angle (as detected by tactile hairs) they would either soon re-contact the odor or the concentration would further decline. In the later case they could reverse the angle or continue turning in a circle that would bring them into contact with the odor, whereupon they could walk directly upwind again. This mechanism is consistent with tracings of tracks of *I. paraconfusus* (Borden and Wood 1966) responding to pheromone in the laboratory olfactometer (see Birch 1984) as well as observations of other species in the genera *Ips*, *Dendroctonus*, *Tomicus*, and *Pityogenes* responding to pheromone or host odors in similar olfactometers (Byers et al. 1979; Byers and Wood 1981a; Lanne et al. 1987; Byers 1983a; Byers et al. 1990a, b).

After the beetle orients and lands on a host tree and begin to release an aggregation pheromone, the likelihood of successful colonization depends on (1) the population level of beetles available for recruitment to the attack and (2) the resistance and health of the tree and its ability to produce defensive resin (Fig. 6). Resistance of conifers, especially pines, to bark beetle attacks has long been attributed to the amount of resin exuded and pitch tubes formed (Webb 1906; Hodges et al. 1985). Dead beetles can often be seen in crystallized resin of pitch tubes. However, species of *Dendroctonus* and other aggressive bark beetles have a great ability to survive the "toxic" monoterpenes and suffocating mucilage and may struggle for hours in copious resin flows (*D. frontalis*, Hodges et al. 1979; *D. brevicomis*, Byers 1995). Drought and poor

water balance lower the resistance of conifers (Hodges and Lorio 1975; Hodges *et al.* 1979) probably by lowering the turgidity of resin duct cells, which lowers the oleoresin exudation pressure (OEP). A correlation between higher OEP and greater resistance of ponderosa pine to attack by *D. brevicomis* and *I. paraconfusus* has been reported (Vité 1961; Wood and Vité 1961; Wood 1962; Brown *et al.* 1987). Oleoresin and the monoterpenes indicate host resistance and therein are repellent to bark beetles in concentrated amounts (Struble 1957; Pitman *et al.* 1966; Berryman and Ashraf 1970; Bordasch and Berryman 1977; Byers *et al.* 2000; El-Sayed and Byers, 2000).

Beetles of many species have specialized areas of the integument or pouches called mycangia where symbiotic fungi are carried, and in some species nourished, until they are introduced inside the entrance tunnel where they grow into the tree (Happ *et al.* 1976; Whitney 1982; Bridges *et al.* 1985; Paine and Stephen 1987; Levieux *et al.* 1991). Some of the fungal species (genera *Ceratocystis=Ophiostoma, Trichosporium*) may attack the living tissues of the tree and paralyze the tree's ability to produce and exude resin for defense against the beetle (Mathre 1964; Horntvedt *et al.* 1983; Paine 1984; Raffa and Berryman 1987; Paine and Stephen 1987; Paine *et al.* 1988). Other fungal species of the beetle's mycangium grow in the galleries after the tree has been killed and appear important to the nutrition and growth of the larvae (Bridges and Perry 1985; Paine *et al.* 1988; Goldhammer *et al.* 1991). In ambrosia beetles, that generally attack unhealthy or dead trees, the adults and larvae feed on fungi lining the galleries instead of on the tree's tissues (Funk 1970; Furniss *et al.* 1987; Kajimura and Hijii 1992).

Successful colonization and reproduction by a bark beetle in a living tree requires release of enough aggregation pheromone to ensure the attraction of sufficient conspecifics to overwhelm the host tree defenses (Fig. 6); however, after killing the tree and securing mates, pheromone should stop in order to avoid further competition for bark areas (Byers *et al.* 1984; Berryman *et al.* 1985). Semiochemicals play a role in "cooperation" among beetles when killing the tree and in their avoidance of competition (discussed later). "Pioneer" beetles that attack the tree first may suffer most from the tree's defensive resin, but these beetles may have no choice but to attack due to low fat reserves. The later that a beetle arrives in the colonization sequence of the host, the poorer is the quality of the bark substrate due to (1) space utilization by established conspecifics (intraspecific competition) and (2) degradation by microorganisms (discussed subsequently).

Under the bark, females lay eggs that hatch to larvae and feed on the phloem for several weeks. Chemicals from both the plant and microorganisms could affect beetle survival at this time, but little is known about these interactions. However, once the tree is dead, there can be no natural selection on the insects to evolve different tree genotypes that produce chemicals harmful to beetles. The larvae pupate in the bark and become yellow, callow adults where they feed and mature until emerging. The beetles may begin a dispersal flight during the same season, or after overwintering in either the tree (*Dendroctonus, Pityogenes* and many *Ips*) or in the forest litter (*I. typographus* in colder climates). *Tomicus minor* and *T. piniperda* emerge from the bark and fly relatively short distances to the tops of pine trees where they bore into a shoot during the summer (Salonen 1973; Långström and Hellqvist 1991). In the autumn, beetles of

T. piniperda crawl down the trunk and bore into its base to overwinter, whereas *T. minor* overwinters in the litter (Salonen 1973; Långström 1983). The next sections will present the details of some olfactory strategies employed during dispersal to find mates and suitable host trees in which to reproduce.

Figure 6. Dendroctonus brevicomis in resin of ponderosa pine.

3. DISPERSAL FROM THE BROOD TREE OR OVERWINTERING SITE

Insects disperse when their habitat becomes unsuitable. This can be from a lack of food resources, mating possibilities, territories and suitable domiciles, or from the need to escape the local buildup of parasites and predators (c.f. Ricklefs 1990). Apparently for the same reasons, bark beetles emerge from the dead brood tree, or litter near the brood tree, and begin a dispersal flight seeking suitable host trees from among many non-host and unsuitable host trees (Fig. 7).

During dispersal, bark beetles and associated predators and parasites feeding or living in brood trees must locate a new host tree from among the relatively few widely scattered suitable hosts in the forest. The host tree is restricted usually to one or a few species and in most cases the bark beetles seek weakened, less resistant trees, or trees that are in the initial stages of death and decay. Also, beetles try to avoid feeding and reproduction in areas heavily colonized by conspecifics and competing species (Byers 1984, 1995; Fig. 8). Thus, it is expected that species have evolved behavioral responses to volatile host-plant chemicals that indicate the presence of a suitable host in which reproduction can occur.

The dispersal flight of a bark beetle may vary from only a few meters (as observed during epidemics) to possibly several kilometers. Several factors interact to cause the dispersal flight distance to vary between individuals. The most obvious

is that a beetle encounters a susceptible tree early in the dispersal flight. However, whether this tree is attacked may depend on the level of fat reserves that can be mobilized for flight (Atkins 1966, 1969; Byers 1999). A beetle should have higher reproductive fitness if it flies far from the brood tree since it can both avoid inbreeding

Figure 7. Many species of bark beetles disperse through a stand of Norway spruce in the spring (Torsby, Sweden).

with siblings and, probably more importantly, escape predators and parasites that are locally denser near the brood tree. Thus, the dispersal distance has been optimized over evolutionary time to balance the probably logarithmically increasing benefits of flying farther against the probably exponentially increasing likelihood of exhaustion and failing to find a host. The fat level required for lengthy dispersal will depend on the conditions in the brood tree during larval development; for example, disease, insect, and climatic factors will affect the nutritional quality of the host (Fig. 9). Severe competition among the larvae will reduce the size of adults as well as their fat content (Atkins 1975; Anderbrant *et al.* 1985). Parasites would reduce the size and fat content of some adults while predators would lessen competition for those remaining locally, thereby increasing the variability of dispersal range in the population. The population density of bark beetles should be stabilized by a frequency-dependant competition for the susceptible trees. This would produce increasingly stronger, longer-flying individuals with decreasing attack and larval density while producing weaker, shorter-flying individuals with increasing competition.

Knowledge of how far and where bark beetle populations disperse comes mainly from (1) mark-release-recapture studies using pheromone traps and from (2) the geographical occurrence of new infestations relative to previous ones. Both lines of

investigation are inconclusive since (1) only a few pheromone traps were used, usually some tens to hundreds of meters from the release site, so that a large proportion of
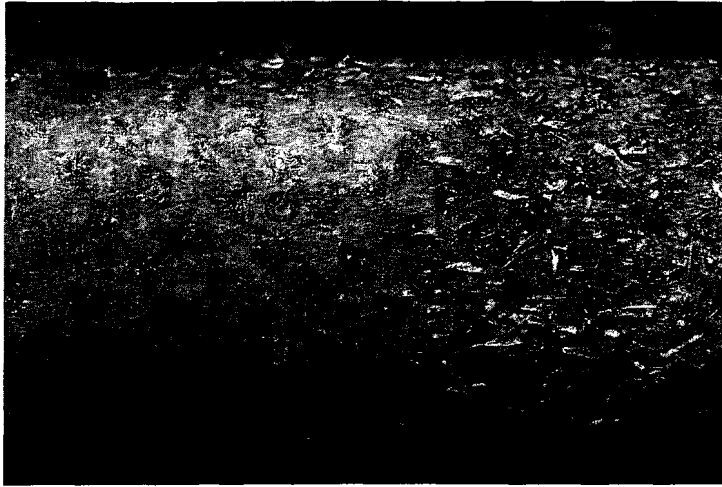

Figure 8. Spacing of attacks of Ips typographus (larger circles) and Pityogenes chalcographus (smaller circles) to avoid competition in the bark of Norway spruce (bark surface scraped smooth on left to reveal attacks that were circled with ink pen).

released beetles escaped, or (2) the origins of attacking beetles were uncertain. Several studies have placed various sized rings of pheromone traps around a source of marked beetles. For example, the spruce bark beetle of Europe, I. typographus, was recaptured at various outer distances from 120 to 1000 m (Botterweg 1982; Zumr 1992; Zolubas and Byers 1995; Duelli et al. 1997). In California, I. paraconfusus was recaptured in outer traps at 2 km (Gara 1963). The ambrosia beetle, Trypodendron lineatum, was recaptured at 500 m (Salom and McLean 1989). As expected, the widely spaced outer traps captured a small proportion of the released beetles, and the large gaps between traps probably allowed many to slip through as they drifted with the wind (e.g., gaps of 785, 1257, and 393 m in Zumr 1992; Gara 1963; and Salom and McLean 1989; respectively). An adverse effect of marking, although discounted, might also influence the dispersal.

The view that bark beetles can fly some tens of km is based less on mark-recapture studies and more on collections of beetles far from forests. Nilssen (1978) found two I. typographus in the stomach of a salmon 35 km from any spruce forest. Miller and Keen (1960) report results of studies by the US Forest Service in California where the western pine beetle, D. brevicomis, infested 'islands' of ponderosa pine, initially free of beetles, that were separated from the main forest by open sagebrush areas. They concluded that significant numbers of bark beetles must have flown a minimum of 3.2 km in one study, and 9.6 or 20 km in another study, to reach the infested trees.

Increasing competition among larvae due to increasing densities of parents laying broods was shown to reduce size and fat content of bark beetles (Atkins 1975; Anderbrant *et al.* 1985) and thus should decrease dispersal ranges. However, this seems in conflict with the statement of Forsse (1991) that flying time of *I. typographus* on flight mills was "similar among populations and appeared unaffected by outbreak

Figure 9. Ips typographus preparing to begin the dispersal flight after emerging from the duff in late May in Sweden.

conditions". Earlier, Forsse and Solbreck (1985) could not find any affect of sex or body size on the duration of flight on mills. Botterweg (1982) also concluded that there was little, if any, affect of beetle size or fat content on dispersal distance as monitored in field traps. However, he did find that fat content of beetles declined over the flight period. This was probably due to consumption of fat during host-seeking rather than later emergence of lower-fat beetles since beetle's sizes (elytral weights) did not decrease over the spring season. Birgersson *et al.* (1988) reported that newly emerged *I. typographus* averaged about 10% fat, while after 24 hours of flight exercise in a plastic box, they declined to only 5% since fat is used for energy. In trees, males with nuptial chambers had about 8% fat (possibly replenishing some after feeding), but after several more days of feeding after females had joined them, the males had 10% fat again.

Bark beetles appear capable of flying quite far in the forest since newly emerged *D. pseudotsugae* flew an average of 2 h on flight mills before resting (3 h total), while some individuals flew up to 8 h uninterrupted (Atkins 1961). Jactel and Gaillard (1991) flew *I. sexdentatus* on rotary flight mills and found that 50% of the beetles could fly more than 20 km, and 10% more than 45 km, based on about 50 interrupted flights. About 25% of *I. typographus* taken from litter in an outbreak area flew for over 1 h, and 10% for more than 2.5 h on flight mills, with a maximum flight of 6 h and 20 min recorded (Forsse and Solbreck 1985). At free-flying speeds of 1.9 to 2 m/s (Gries *et al.* 1989; Byers 1996a), a maximum range would be 41 to 45.6 km without wind transport. However, wing beat frequency declines with flight duration, which may affect flight range. In the only case studied, the wing beat frequency of *D. pseudotsugae* of about 95 Hz declines 18 % with flight time over 4 h to about 75 Hz (Atkins 1960). Speed on flight mills also declined from 1.11 m/s to 0.99 m/s (Atkins 1961).

4. DECIDING WHETHER TO ACCEPT A HOST OR CONTINUE TO DISPERSE

Tradeoffs regarding host plant acceptance by insects have been reviewed by Miller and Strickler (1984). They present a model (their Fig. 6.1) by Dethier (1982) where the decision by the insect whether to accept the plant is dependent on external (olfaction, vision, mechanoreception, and gustation) stimulatory and inhibitory inputs balanced against internal excitatory and inhibitory inputs. A graphical, and simplified, model of host acceptance is shown in Fig. 10 that is directly applicable to pioneer bark beetles. In this model, as the bark beetle flies around searching for suitable host trees (usually trees already under attack by conspecifics) they use up energy reserves of lipids (Atkins 1969; Thompson and Bennett 1971) and probably become increasingly willing to accept substandard hosts.

The beetle may, by chance, encounter several hosts during the dispersal flight that are more or less suitable for reproduction. The beetle will accept a host if the combination of the host suitability and fatigue level of the beetle is above the curve (Fig. 10); otherwise the beetle will continue searching for more suitable hosts. The curve is asymptotic to the Y-axis for those beetles that require flight before responding to semiochemicals, whereas the curve would intersect the Y-axis for species that are immediately responsive after emergence. The suitability of the host is determined by the nutritional quality, as well as by the density of established attacks by the same or other species of bark beetle that indicate the potential for damaging competition.

At the beginning of a dispersal flight, bark beetles are considered rather unresponsive to pheromone or host volatiles. The theory is that fat reserves are higher in freshly emerged beetles so that they have the ability for extended flight and can gain adaptive benefits from dispersal before responding to hosts (Borden *et al.* 1986; Anderbrant *et al.* 1985; Gries *et al.* 1990). Graham (1959) showed that continued flight exercise by *T. lineatum* caused an increase in responsiveness to visual and olfactory stimuli of the host. Freshly emerged *T. lineatum* and *D. pseudotsugae* required 30 or 90 min of flight, respectively, before responding to pheromone from female frass (Bennett and Borden 1971). Atkins (1966) found that female *D. pseudotsugae* with more than 20 %

fat (dry weight) were usually not responsive to the host, while those under 20 % fat were responsive and still could fly. Beetles with less than 10% fat had trouble flying since fat was required as an energy source (Atkins 1969). The fat metabolized by *D. pseudotsugae* consists mainly of C16 and C18 fatty acids (Thompson and Bennett 1971). Other studies have found that scolytid beetles in the genera *Trypodendron*, *Dendroctonus*, *Scolytus*, and *Ips* increased their responsiveness or upwind orientation to host and pheromone after continued flight exercise (Choudhury and Kennedy 1980; and cf. Borden *et al.* 1986).
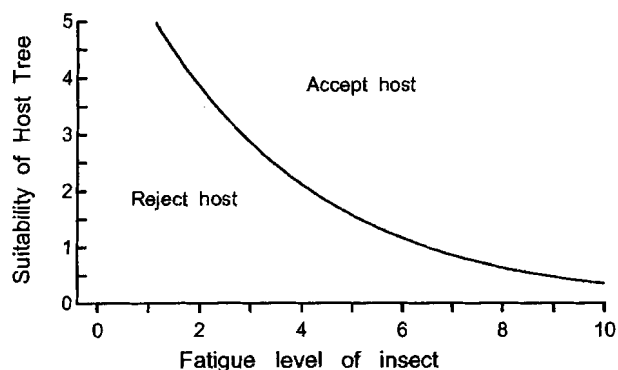

Figure 10. Theoretical curve for the acceptance of host trees by bark beetles depending on prerequisite flight exercise (asymptotic y-axis) and level of fatigue (amount of flight) and suitability of the host for reproduction (which depends on nutritional quality and density of colonization by competing bark beetles).

However, some bark beetles appear responsive to pheromone upon emergence. Lindelöw and Weslien (1986) found that overwintered *I. typographus*, collected and marked as they emerged from tents over forest litter, were caught in synthetic pheromone traps within minutes of release. Schlyter and Löfqvist (1986) suggested that preliminary experiments indicated *I. typographus* became more responsive to pheromone with flight exercise, but further details were not reported. The majority of *I. paraconfusus* in California responded to aggregation pheromone soon after emergence (Wood and Bushing 1963; Gara 1963; Hagen and Atkins 1975). Botterweg (1982) also found that *I. typographus* can immediately respond to pheromone when beginning dispersal, and this is in accordance with his finding that beetles lost 40-50% of their fat over the winter. Possibly, second generation beetles in southern Europe would have higher fat content and consequently disperse further.

5. THEORIES OF HOW BARK BEETLES FIND SUITABLE HOST TREES

There are two general theories on how bark beetles find suitable host trees that have not been previously colonized by conspecifics releasing pheromone (McMullen and Atkins 1962). The first is that beetles locate such trees by orienting over several meters to volatile chemicals usually released by damaged or diseased trees (called "primary

attraction"). It seems that *Tomicus piniperda* finds hosts by primary attraction as the species is attracted to monoterpenes in the resin (Fig. 11).

The second theory is that beetles fly about and encounter suitable host trees at random, whereupon they land and test them by short-range olfaction or by taste. The two theories are not mutually exclusive, and one or the other may primarily operate in a particular species. In California, host finding by the important pests *D. brevicomis* and *I. paraconfusus* is thought to be a random process. Ponderosa pines that were killed by freezing with dry ice and then screened to prohibit bark beetle attack, did not have higher landing rates for the prevalent *D. brevicomis* and *I. paraconfusus* bark beetles (among other species) than did living trees. Landing rates on diseased and healthy trees also were similar. It was estimated that about one *D. brevicomis* beetle visited each tree in the forest each day (Moeck *et al.* 1981; D.L. Wood 1982). Logs of freshly cut ponderosa pine placed in sticky screen traps did not catch beetles of these species, while at the same time high numbers were attracted to synthetic pheromone or infested logs (Moeck *et al.* 1981).

In addition to *I. paraconfusus* and *D. brevicomis*, many species probably visit trees at random, whereupon the tree's resistance is tested during an attack. For example, *Scolytus quadrispinosus* was caught equally on traps placed in host shagbark hickory, *Carya ovata*, and nonhost white oak, *Quercus alba* (Goeden and Norris 1965). Berryman and Ashraf (1970) found attacks by *Scolytus ventralis* in the basal section of 74% of grand fir examined, while only 3.5% of these trees were colonized. Most unsuccessful attacks were abandoned before beginning the gallery. The attacks on grand fir appeared random during the early part of the flight period before aggregations resulted. Hynum and Berryman (1980) caught *D. ponderosae* in traps on 96% of the lodgepole pines (*P. contorta*) sampled, but only 66% of these pines were killed. Also, they found no differences in landing rates between killed and surviving lodgepole pines or between host and nonhost trees. A direct relationship between the numbers of *D. ponderosae* caught on unattacked trees and the numbers of trees upon which beetles landed was found in a study of lodgepole pines (Raffa and Berryman 1979). *I. grandicollis* landed equally on sticky traps on trees judged resistant or susceptible based on crown area (Witanachchi and Morgan 1981). However, Schroeder (1987) found an average of 35 *T. piniperda* landing on lower vigor Scots pine, *P. sylvestris* (as judged by less crown area), than on higher vigor trees (mean of 22 landing per tree). These differences could be due to secondary release of monoterpenes by beetles boring in the low vigor trees that were less able to resist attack.

There is some evidence that *I. typographus* is weakly attracted to host volatiles (Austarå *et al.* 1986; Lindelöw *et al.* 1992) or monoterpenes such as α-pinene (Rudinsky *et al.* 1971), but other studies have not observed any attraction to host volatiles or synergism of pheromone and host volatiles (Schlyter *et al.* 1987a). A computer model by Gries *et al.* (1989), in which "beetles" must take a series of flights between trees in a grid (each flight to one of eight neighboring trees) and test each tree for suitability, showed that few beetles would find the widely scattered hosts designated as susceptible. Thus, they concluded that a mechanism of long-range

primary attraction would be required for maintenance of the population. However, a more recent computer model, in which beetles "fly" more naturally among randomly

Figure 11. Attraction of Tomicus piniperda to monoterpenes released from oleoresin exuding from cut end of a Scots pine log.

dispersed susceptible trees indicated that a significant proportion of the population could find the susceptible trees by chance interception of the trunk diameter (Byers 1993a, 1996a). If beetles then test the defenses of the potential host (although this rarely has been observed) then weaker, more susceptible, trees will not exude adequate resin and allow the beetle to produce aggregation pheromone. According to the later model, this will in effect greatly increase the effective "radius" of the tree (or EAR) so that many more in the population can quickly find and colonize these trees (Byers 1993a, 1996a).

In addition to the "random landing" and "primary attraction" to host volatile theories, some bark beetles may find weakened and susceptible host trees by orienting to volatiles produced by competing species during colonization. The volatiles can be host compounds that virtually any bark beetle would release upon attack (e.g., monoterpenes) or pheromone components of these other species. For example, *D. brevicomis* responds to pheromone components of *I. paraconfusus* in the laboratory (Byers and Wood 1981a); *I. typographus* responds to *exo*-brevicomin (from *D. micans* and *Dryocoetes* spp., Borden *et al.* 1987) when combined with its pheromone components (Tommerås *et al.* 1984); and several sympatric species of *Ips* in the southeastern United States are cross-attracted to infested pine logs in the field (Birch *et al.* 1980b).

Finally, bark beetles may be aided in locating suitable host trees by avoiding volatiles from (1) hosts fully colonized by conspecifics or competing species and (2) nonhost trees and plants. Avoidance of these types of substrates will be covered in

more detail in later sections on discriminating suitability of hosts, avoidance of competition and decaying colonized hosts, and avoidance of nonhosts.
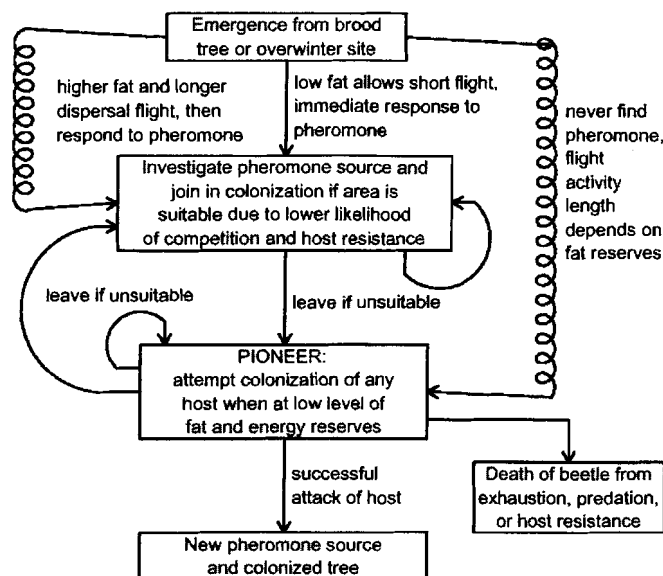
6. STRATEGIES OF "PIONEER" BARK BEETLES

Figure 12. Conceptual model of dispersal and host-seeking ecology of "aggressive" bark beetles that use aggregation pheromones. Factors such as the beetle's fat reserves, chances of encountering pheromone, and level of competition and host suitability determine whether a beetle joins resident beetles in colonizing a tree or is the first "pioneer" to attack.

A beetle that lands on a tree and attempts to find a place on the bark to bore is termed a "pioneer" if there are few others present. Pioneers are presumed to encounter significant host resistance and resin when attacking compared to later arrivals ("joiners") when the tree is weakened or has succumbed (Berryman 1974; Raffa and Berryman 1979; Wood 1982; Byers 1995). Only males, in the case of *Ips* and *Pityogenes*, or females, in the case of *Dendroctonus*, initiate the entrance tunnel and can be pioneers, but the joining sex in the early stages of colonization must incur some increased risks of resinosis as well. One hypothesis is that since a few pioneers must attack the tree and survive to produce pheromone before numerous others of the population can exploit the resource, pioneers must be the largest and most vigorous beetles of the population. In Fig. 12, an alternative theory is presented for the dispersal and host-seeking flight under various conditions and circumstances. An individual should prefer to orient to pheromone and a tree under colonization, but if fat reserves become relatively low during dispersal, then a pioneer strategy becomes advantageous

compared to exhaustion in flight (as in Fig. 10). As fat reserves become dangerously low, the beetle might attempt to bore into any host tree in the expectation of encountering one of low resistance (Fig. 2). Thus, smaller beetles, such as those that suffered severe larval competition and have low fat (Anderbrant *et al.* 1985; Anderbrant and Schlyter 1989), or those that have used up their fat reserves during a host-seeking flight, regardless of size, are hypothesized to be the pioneers (Byers 1999).

If the pioneer beetle lands on a tree of low resistance that cannot produce sufficient resin to repel the beetle, then it has time to feed and excrete pheromone components with the fecal pellets. This then functions as a beacon to individuals of the population in the surrounding area that a weakened host can be exploited as a food and mate resource (Byers 1996a). Aggregation pheromone is an evolutionarily adaptive signal since only trees too weak to vigorously repel beetles with resin will allow beetles to produce pheromone and joining beetles will likely suffer less mortality than as a pioneer. Some species, usually termed less aggressive ones, such as the European pine shoot beetle, *Tomicus piniperda*, are attracted to monoterpene volatiles produced after injury to the host tree by biotic or abiotic factors that indicate susceptibility (Byers *et al.* 1985; Byers 1995, 1996a).

7. HOST SEMIOCHEMICALS ATTRACTIVE TO BARK BEETLES

Species of bark beetle that regularly attack and kill living trees (termed "aggressive") have been shown nearly always to possess an aggregation pheromone, usually of two or more components, but are weakly, if at all, attracted by host volatiles alone (Vité and Pitman 1969; Byers 1989a, 1995). However, so-called "secondary" bark beetle species (those that arrive later after the tree has already been killed by the aggressive bark beetles or that feed as saprophytes in decaying trees) may not use an aggregation pheromone, but generally are strongly attracted to either host monoterpenes, ethanol or a combination (Kohnle 1985; Klimetzek *et al.* 1986; Schroeder 1988; Schroeder and Lindelöw 1989). Host volatiles are attractive to a number of forest scolytids including species in the genera *Scolytus, Dendroctonus, Hylurgops, Trypodendron* and *Tomicus* (Goeden and Norris 1964; Rudinsky 1966; Meyer and Norris 1967a; Moeck 1970; Byers *et al.* 1985; Lanne *et al.* 1987; Volz 1988; Lindelöw *et al.* 1992; Hobson *et al.* 1993; Macias-Samano *et al.* 1998).

Ethanol, probably released by microorganisms in decaying woody tissue (Graham 1968; Moeck 1970; Cade *et al.* 1970) and by alcoholic fermentation processes in stressed plants (Kimmerer and Kozlowski 1982; Kelsey 1994, 1996; Kelsey and Joseph 1997, 1999), is attractive to a wide variety of species of bark beetles (Moeck 1970, 1981; Magema *et al.* 1982; Montgomery and Wargo 1983; Kohnle 1985; Klimetzek *et al.* 1986; Schroeder 1987, 1988; Schroeder and Eidmann 1987; Phillips *et al.* 1988; Volz 1988; Chénier and Philogène 1989; Schroeder and Lindelöw 1989; Byers 1992a). Primary alcohols other than ethanol have not been reported as being attractive to scolytids. However, only a few studies have tested methanol (Moeck 1970; Montgomery and Wargo 1983; Byers 1992a); longer chain alcohols up to hexanol did not attract Scolytids in Sweden when they were known to be flying (Byers

1992a). Electroantennogram (EAG) responses of *T. piniperda* to a series of straight-chain alcohols indicated that the antennae respond increasingly to longer chain length up to a maximum between pentanol, and heptanol, and then decrease in responsiveness (Lanne *et al.* 1987). The response spectrum could be due in part to differences in volatility. Thus, although ethanol plays a role in host selection (discussed subsequently), the EAG response for ethanol is lower than for longer-chain alcohols, which are not attractive but rather repellent. 1-Hexanol (from deciduous trees) inhibits response of *T. piniperda* to attractive monoterpenes (Schlyter *et al.* 2000). Ethanol and CO_2 are the usual end products of sugar fermentation by microorganisms whereas methanol is not, which probably explains the evolution of the use of ethanol by forest insects. Moeck (1970) found methanol to be a minor constituent and ethanol a major constituent of extracts from Douglas-fir sapwood attractive to *T. lineatum*.

Various tree monoterpenes (e.g. α-pinene, myrcene, terpinolene, ß-pinene, Fig. 5) and turpentine are also attractive to a large number of bark beetle species (Byers *et al.* 1985, 1992a; Phillips *et al.* 1988; Schroeder 1988; Chénier and Philogène 1989; Schroeder and Lindelöw 1989; Miller and Borden 1990; Phillips 1990; Hobson *et al.* 1993). Synergism between ethanol and various monoterpenes (or turpentine) is also of widespread occurrence (Nijholt and Schönherr 1976; Kohnle 1985; Vité *et al.* 1986; Phillips *et al.* 1988; Volz 1988; Schroeder 1988; Chénier and Philogène 1989; Schroeder and Lindelöw 1989; Phillips 1990). These compounds are not only important for primary attraction to plants, but also may play a role in enhancing the bark beetles' response to aggregation pheromone (Bedard *et al.* 1969, 1970; Pitman *et al.* 1975; McLean and Borden 1977; Borden *et al.* 1980, 1981; Paiva and Kiesel 1985; Byers *et al.* 1988; Miller and Borden 1990). Host-tree compounds, ethanol and monoterpenes, elicited increased entering rates of bark beetles *T. lineatum* and *P. chalcographus*, respectively, into pipe traps baited with aggregation pheromone (Vité and Bakke 1979; Bakke 1983; Byers *et al.* 1988). ß-Phellandrene (Fig. 5) is slightly attractive alone to *I. pini* and enhances response to pheromone (Miller and Borden 1990), and so the monoterpene might induce entering of holes.

In most of the previously discussed studies, the discovery of host compounds attractive to bark beetles has been by the comparative approach (similar species are known to be attracted) or by surmising that identified chemicals in the host would be attractive. Thus, most studies are incomplete because of the possibility that there are still undiscovered chemicals important for attraction to the host. Byers *et al.* (1985) used the subtractive-combination bioassay and fractionation method (Byers 1992b) to rigorously identify the host volatiles responsible for aggregation of *T. piniperda*. A combination of (-)-(*S*)-α-pinene, (+)-(*R*)-α-pinene, (+)-3-carene, and terpinolene, or each alone, was effective in attracting both sexes (Fig. 5 and 11). During the isolation study, designed for detection of synergistic pheromone components, no evidence was found for beetle-produced compounds being attractive, in contrast to most bark beetles that aggregate en masse on hosts (Byers 1989a). Byers *et al.* (1985) quantified the release rates of α-pinene, terpinolene, and 3-carene from a freshly cut log of Scots pine (28 cm x 13 cm diam.) and found them each to be about 15 mg/day. Release of comparable amounts in the field competed favorably with a host log in attracting *T. piniperda*. They theorized that the beetle's attraction to monoterpenes functioned in

the selection of host species because other common tree species have less monoterpenes. In addition, this attraction to monoterpenes served in the beetle's recognition of its host's susceptibility since storm-damaged or felled trees have resinous wounds releasing monoterpenes and are less able to resist attack due to the injuries.

In the isolation of host volatiles attractive to *T. piniperda*, a gas-chromatographic adsorbent (Porapak Q), widely used for trapping insect pheromones, was used to collect headspace air from the infested pine logs. Unfortunately, Porapak Q will not retain ethanol molecules due to their small size. Thus ethanol could be a constituent of the attractive host odor. Vité *et al.* (1986) presented evidence that ethanol enhanced the attraction of *T. piniperda* to α-pinene and terpinolene (identified above) by about eight-fold, but these results are difficult to confirm since the chemical release rates were not given. They proposed that ethanol would be released from diseased trees and thus indicate their suitability to *T. piniperda*. Ethanol is attractive when released on healthy trees since *T. piniperda* were caught in ethanol-baited traps on trees; and these beetles also attacked trees baited with ethanol (Schroeder and Eidmann 1987; Byers 1992a). However, the attraction to ethanol in traps away from trees is weak or negligible, while monoterpenes in these traps are attractive (Schroeder 1988; Schroeder and Lindelöw 1989; Byers 1992a).

Ethylene is another chemical that may be released by diseased or dying trees that could be attractive to bark beetles. Campos *et al.* (1994) found that the olive bark beetle, *Phloeotribus scarabaeoides*, was attracted to logs of olive that released higher amounts of ethylene. Also, a chemical reaction of 2-chloroethylphosphonic acid caused ethylene to be released, which attracted the beetles in the laboratory (Campos and Pena 1995). Trees treated with the chemical released more ethylene and caught more beetles on traps than traps on control trees (Gonzalez and Campos 1995). Treated wood also released more ethylene that resulted in higher densities of attacks by olive bark beetles (Gonzales and Campos 1996). Inoculation of bark beetle-vectored fungi, *Ophiostoma minus* and *O. nigrocarpa,* into slash and loblolly pines induced ethylene release (Popp *et al.* 1995). Ethylene was also released from needles of Monterey pine inoculated with the pitch canker fungal pathogen, *Fusarium circinatum*. However, the twig-infesting *Pityophthorus* spp. was not attracted to ethylene, cut branches, or to branches plus ethylene (Bonello *et al.* 2001), although fungal infected branches were not tested. The authors concluded that host discrimination occurs after landing. More research is needed to determine if ethylene plays a role in primary attraction of other bark beetles to weakened hosts.

8. DISCRIMINATING THE SUITABILITY OF HOSTS

Plant suitability in insects was reviewed by Scriber (1984). A plant's suitability to bark beetles varies with its nutritional quality and composition of deterrents and toxins. Nonhost trees are probably less nutritional to a particular beetle than its hosts. The beetle in most cases would not be expected to be able to detoxify some of the toxins in nonhosts (which are avoided or not usually encountered) that may have evolved for use against herbivorous insects. A beetle would save much time and energy if it could

discriminate between the host and the nonhost and determine the suitability of the host by olfactory means from a distance without the need to land. Sometimes host and nonhost trees are adjacent and the beetle could land by mistake on the nonhost; however, short-range olfactory cues might indicate the inappropriateness of the nonhost bark substrate (Byers *et al.* 1998, 2000). If the beetle still could not decide, boring a short distance into the nonhost might reveal the lack of feeding stimulants or the presence of deterrents causing the beetle to leave (Elkinton and Wood 1980; Byers *et al.* 2000).

9. AVOIDANCE OF COMPETITION AND UNSUITABLE AREAS OF HOSTS

Verbenone is found in relatively large amounts (μg) in male hindguts of several bark beetles of North America, *D. frontalis*, *D. brevicomis*, *D. ponderosae*, and *D. pseudotsugae* (Renwick and Vité 1968; Rudinsky *et al.* 1974; Byers *et al.* 1984; Pierce *et al.* 1987) but in low amounts (ng) in *T. piniperda* (Lanne *et al.* 1987), or essentially absent in *I. paraconfusus*, *I. typographus*, and *P. chalcographus* (Byers 1983b; Birgersson *et al.* 1984, 1990). Verbenone (Fig. 13) inhibits the attraction of these beetles to their respective aggregation pheromones (Renwick and Vité 1969, 1970; Byers and Wood 1980; Bakke 1981; Byers *et al.* 1989c; Byers 1993b).

Exposure of male and female *D. brevicomis* to (+)- and (-)- enantiomers of α-pinene for several hours caused them to produce large amounts of (+)- and (-)-*trans*-verbenol in their hindguts (Fig. 13, Byers 1983c). However, the biosynthesis of verbenone in these beetles was not affected by exposure to α-pinene enantiomers, even though verbenone is structurally similar to α-pinene (Fig. 5) and is found in males landing on trees (Renwick and Vité 1968, 1970; Byers *et al.* 1984). The (-)-enantiomer of *trans*-verbenol (Fig. 13) inhibits female *D. brevicomis* from entering holes and may serve as a signal to arriving females that they should avoid areas colonized by conspecifics (Byers 1983c).

Both verbenone and *trans*-verbenol are produced by *D. brevicomis* beetles in the greatest amounts early in colonization so it was suggested that they play a role in reducing intraspecific competition (Byers *et al.* 1984), as well as interspecific competition with *I. paraconfusus* (Byers and Wood 1980). However, verbenone (and possibly *trans*-verbenol) are also produced increasingly in ageing logs infested by bark beetles (Birgersson and Bergström 1989; Byers *et al.* 1989c). A common bacterium, *Bacillus cereus*, also isolated from *I. paraconfusus*, can make *cis*- and *trans*-verbenol from α-pinene (Brand *et al.* 1975). Several yeasts from *I. typographus* can interconvert the verbenols, and when grown in a phloem medium they produced the oxygenated monoterpenes α-terpineol, borneol, myrtenol, terpenene-4-ol and *trans*-pinocarveol, compounds also shown to be released increasingly from bark beetle holes with age of attack (Leufvén *et al.* 1984, 1988; Birgersson and Bergström 1989). A mycangial fungus grown in culture media converted alcohol products of α-pinene to verbenone, the end product (Brand *et al.* 1976). These microorganisms are introduced by bark beetles during colonization and after buildup may release verbenone, thus signaling to flying beetles that remaining in these bark substrates would entail competition with established bark beetle colonies. Recently, verbenone was found in twigs of eastern
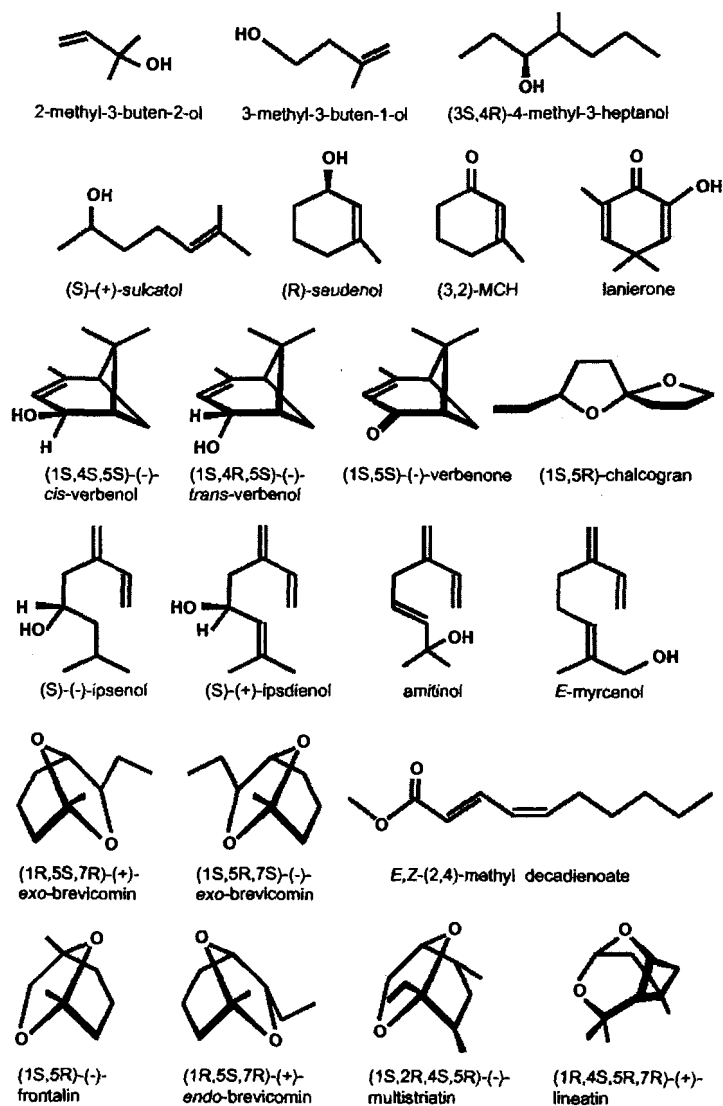
Figure 13. Pheromone components of bark beetles. Key: aggregation component (a), inhibitor of aggregation (i). Row 1: 2-methyl-3-buten-2-ol (a, I. typographus); 3-methyl-3-buten-1-ol (a, I. cembrae), 4-methyl-3-heptanol (a, S. multistriatus). Row 2: sulcatol (a, G. sulcatus, G. retusus); seudenol (D. pseudotsugae, D. rufipennis, D. simplex); MCH (i, D. pseudotsugae); lanierone (a, I. pini). Row 3: cis-verbenol (a, I. paraconfusus, I. typographus, I. calligraphus); trans-verbenol (a, D. ponderosae, T. minor; i, D. brevicomis); verbenone (i, Dendroctonus); chalcogran (a, Pityogenes). Row 4: ipsenol (a, Pityokteines curvidens, and many Ips: e.g. I. paraconfusus, I. grandicollis), ipsdienol (a, many Ips, e.g. I. paraconfusus, I. duplicatus, I. pini, I. calligraphus, I.

*avulsus); amitinol (a, I. amitinus); E-myrcenol (a, I. duplicatus). Row 5: (+)-exo-brevicomin (a,
D. brevicomis, Dryocoetes); (-)-exo-brevicomin (a, Dryocoetes); methyl decadienoate (P.
chalcographus). Row 6: frontalin (a, many Dendroctonus); endo-brevicomin (i, D. frontalis);
multistriatin (a, S. multistriatus); lineatin (a, T. lineatum). References to above pheromones are
in reviews by Borden (1982) and Byers (1989a), and the following (Bakke 1975; Baker et al.
1977; Lanne et al. 1987; Borden et al. 1987; Byers et al. 1989b, 1990a, b; Teale et al. 1991;
Camacho et al. 1993).*

cottonwood, *Populus deltoids* (personal comm. from Carlos Flechtmann, in Huber *et al.* 1999).

Myrcene and α-pinene from host trees can be used as precursors of pheromones and allomones in some species of conifer-feeding bark beetles. However, recent research has shown that the majority of ipsdienol and ipsenol in *Ips* bark beetles results from *de novo* biosynthesis from simple acetate and mevalonate precursors (Seybold and Tittiger 2003). The later steps in the isoprenoid pathway lead to geranyl diphosphate and myrcene before being stereoslectively, and species-specifically, converted to various enantiomers of myrcene-like alcohols (e.g., ipsdienol, ipsenol, *E*-myrcenol, amitinol) that are pheromone components (Seybold *et al.* 2000; Seybold and Tittiger 2003). *D. brevicomis, I. paraconfusus* and *I. pini* occur sympatrically in California and Oregon and compete for ponderosa pine bark. Myrcene vapors can be converted only by male *D. brevicomis* to (+)-ipsdienol (Fig. 13), also a pheromone component of its competitor *I. paraconfusus* (Hughes 1973; Byers 1982). (+)-Ipsdienol inhibits response of both *D. brevicomis* and *I. pini* to their synthetic aggregation pheromones (Birch *et al.* 1980a; Lanier *et al.* 1980; Byers 1982). In Europe, ipsdienol, a pheromone component of *I. duplicatus* could act as an allomone to inhibit response of *I. typographus* (Byers *et al.* 1990b; Schlyter *et al.* 1992). Mated males of *I. typographus* produce small amounts of ipsdienol and ipsenol during colonization that might function in avoiding competition (Birgersson *et al.* 1984; Birgersson and Leufvén 1988; Birgersson *et al.* 1988). Although, ipsdienol was previously thought to be an aggregation pheromone component of *I. typographus* (Bakke *et al.* 1977), other studies have shown the compound to be either inactive or inhibit attraction of these beetles to *cis*-verbenol and methyl butenol, the most potent components (Schlyter *et al.* 1987b, c). Also, ipsdienol was not found in single males in a nuptial chamber, while it was detected in small amounts in later phases of attack when males had been joined by one or more females (Birgersson *et al.* 1988).

P. chalcographus of Europe (Fig. 14) produces a two- component aggregation pheromone consisting of chalcogran and methyl decadienoate (Francke *et al.* 1977; Byers *et al.* 1988, 1990a). Both chalcogran and methyl decadienoate (Fig. 13) cause *I. typographus* to avoid landing on traps releasing their aggregation pheromone components (*cis*-verbenol and methyl butenol) (Byers 1993b). However, *P. chalcographus* attraction to its pheromone was not inhibited by pheromone components of *I. typographus* even though the latter, and larger, beetle wins in competitive situations when both species attack simultaneously (Byers, unpublished).

Figure 14. P. chalcographus searching for a boring site on the bark of Norway spruce

However, if *P. chalcographus* precedes *I. typographus* on the host by just a few days then the former species will win in competitive situations (Byers, unpublished). Verbenone is increasingly released as colonized areas of *I. typographus* age (Birgersson and Bergström 1989) and the compound is inhibitory to *P. chalcographus* (Byers 1993b), as well as to *I. typographus* (Bakke 1981; Schlyter *et al.* 1989).

10. AVOIDANCE OF DECAYING OR FULLY COLONIZED HOSTS

As mentioned above, some microorganisms isolated from bark beetles or their gallery walls, may convert α-pinene to *cis-* and *trans-*verbenol, or *trans-*verbenol to verbenone. It was proposed that this process may account for termination of attack (Brand *et al.* 1976). Verbenone is increasingly released from ageing logs of spruce and pine colonized by bark beetles (*I. typographus*, Birgersson and Bergström 1989; *T. piniperda*, Byers *et al.* 1989c), possibly due to the activity of microorganisms. Byers (1989a, b) speculated that if verbenone is a consistent signal of microbial activity in decaying hosts, then bark beetle species may have evolved an avoidance to this compound (a kairomone) in order to avoid unsuitable hosts. The bark beetle then could have evolved to produce verbenone as a pheromone that reduced intraspecific competition, since the avoidance response was already existent. Other bark beetle species might then evolve to avoid species that produced verbenone (as an allomone), and so avoid interspecific competition. Sympatric species on the same host might coevolve responses to, and/or production of, verbenone since the chemical could serve as a signal for several types of beneficial information (kairomone, pheromone, and allomone).

Verbenone was reported to inhibit pheromone responses of over 10 species of bark beetle (Borden 1997). However, verbenone does not always inhibit bark beetles. For example, *H. palliatus* feeds in unhealthy or dying Scots pines that release verbenone

(Byers *et al.* 1989c), and the beetle's attraction to ethanol was not inhibited by verbenone (Byers 1992a). Angiosperm trees in a state of decay may not release verbenone since they probably do not have α-pinene, thus *T. domesticum* could evolve to avoid degrading nonhost pines by avoiding verbenone (Byers 1992a). Another bark beetle, *P. bidentatus*, attacks diseased limbs of Scots pine and is not affected by release rates of verbenone, which inhibit more aggressive bark beetles. This is probably because verbenone is expected to be present from the diseased host limbs (Byers *et al.* 2000). In the case of conifer bark beetles, Verbenone is increasingly implicated as a general sign of host unsuitability in conifer-killing bark beetles (due to microbial decay or competition with bark beetles). Therefore, it is paradoxical that conifers have not evolved the capacity to convert α-pinene, which they have in abundance, to verbenone in order to repel aggressive bark beetles.

Ethanol, also, sometimes reduces response to attractive baits. Klimetzek *et al.* (1986) tested different release rates of ethanol (24 to 125 mg/day) with an unreported release rate of α-pinene and terpinolene and found that the higher releases of ethanol inhibited attraction of *T. piniperda*. However, a control with either ethanol alone or terpenes alone was not reported. Schroeder (1988) increased the release of ethanol in five dosages over an even wider range from 0 to 50 g/day in combination with a 240-mg/day α-pinene release. In this case, the attraction of *T. piniperda* declined linearly with the logarithm of ethanol release, which is in conflict with the theory of Vité *et al.* (1986) that ethanol was synergistic with monoterpenes.

Schroeder and Lindelöw (1989) provided the first evidence that could integrate the disparate results. They found that high release rates of α-pinene were most attractive to beetles and that ethanol releases alone from 0 to 3 g/day were barely attractive. At a low release rate of α-pinene (2.4 or 22 mg/day), and thus low attraction, lower release rates of ethanol from 0 to 3 g/day had a synergistic effect when combined with α-pinene in attracting beetles (Schroeder and Lindelöw 1989). Their results are supported by Byers (1992a); i.e., a weak enhancement of attraction by ethanol at low release rates when blended with three host monoterpenes, but no observable effect of ethanol on the greater attraction to higher release rates of monoterpenes.

Ethanol released at even higher rates, 120 mg/day (Klimetzek *et al.* 1986) or 50 g/day (Schroeder 1988), inhibited the response of *T. piniperda* to monoterpenes. Therefore, the beetle could find diseased, but physically uninjured, trees by a weak response to a synergism between low monoterpene release rates and moderate ethanol rates - the hypothesis of Vité *et al.* (1986). Beetles would occasionally penetrate these trees, and if low in resistance would permit continued feeding. Resinosis and monoterpene release from the entrance holes would elicit increased numbers of beetles joining in a mass attack. Injured trees with wound oleoresin, and trees under attack with "pitch tubes", would have a higher monoterpene release and attract the greatest numbers of beetles, according to Byers *et al.* (1985). Trees with high ethanol release rates would indicate a tree in advanced decay and unsuitable for reproduction, and thus to be avoided, as theorized by Klimetzek *et al.* (1986). High monoterpene releases from trees (freshly wounded and not dead) would not naturally coincide with high ethanol release rates (presumably during decay after death). In addition, other compounds such as verbenone from decaying hosts would inhibit response to

monoterpenes from unsuitable hosts (discussed in the next part). These studies emphasize the need for releasing semiochemicals at known rates during tests in the field. In addition, measurements of the natural release rates of ethanol and monoterpenes from various host and nonhost substrates are necessary for further understanding of bark beetle chemical ecology.

11. AVOIDANCE OF NONHOSTS

According to studies discussed previously, bark beetles find their host tree by attraction to host volatiles (or after random landing and probing), as well as by avoiding chemicals from colonized hosts or decaying hosts. However, it is becoming increasingly apparent that many beetles avoid nonhost trees due to specific odors. It is inherently more difficult to isolate repellents and inhibitors used in avoidance behavior than to isolate attractants since tests of avoidance require one to first isolate the attractive host odors and then present these with and without the possibly inhibitory nonhost odors. Several studies indicate that at least some species of bark beetle avoid nonhost volatiles during their search for host trees. The attraction of both *T. piniperda* and *H. palliatus* to ethanol (1-6 g/day) was reduced by odors from cut logs of nonhost trees, birch, *Betula pendula*, and aspen, *Populus tremula* (Schroeder 1992). In future experiments, host logs (or monoterpenes and ethanol) should be tested instead of ethanol alone to simulate the host tree. Dickens *et al.* (1992) reduced the attraction response of *D. frontalis*, *I. grandicollis* and *I. avulsus* to aggregation pheromone by releasing the green-leaf volatiles, 1-hexanol and hexanal. *T. domesticum* colonizes wood of deciduous trees (e.g. *Fagus sylvatica*, *Quercus* spp. *Betula* spp.) and is known to be attracted to ethanol (Magema *et al.* 1982; Paiva and Kiesel 1985). Monoterpenes of Scots pine and verbenone (from decaying conifers) reduced response of this species to ethanol (Byers 1992a) and would provide a mechanism for avoiding nonhosts and unsuitable colonization areas. This also is valid for the hardwood-breeding species *Anisandrus dispar* (Schroeder and Lindelöw 1989).

Recently, the spruce bark beetles *Ips typographus* and *Pityogenes chalcographus* were shown to avoid volatiles of nonhost birch trees (both from bark and leaves, Fig. 15), which suggests the possibility that beetles may not enter areas of primarily birch (Byers *et al.* 1998). However, it is more certain that the beetle would leave a birch tree after landing due to a relatively high concentration of repellent nonhost volatiles at the surface of the bark.

There is increasing evidence that aggregation responses to semiochemicals by conifer-infesting bark beetles in several genera are reduced by volatiles from nonhost angiosperm trees (e.g. *Betula, Populus, Acer*) (Dickens *et al.* 1992; Schroeder 1992; Schlyter *et al.* 1995; Wilson *et al.* 1996; Guerrero *et al.* 1997; Borden *et al.* 1997, 1998; Deglow and Borden 1998; Byers *et al.* 1998, 2000; Poland *et al.* 1998; Zhang *et al.* 1999a, b, 2000, 2001; Huber *et al.* 1999, 2000, 2001; Huber and Borden 2001a, b; Poland and Haack 2000; Schlyter *et al.* 2000; Zhang 2003; Zhang and Schlyter 2003). These studies have found that some of the most important nonhost angiosperm compounds are (Z)-3-hexen-1-ol, (E)-2-hexen-1-ol, and 1-hexanol mostly from leaves, as well as *trans*-conophthorin from bark.

Figure 15. Pityogenes chalcographus were induced to land on birch trees by baits of aggregation pheromone but the individuals did not stay more than about 2 minutes due to odors from the bark (probably 1-hexanol, trans-conophthorin, and other unidentified compounds, Byers et al. 1998).

Volatiles from leaves or bark of nonhosts birch (*Betula pendula*) and Norway spruce (*Picea abies*) also dramatically reduced the attraction of the bark beetle, *Pityogenes bidentatus*, to their aggregation pheromone components (*cis*-verbenol and grandisol) in the field. Surprisingly, odors from either the needles or bark of the host Scots pine, *Pinus sylvestris*, similarly inhibited attraction. Monoterpenes of pine and spruce (α-pinene, ß-pinene, terpinolene, and 3-carene), as well as ethanol, chalcogran and some nonhost green leaf alcohols [(Z)-3-hexen-1-ol, (E)-2-hexen-1-ol, and 1-hexanol], also reduced catches. Collections of volatiles from the field-tested plant tissues indicated they released monoterpenes in amounts similar to the synthetics that inhibited responses. The varied plant and insect sources of these inhibitory compounds indicate that *P. bidentatus* bark beetles have evolved several strategies to increase their fitness by avoiding nonhost and unsuitable host trees in a complex olfactory landscape.

12. FEEDING STIMULANTS AND DETERRENTS

Presumably, a beetle must not only determine that the bark underneath is the proper host and is suitable for reproduction, but it must also judge potential competition by whether nearby areas have bark beetles beginning their attacks. Many species of bark beetle bore their entrance holes in a spaced or uniform pattern, indicating the beetles try to avoid competition (Byers 1984, 1992c, 1996c). In some cases, the beetle will bore through the outer bark, regardless of the host, until it encounters the phloem. For example, *I. paraconfusus* will bore through the outer bark of the nonhost white fir, *Abies concolor*, as readily as through bark of the host ponderosa pine. However, the

beetle only bores about 1 mm in white fir phloem and then leaves (Elkinton and Wood 1980). In the initial boring phase, gustatory (and possibly olfactory) stimulants, deterrents, and physiological factors are considered in a decision whether to continue feeding and excavating the gallery. The beetle probably can determine whether the host tissue is of good quality in terms of nutritional and moisture factors (Webb and Franklin 1978). The phloem of ponderosa pine, sugar pine (*P. lambertiana)*, Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*), and several other conifers contain about equal amounts of glucose, fructose and sucrose (Smith and Zavarin 1960). Bark beetles have been induced to feed or lay eggs on several diets, but the most successful diets contained some percentage of host (usually phloem) tissue (Jones and Brindley 1970; Richeson *et al.* 1970; Whitney and Spanier 1982; Conn *et al.* 1984; Byers and Wood 1981b), indicating the presence of feeding or ovipositional stimulants. In experiments to introduce antibiotics, sucrose was found to increase feeding by *I. paraconfusus* in powdered cellulose diets (Byers and Wood 1981b).

Few studies have attempted to isolate feeding stimulants in conifer-feeding bark beetles, and none have isolated specific compounds. Elkinton *et al.* (1981) extracted ponderosa pine phloem successively with diethyl ether (partitioned with water), water and then methanol, and added these extracts to powdered cellulose diets. *I. paraconfusus* beetles were then given a choice between a control diet and a diet with extract. The diet with the ether extract did not cause beetles to remain longer and there was no preferential boring, but the extract did cause more feeding compared to the control. The water partition of the ether extract only caused beetles to remain longer. The water extract elicited more boring and feeding, while the methanol extract was inactive since feeding stimulants had already been extracted by the ether and water treatments. These results indicate that several compounds function in gustatory preferences. Solvent (methanol-water-benzene) extracts of lodgepole pine (*Pinus contorta*) bark were absorbed by tissue paper and shown to induce feeding by *D. ponderosae* (Raffa and Berryman 1982). The benzene fraction induced biting but not feeding while the polar fraction (water-methanol) caused continued feeding. Differences in feeding preferences for bark extracts varied widely between trees, but these differences could not be attributed to amounts of 13 monoterpenes as determined by gas chromatography (GC). Also, extracts of trees judged resistant, because beetles that had been forced to attack in cages either refused or discontinued attack, were as stimulatory to feeding beetles as those from susceptible trees. In contrast, Hynum and Berryman (1980) found greater feeding preferences for bark extracts of susceptible lodgepole pines than for comparable extracts of resistant lodgepole pine. However, the susceptible trees had been killed by the beetles before solvent extraction, which might have allowed microorganisms to produce additional feeding stimulants. White (1981) also found differences in gustatory deterrent and stimulatory properties of bark extracts from different trees of loblolly pine, *P. taeda*.

Most work on feeding stimulants and deterrents in beetles of deciduous trees involves the elm bark beetle, *Scolytus multistriatus*. Vanillin and syringaldehyde are short-range attractants inducing feeding in *S. multistriatus* (Meyer and Norris 1967b). Feeding stimulants were isolated from the bark of American elm, *Ulmus americana*, of which one was partially identified as a pentacyclic triterpene (Baker and Norris 1967).

Later some lignin intermediates and phenolics were suggested (Meyer and Norris 1974). Doskotch *et al.* (1973) succeeded in identifying another feeding stimulant in elm bark as a catechin xyloside. A tritiated catechol-feeding stimulant was shown to penetrate the gustatory receptor of *S. multistriatus* (Borg and Norris 1971). *Scolytus rugulosus* is stimulated to feed in fruit trees by several phenolic compounds (Chararas *et al.* 1982).

Scolytus multistriatus was induced to feed on sucrose pith disks when volatiles from benzene extracts of bark of nonhost trees (Eastern cottonwood, *Populus deltoides*, and yellow buckeye, *Aesculus octandra*) were placed 7 mm away (Baker and Norris 1968). However, these nonhost trees were not fed upon since they contained nonvolatile feeding deterrents, as shown by lowered feeding on a mixture of host and nonhost extracts compared to host extracts. *S. multistriatus* beetles do not attack the nonhost hickory, *C. ovata*, due to the presence of juglone (5-hydroxy-1,4-napthoquinone), a feeding deterrent (Gilbert *et al.* 1967). Elm tree tissue infected by the fungus *Phomopsis oblonga* is avoided by *S. multistriatus* due to several complex feeding deterrents. These include oblongolide (isomer of dimethylnapthofuranone), a norsesquiterpene lactone, two tiglic esters of 5,6-dihydro-5-hydroxy-2-pyrones, nectriapyrone, 4-hydroxyphenylethanol, 5-methylmellein as well as acids of 2-furoic, orsellinic, 3-nitropropanoic, and mellein-5-carboxylic (Begley and Grove 1985; Claydon *et al.* 1985).

Diterpene acids (e.g., abietic, levopimaric, neoabietic and palustric acids) have been isolated from ponderosa pine oleoresin (Anderson *et al.* 1969; Himejima *et al.* 1992) and these are known to be antifeedants against aphids and sawflies (Wagner *et al.* 1983; Schuh and Benjamin 1984; Rose *et al.* 1981). However, these compounds have not been tested on bark beetles. Tannins, phenolics and terpenoids that can inhibit feeding or digestion in other insects (Berenbaum and Isman 1989) could also affect bark beetles. Ponderosa pine bark extracted first with ether yields behenic and lignoceric acids, fatty alcohols, resin acids, and flavonols (quercetin and myricetin, pinoquercetin, pinomyricetin and dihydroquercetin). A subsequent acetone extract contains tannins and phlobaphenes, while a third hot-water extract has tannin (6-11 % dry weight of bark) and carbohydrates (Anderson 1962; Anderson *et al.* 1969). Many of these compounds are found only in the outer bark and although they may be important in deterring nonhost bark beetles, at least the host-adapted *I. paraconfusus* does not eat the outer bark (Elkinton and Wood 1980). However, host compounds of lower volatility at close range may be important in deterring attacks after landing. For example, Byers *et al.* (1998, 2000) found that *P. chalcographus* and *P. bidentatus* would not attack non-host birch or spruce, respectively, after briefly landing in response to pheromone baits (Fig. 13).

13. MANAGEMENT OF BARK BEETLES USING SEMIOCHEMICALS

Pheromones have been used in the field to disrupt mate finding in moths (Hodges *et al.* 1984; Zvirgzdins *et al.* 1984; Flint and Merkle 1984; Campion *et al.* 1989), beetles (Villavaso and McGovern 1981; Villavaso 1982), and flies (Jones *et al.* 1982). In most cases, relatively large quantities of pheromone (consisting of several pheromone

components) are more or less evenly distributed throughout the field to adapt (overload) sensory receptors or habituate behavioral response ('confusion') or to exhaust the individuals in orientation attempts (i.e. "wild-goose chases"). The best successes so far have involved straight-chain olefinic acetates, alcohols, and aldehydes of moths (Baker 1989; Byers 2002).

Bark beetles that colonize forest trees may present problems for disruption techniques for several reasons, one is that their pheromone components, usually oxygenated monoterpenes, are more volatile than moth straight-chain hydrocarbons (Byers 1989a). More important perhaps is that compared to moths even larger quantities are expected to be required for disruption of bark beetles since the latter individuals generally release higher rates (ng to μg/h) of pheromone components than moths (pg to ng/h) (Browne *et al.* 1979; Schlyter *et al.* 1987a; Birgersson and Bergström 1989; Byers *et al.* 1990a, b; Ramaswamy and Cardé 1984; Du *et al.* 1987). Furthermore, even higher quantities of synthetic pheromone are required to compete with pest bark beetles that typically release semiochemicals in large aggregations on their host tree as compared to individual female moths. Possibly because of these reasons, as well as the fact that both sexes are attracted by pheromone, several attempts to control bark beetles have used the mass-trapping method. This method employs traps, either sticky-screen (Browne 1978) or cylinder with holes/barrier type (Bakke 1989), baited with synthetic pheromone components. Traps releasing pheromone components have been used in control programs to lure other pest insects such as moths to their death (Haniotakis *et al.* 1991; Sternlicht *et al.* 1990).

Previous theoretical attempts at determining the effectiveness of pheromone mass trapping have used population dynamic models (Knipling and McGuire 1966; Roelofs *et al.* 1970; Beroza and Knipling 1972; Nakasuji and Fujita 1980; Nakamura 1982; Barclay 1984; Fisher *et al.* 1985; Barclay 1988; Barclay and Li 1991). These models are mathematically complex and make several assumptions about beetle survival and mating rates, as well as attraction rates to pheromone traps, which limits their application. There have been no models where 'insects' are moved in 'real' time and space in relation to traps of specific dimensions and positions, although two-dimensional models of 'correlated random walks' are probably close to reality (Byers 1993a, 1996a, b, 1999, 2000, 2001).

The first major attempt to control bark beetle populations using pheromone-baited traps was done in 1970 in California (Bedard *et al.* 1979; Wood 1980; DeMars *et al.* 1980). Large (1 x 2 m) sticky screens baited with *exo*-brevicomin and frontalin, pheromone components of the western pine beetle, *Dendroctonus brevicomis* (Silverstein *et al.* 1968; Kinzer *et al.* 1969), plus the host monoterpene, myrcene (Bedard *et al.* 1969), were placed in ponderosa pine forests at Bass Lake, California. In four plots of 1.3 km^2 each, 66 pheromone traps were deployed in a grid of about 161 m spacing. Over a million beetles were caught and the test appeared to be successful since the number of trees killed by the beetle declined to 10% the pre-treatment level for several years (Bedard *et al.* 1979; Wood 1980; DeMars *et al.* 1980).

Norway and Sweden have extensive conifer forests, and in the 1970's a major outbreak of the European spruce engraver, *I. typographus*, devastated many areas (Austarå *et al.* 1984). Since the pheromone of this beetle had recently been identified

as a mixture of 2-methyl-3-buten-2-ol and $(1S,4S,5S)$-*cis*-verbenol (Bakke *et al.* 1977), an extensive mass-trapping control program was initiated in 1979 and may have led to the decline of outbreaks after 1980 (Bakke 1985, 1989; Vité 1989). Several other European studies have reported successful control of bark beetles with the intensive use of pheromone-baited traps (Vrkoc 1989; Richter 1991; Jakus 1998).

These pioneering studies of mass trapping using pheromones did have some deficiencies. Many of these studies lacked appropriate controls or check plots so it is not possible to determine the success of the control programs. Also, a combination of experience and intuition led to subjective estimates as to the level of trapping and the pheromone release rate ultimately employed for control of the population. Certainly, these questions are complex and it is not surprising that they were not solved entirely. Models that employ various parameters can help to understand mass trapping. The parameters include types of pheromone traps and spacings, bait strengths, and treatment durations in conjunction with different population densities and host stand conditions. This is a task with nearly unlimited possibilities. However, the models will not be a substitute for experimentation with some of the parameters in the field.

Weber (1987) was critical of pheromone trapping of bark beetles for control since he calculated that enough beetles would remain untrapped to then colonize susceptible hosts and replenish the population density due to an absence of competition. This assessment is conjectural since trapping experiments with different traps and pheromone dosages were not done. Also, the complementary effects of other forest management practices, such as removal of slash and infested trees to reduce populations, were not considered. The consequences of population reduction to densities below the threshold required to overcome tree resistance by means of a mass attack were also not considered (Berryman and Stenseth 1989; Berryman *et al.* 1989). In contrast, some models (Byers 1993a, 1996a) indicate that insect populations can potentially be drastically reduced with a small number of traps with an effective radius that seems smaller than what one might intuitively expect for pheromone baits. However, whether this population reduction is sufficient to affect natural matings and population levels over several generations is still an open question.

In many past control programs that used pheromone trapping, there has been the problem of finding control areas to determine whether the treatment has been effective. However, several monitor traps placed inside the control area (or even the control traps themselves) will indicate the population density and the progress of the control program. If no more insects are being caught, then obviously the control is a success, unless the flight period is over. This can be determined by monitoring traps placed in untreated areas, some distance away, but still within the same general biotope and climatic regime. Usually only one beetle or pair of bark beetles begin attack of a tree and at this time pheromone release is relatively low compared to a few days later when thousands of beetles participate in the mass attack. Thus, it seems advantageous to initiate mass trapping before beetles swarm in the spring and have time to build aggregations that can compete with traps for attraction of dispersing beetles. The population levels need only be reduced below the thresholds required to kill trees. In moths, reproduction can occur despite high trapping efficiency suggested

by the model because male moths may mate with females before being trapped (Roelofs *et al.* 1970).

There are several variables that can influence the trapping of the population so it does not follow the predictions based on simulation models or iterative equations. For example, the `flight' speed used in models (2 m/s, Byers *et al.* 1989a) may be more than the speed observed for flying or wind-blown insects since they often stop to rest or feed (Byers 1996a). Also, in the case of bark beetles, there can be host volatiles that attract the beetles during their swarming flight, or trees under colonization where aggregation pheromones are released (Byers 1989a). Several studies have indicated that as the density of calling female moths increase, the catches on pheromone-baited traps increase relatively less or may decline, probably due to competition between the natural and synthetic sources (Raulston *et al.* 1979; Nakamura 1982; Witz *et al.* 1992). Traps can also be overloaded with caught insects, and synthetic pheromone release rates can diminish over time, which will cause catches in nature to differ from model predictions. Pheromone release rates can decrease (and the effective pheromone trap radius) due to compound degradation and in other cases due to exponential decline from substrates (e.g. rubber septa). Methyl decadienoate, a pheromone component of the bark beetle *Pityogenes chalcographus*, is especially sensitive to sunlight, and attraction rates can be halved in a few hours unless the compound is shaded. In models, the shape of pheromone plumes emanating from traps has been transformed to the *EAR*, which also reduces the correspondence between reality (some type of Gaussian time-averaged plume depending on the wind) and the models (a circle). Much research in the practical area is needed, unfortunately this is expensive and time and labor consuming.

14. ECOLOGICAL ASPECTS AND CONCLUDING REMARKS

Bark beetles are a keystone species, meaning that they are evolutionarily and historically a dominant component of the natural forest ecosystem. Without bark beetles, many thousands of microbial, nematode, mite, and insect species would become extinct since they rely on bark beetles to create a habitat for them (Dahlsten and Stephen 1974). The aggressive interactions between bark beetles and trees also must affect population genetics and evolution. Trees and parts of trees (shoots, cones, limbs) are killed when eaten by bark beetles or by fungi introduced during feeding so there is certainly a severe selection pressure on trees to evolve resistance mechanisms, which they have, but bark beetles have also evolved counter-resistance mechanisms (Byers 1995). This so-called evolutionary arms race continues, especially with man's activities introducing new species of tree and bark beetle. In spite of a general resistance having evolved in conifers, older, weak and unhealthy trees are removed by bark beetles, and microbial diseases, which greatly influences the age and species structure of the forest.

The main reason bark beetles have been studied so extensively is that they are perceived as pests that damage forests. Certainly at outbreak levels, bark beetles kill vast areas of conifer forests, which drastically affect the ecology and species composition for a considerable time. In forest plantations used only for the production

of fiber, bark beetles are indeed pests. In forests with residential tracts, bark beetles are a threat to the desired stability of old-growth stands. In wilderness areas and recreational forests, bark beetles may be tolerated as part of the natural ecosystem. In fact, bark beetles are a keystone species that naturally fluctuates in abundance as the forest ages and succession processes occur. Many forests are designated as multi-use, meaning that they are for recreation and for timber production. Obviously some uses preclude other uses, or are at least in conflict. There often must be a compromise between producing the most fiber per unit area (short term interest) and the maintenance of natural forest biodiversity (long term interest). Over the long term (longer than a human's lifetime), most forest ecosystems require disturbances that remove old trees and open the land to a succession of plant and animal species guilds. Either bark beetles or fire, or both, are well known to carry out this natural long-term cycling function. Man, however, usually does not appreciate these perturbative cycles that progress over many decades. The discussion about the role of bark beetles, fire, and overuse of forests by mankind will continue for many years to come, but research in all these areas will help to understand how to better utilize and enjoy nature.

15. REFERENCES

Anderbrant, O., Schlyter, F. 1989. Causes and effects of individual quality in bark beetles. Holarctic Ecology, 12, 488-93.

Anderbrant, O., Schlyter, F., & Birgersson, G. 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. Oikos, 45, 89-98.

Anderson, A.B. 1962. The influence of extractives on tree properties II. Ponderosa pine (*Pinus ponderosa* Dougl.). Journal of the Institute of Wood Science, 10, 29-47.

Anderson, A.B., Riffer, R., & Wong, A. 1969. Monoterpenes, fatty and resin acids of *Pinus ponderosa* and *Pinus jeffreyi*. Phytochemistry, 8, 873-5.

Atkins, M.D. 1960. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae) II. Flight Movements. Canadian Entomologist, 92, 941-54.

Atkins, M.D. 1961a. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae) III. Flight capacity. Canadian Entomologist, 93, 467-74.

Atkins, M.D. 1966. Laboratory studies on the behavior of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. Canadian Entomologist, 98, 953-91.

Atkins, M.D. 1969. Lipid loss with flight in the Douglas-fir beetle. Canadian Entomologist, 101, 164-65.

Atkins, M.D. 1975. On factors affecting the size, fat content and behavior of a scolytid. Zeitschrift für angewandte Entomologie, 78, 209-18.

Austarå, O., Annila, E., Bejer, B., & Ehnström, B. 1984. Insect pests in forests of the nordic countries 1977-1981. Fauna Norvegica, Series B, 31, 8-15.

Austarå, O., Bakke, A., & Midtgaard, F. 1986. Response in *Ips typographus* to logging waste odors and synthetic pheromones. Journal of Applied Entomology, 101, 194-98.

Baker, B.H., Hostetler, B.B., & Furniss, M.M. 1977. Response of eastern larch beetle (Coleoptera: Scolytidae) in Alaska to its natural attractant and to Douglas-fir beetle pheromones. Canadian Entomologist, 109, 289-94.

Baker, J.E., & Norris, D.M. 1967. A feeding stimulant for *Scolytus multistriatus* (Coleoptera: Scolytidae) isolated from the bark of *Ulmus americana*. Annals of the Entomological Society of America, 60, 1213-15.

Baker, J.E., & Norris, D.M. 1968. Further biological and chemical aspects of host selection by *Scolytus multistriatus*. Annals of the Entomological Society of America, 61, 1248-55.

Baker, T.C. 1989. Sex pheromone communication in the Lepidoptera: new research progress. Experientia, 45, 248-62.

Baker, T.C., Hansson, B.S., Löfstedt, C., & Löfqvist, J. 1988. Adaptation of antennal neurones in moths is associated with cessation of pheromone-mediated upwind flight. Proceedings of the National Academy of Sciences, U.S.A., 85, 9826-30.

Bakke, A. 1975. Aggregation pheromone in the bark beetle *Ips duplicatus* (Sahlberg). Norwegian Journal of Entomology, 22, 67-69.

Bakke, A. 1981. Inhibition of the response in *Ips typographus* to the aggregation pheromone; field evaluation of verbenone and ipsenol. Zeitschrift für angewandte Entomologie, 92, 172-77.

Bakke, A. 1983. Dosage response of the ambrosia beetle *Trypodendron lineatum* (Oliver) (Coleoptera, Scolytidae) to semiochemicals. Zeitschrift für angewandte Entomologie, 95, 158-61.

Bakke, A. 1985. Deploying pheromone-baited traps for monitoring *Ips typographus* populations. Zeitschrift für angewandte Entomologie, 99, 33-9.

Bakke, A. 1989. The recent *Ips typographus* outbreak in Norway: Experiences from a control program. Holarctic Ecology, 12, 515-19.

Bakke, A., Frøyen, P., & Skattebøl, L. 1977. Field response to a new pheromonal compound isolated from *Ips typographus*. Naturwissenschaften, 64, 98.

Barclay, H.J. 1984. Pheromone trapping models for pest control: Effects of mating patterns and immigration. Researches on Population Ecology, 26, 303-11.

Barclay, H.J. 1988.. Models for combining methods of pest control: food-baited and pheromone-baited traps containing either insecticide or chemosterilant. Bulletin of Entomological Research, 78, 573-90.

Barclay, H.J., & Li, C. 1991. Combining methods of pest control: Minimizing cost during the control program. Theoretical Population Biology, 40, 105-23.

Bedard, W.D., Tilden, P.E., Wood, D.L., Silverstein, R.M., Brownlee, R.G., & Rodin, J.O. 1969. Western pine beetle: field response to its sex pheromone and a synergistic host terpene, myrcene. Science, 164, 1284-85.

Bedard, W.D., Silverstein, R.M., & Wood, D.L. 1970. Bark beetle pheromones. Science, 167, 1638-39.

Bedard, W.D., Wood, D.L., & Tilden, P.E. 1979. Using behavior modifying chemicals to reduce western pine beetle-caused tree mortality and protect trees. In. *Current Topics in Forest Entomology*, W.E. Waters (ed.). U.S. Forest Service General Technical Report, WO-8.

Begley, M.J., & Grove, J.F. 1985. Metabolic products of *Phomopsis oblonga* I. 3a,5a,6,7,8,9,9a,9b-octahydro- 7,9b-dimethylnaphtho-1,2-c-furan-1-3h-one oblongolide. Journal of the Chemical Society, Perkin Transactions 1, 0,861-4.

Bennett, R.B., & Borden, J.H. 1971. Flight arrestment of tethered *Dendroctonus pseudotsugae* and *Trypodendron lineatum* (Coleoptera: Scolytidae) in response to olfactory stimuli. Annals of the Entomological Society of America, 64, 1273-86.

Berenbaum, M.R., & Isman, M.B. 1989. Herbivory in holometabolous and hemimetabolous insects: contrasts between Orthoptera and Lepidoptera. Experientia, 45, 229-36.

Beroza, M., & Knipling, E.F. 1972. Gypsy moth control with the sex attractant pheromone. Science, 177, 19-27.

Berryman, A.A. 1974. Dynamics of bark beetle populations towards a general productivity model. Environmental Entomology, 3, 579-85.

Berryman, A.A., & Ashraf, M. 1970. Effects of *Abies grandis* resin on the attack behavior and brood survival of *Scolytus ventralis* (Coleoptera: Scolytidae). Canadian Entomologist, 102, 1229-36.

Berryman, A.A., & Stenseth, N.C. 1989. A theoretical basis for understanding and managing biological populations with particular reference to the spruce bark beetle. Holarctic Ecology, 12, 387-94.

Berryman, A.A., Dennis, B., Raffa, K.F., & Stenseth, N.C. 1985. Evolution of optimal group attack with particular reference to bark beetles (Coleoptera: Scolytidae). Ecology, 66, 898-903.

Berryman, A.A., Raffa, K.F., Millstein, J.A., & Stenseth, N.C. 1989. Interaction dynamics of bark beetle aggregation and conifer defense rates. Oikos, 56, 256-63.

Birch, M.C. 1984. Aggregation in bark beetles. In. *Chemical Ecology of Insects*, W.J. Bell, R.T. Cardé (Eds.). Chapman and Hall, London.

Birch, M.C., Light, D.M., Wood, D.L., Browne, L.E., Silverstein, R.M., Bergot, B.J., Ohloff, G., West, J.F., & Young, J.C. 1980a. Pheromonal attraction and allomonal interruption of *Ips pini* in California by the two enantiomers of ipsdienol. Journal of Chemical Ecology, 6, 703-17.

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

Birgersson, G., & Bergström, G. 1989. Volatiles released from individual spruce bark beetle entrance holes: quantitative variations during the first week of attack. Journal of Chemical Ecology, 15, 2465-84.

Birgersson, G., & Leufvén, A. 1988. The influence of host tree response to *Ips typographus* and fungal attack on production of semiochemicals. Insect Biochemistry, 18, 761-70.

Birgersson, G., Schlyter, F., Bergström, G., & Löfqvist, J. 1988. Individual variation in aggregation pheromone content of the bark beetle, *Ips typographus*. Journal of Chemical Ecology, 14, 1737-1762.

Birgersson, G., Byers, J. A., Bergström, G., & Löfqvist, J. 1990. Production of pheromone components, chalcogran and methyl (E,Z)-2,4-decadienoate, in the spruce engraver *Pityogenes chalcographus*. Journal of Insect Physiology, 36, 391-5.

Birgersson, G., Schlyter, F., Löfqvist, J., & Bergström, G. 1984. Quantitative variation of pheromone components in the spruce bark beetle *Ips typographus* from different attack phases. Journal of Chemical Ecology, 10, 1029-55.

Bombosch, S., Engler, I., Gossenauer, H., & Herrmann, B. 1985. On the role of pheroprax influencing the settlement of *Ips typographus* on spruce. Zeitschrift für angewandte Entomologie, 100, 458-63.

Bonello, P., Mcnee, W.R., Storer, A.J., Wood, D.L., & Gordon, T.R. 2001. The role of olfactory stimuli in the location of weakened hosts by twig-infesting *Pityophthorus* spp. Ecological Entomology, 26, 8-15.

Bordasch, R.P., & Berryman, A.A. 1977. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae) 2. repellency of *Abies grandis* resins and some monoterpenes. Canadian Entomologist, 109, 95-100.

Borden, J.H. 1982. Aggregation pheromones. In. *Bark beetles in North American Conifers: a System for the Study of Evolutionary Biology,* J.B. Mitton, K.M. Sturgeon (Eds.). University of Texas. Austin, USA.

Borden, J.H. 1997. Disruption of semiochemical-mediated aggregation in bark beetles. In. *Pheromone Research: New Directions,* R.T. Cardé, A.K. Minks (Eds.). Chapman and Hall, New York.

Borden, J.H., & Wood, D.L. 1966. The antennal receptors and olfactory response of *Ips confusus* (Coleoptera: Scolytidae) to male sex attractant in the laboratory. Annals of the Entomological Society of America, 59, 253-61.

Borden, J.H., Handley, J.R., McLean, J.A., Silverstein, R.M., Chong, L., Slessor, K.N., Johnston, B.D., & Schuler, H.R. 1980. Enantiomer-based specificity in pheromone communication by two sympatric *Gnathotrichus* species (Coleoptera: Scolytidae). Journal of Chemical Ecology, 6, 445-56.

Borden, J.H., Chong, L., Slessor, K.N., Oehlschlager, A.C., Pierce, Jr., H.D., & Lindgren, B.S. 1981. Allelochemic activity of aggregation pheromones between three sympatric species of ambrosia beetles (Coleoptera: Scolytidae). Canadian Entomologist, 113, 557-63.

Borden, J.H., King, C.J., Lindgren, S., Chong, L., Gray, D.R., Oehlschlager, A.C., Slessor, K.N., & Pierce, Jr., H.D. 1982. Variation in response of *Trypodendron lineatum* from two continents to semiochemicals and trap form. Environmental Entomology, 11, 403-8.

Borden, J.H., Hunt, D.W.A., Miller, D.R., & Slessor, K.N. 1986. Orientation in forest Coleoptera: an uncertain outcome of responses by individual beetles to variable stimuli. In. *Mechanisms in Insect Olfaction,* T.L. Payne, M.C. Birch, C.E.J. Kennedy (Eds.). Clarendon Press, Oxford.

Borden, J.H., Pierce, A.M., Pierce, Jr., H.D., Chong, L.J., Stock, A.J., & Oehlschlager, A.C. 1987. Semiochemicals produced by western balsam bark beetle *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae). Journal of Chemical Ecology, 13, 823-36.

Borden, J.H., Chong, L.J., Savoie, A., & Wilson, I.M. 1997. Responses to green leaf volatiles in two biogeoclimatic zones by striped ambrosia beetle, *Trypodendron lineatum.* Journal of Chemical Ecology, 23, 2479-91.

Borden, J.H., Wilson, I.M., Gries, R., Chong, I.J., & Pierce, H.D. Jr. 1998. Volatiles from the bark of trembling aspen, *Populus tremuloides* Michx. (Salicaceae) disrupt secondary attraction by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Chemoecology, 8, 69-75.

Borg, T.K., & Norris, D.M. 1971. Penetration of tritiated catechol: a feeding stimulant into chemo receptor sensilla of *Scolytus multistriatus* (Coleoptera: Scolytidae). Annals of the Entomological Society of America, 64, 544-7.

Botterweg, P.F. 1982. Dispersal and flight behavior of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. Zeitschrift für angewandte Entomologie, 94, 466-89.

Brand, J.M., Bracke, J.W., Markovetz, A.J., Wood, D.L., & Browne, L.E. 1975. Production of verbenol pheromone by a bacterium isolated from bark beetles. Nature, 254, 136-7.

Brand, J.M., Bracke, J.W., Britton, L.N., Markovetz, A.J., & Barras, S.J. 1976. Bark beetle pheromones: production of verbenone by a mycangial fungus of *Dendroctonus frontalis*. Journal of Chemical Ecology, 2, 195-9.

Bridges, J.R., Nettleton, W.A., & Connor, M.D. 1985. Southern pine beetle *Dendroctonus frontalis* (Coleoptera: Scolytidae) infestations without the bluestain fungus *Ceratocystis minor*. Journal of Economic Entomology, 78, 325-7.

Bridges, J.R., & Perry, T.J. 1985. Effects of mycangial fungi on gallery construction and distribution of bluestain in southern pine beetle *Dendroctonus frontalis* infested pine bolts. Journal of Entomological Science, 20, 271-5.

Brown, M.W., Nebeker, T.E., & Honea, C.R. 1987. Thinning increases loblolly pine vigor and resistance to bark beetles. Southern Journal of Applied Forestry, 11, 28-31.

Browne, L.E. 1978. A trapping system for the western pine beetle using attractive pheromones. Journal of Chemical Ecology, 4, 261-75.

Browne, L.E., Wood, D.L., Bedard, W.D., Silverstein, R.M., & West, J.R. 1979. Quantitative estimates of the Western pine beetle attractive pheromone components, *exo*-brevicomin, frontalin, and myrcene in nature. Journal of Chemical Ecology, 5, 397-414.

Byers, J.A. 1982. Male-specific conversion of the host plant compound, myrcene, to the pheromone, (+)-ipsdienol, in the bark beetle, *Dendroctonus brevicomis*. Journal of Chemical Ecology, 8, 363-72.

Byers, J.A. 1983a. Sex-specific responses to aggregation pheromone: regulation of colonization density by the bark beetle *Ips paraconfusus*. Journal of Chemical Ecology, 9, 129-42.

Byers, J.A. 1983b. Influence of sex, maturity and host substances on pheromones in the guts of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus*. Journal of Insect Physiology, 29, 5-13.

Byers, J.A. 1983c. Bark beetle conversion of a plant compound to a sex-specific inhibitor of pheromone attraction. Science, 220, 624-26.

Byers, J.A. 1984. Nearest neighbor analysis and simulation of distribution patterns indicates an attack spacing mechanism in the bark beetle, *Ips typographus* (Coleoptera: Scolytidae). Environmental Entomology, 13, 1191-2000.

Byers, J.A. 1989a. Chemical ecology of bark beetles. Experientia, 45, 271-83.

Byers, J.A. 1989b. Behavioral mechanisms involved in reducing competition in bark beetles. Holarctic Ecology, 12, 466-76.

Byers, J.A. 1991. Simulation of mate finding behaviour in pine shoot beetles, *Tomicus piniperda*. Animal Behaviour, 41, 649-60.

Byers, J.A. 1992a. Attraction of bark beetles, *Tomicus piniperda, Hylurgops palliatus*, and *Trypodendron domesticum* and other insects to short-chain alcohols and monoterpenes. Journal of Chemical Ecology, 18, 2385-2402.

Byers, J.A. 1992b. Optimal fractionation and bioassay plans for isolation of synergistic chemicals: the subtractive-combination method. Journal of Chemical Ecology, 18, 1603-21.

Byers, J.A. 1992c. Dirichlet tessellation of bark beetle spatial attack points. Journal of Animal Ecology, 61, 759-68.

Byers, J.A. 1993a. Simulation and equation models of insect population control by pheromone-baited traps. Journal of Chemical Ecology, 19, 1939-56.

Byers, J.A. 1993b. Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityogenes chalcographus*. Experientia, 49, 272-5.

Byers, J.A. 1995. Host tree chemistry affecting colonization in bark beetles, In. *Chemical Ecology of Insects 2*. R.T. Cardé, W.J. Bell (Eds.). Chapman and Hall, New York.

Byers, J.A. 1996a. An encounter rate model for bark beetle populations searching at random for susceptible host trees. Ecological Modelling, 91, 57-66.

Byers, J.A. 1996b. Temporal clumping of bark beetle arrival at pheromone traps: Modeling anemotaxis in chaotic plumes. Journal of Chemical Ecology, 22, 2133-55.

Byers, J.A. 1996c. Correct calculation of Dirichlet polygon areas. Journal of Animal Ecology, 65, 528-9.

Byers, J.A. 1999. Effects of attraction radius and flight paths on catch of scolytid beetles dispersing outward through rings of pheromone traps. Journal of Chemical Ecology, 25, 985-1005.

Byers, J.A. 2000. Wind-aided dispersal of simulated bark beetles flying through forests. Ecological Modelling, 125, 231-43.

Byers, J.A. 2001. Correlated random walk equations of animal dispersal resolved by simulation. Ecology, 82, 1680-90.

Byers, J.A. 2002. Internet programs for drawing moth pheromone analogs and searching literature database. Journal of Chemical Ecology, 28, 807-17.

Byers, J.A., & Löfqvist, J. 1989. Flight initiation and survival in the bark beetle *Ips typographus* (Coleoptera: Scolytidae) during the spring dispersal. Holarctic Ecology, 12, 432-40.

Byers, J.A., & Wood, D.L. 1980. Interspecific inhibition of the response of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus*, to their pheromones in the field. Journal of Chemical Ecology, 6, 149-64.

Byers, J.A., & Wood, D.L. 1981a. Interspecific effects of pheromones on the attraction of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus* in the laboratory. Journal of Chemical Ecology, 7, 9-18.

Byers, J.A., & Wood, D.L. 1981b. Antibiotic-induced inhibition of pheromone synthesis in a bark beetle. Science, 213, 763-4.

Byers, J.A., Wood, D.L., Browne, L.E., Fish, R.H., Piatek, B., & Hendry, L.B. 1979. Relationship between a host plant compound, myrcene and pheromone production in the bark beetle, *Ips paraconfusus*. Journal of Insect Physiology, 25, 477-82.

Byers, J.A., Wood, D.L., Craig, J., & Hendry, L.B. 1984. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter- and intraspecific competition. Journal of Chemical Ecology, 10, 861-77.

Byers, J.A., Lanne, B.S., Schlyter, F., Löfqvist, J., & Bergström, G. 1985. Olfactory recognition of host-tree susceptibility by pine shoot beetles. Naturwissenschaften, 72, 324-6.

Byers, J.A., Birgersson, G., Löfqvist, J., & Bergström, G. 1988. Synergistic pheromones and monoterpenes enable aggregation and host recognition by a bark beetle. Naturwissenschaften, 75,1 53-5.

Byers, J.A., Anderbrant, O., & Löfqvist, J. 1989a. Effective attraction radius: a method for comparing species attractants and determining densities of flying insects. Journal of Chemical Ecology, 15, 749-65.

Byers, J.A., Högberg, H.E., Unelius, R., Birgersson, G., & Löfqvist, J. 1989b. Structure-activity studies on aggregation pheromone components of *Pityogenes chalcographus* (Coleoptera: Scolytidae): all stereoisomers of chalcogran and methyl 2,4-decadienoate. Journal of Chemical Ecology, 15, 685-95.

Byers, J.A., Lanne, B.S., & Löfqvist, J. 1989c. Host-tree unsuitability recognized by pine shoot beetles in flight. Experientia, 45, 489-92.

Byers, J.A., Birgersson, G., Löfqvist, J., Appelgren, M., & Bergström, G. 1990a. Isolation of pheromone synergists of bark beetle, *Pityogenes chalcographus*, from complex insect-plant odors by fractionation and subtractive-combination bioassay. Journal of Chemical Ecology, 16, 861-76.

Byers, J.A., Schlyter, F., Birgersson, G., & Francke, W. 1990b. *E*-myrcenol in *Ips duplicatus*: an aggregation pheromone component new for bark beetles. Experientia, 46, 1209-11.

Byers, J.A., Zhang, Q.H., Schlyter, F., & Birgersson, G. 1998. Volatiles from nonhost birch trees inhibit pheromone response in spruce bark beetles. Naturwissenschaften, 85, 557-61.

Byers, J.A., Zhang, Q.H., & Birgersson, G. 2000. Strategies of a bark beetle, *Pityogenes bidentatus*, in an olfactory landscape. Naturwissenschaften, 87, 503-7.

Cade, S.C., Hrutfiord, B.F., & Gara, R.I. 1970. Identification of a primary attractant for *Gnathotrichus sulcatus* isolated from western hemlock logs. Journal of Economic Entomology, 63, 1014-15.

Camacho, A.D., Pierce, Jr., H.D., & Borden, J.A. 1993. Aggregation pheromones in *Dryocoetes affaber* (Mann.) (Coleoptera: Scolytidae): stereoisomerism and species specificity. Journal of Chemical Ecology, 20, 111-24.

Campion, D.G., Critchley, B.R., & McVeigh, L.J. 1989. Mating disruption. In. *Insect Pheromones in Plant Protection*, A.R. Jutsum, R.F.S. Gordon (Eds.). Wiley and Sons, New York.

Campos, M., Pena, A., & Sanchez-Raya, A.J. 1994. Release of ethylene from pruned olive logs: Influence on attack by bark beetles (Coleoptera, Scolytidae). Journal of Chemical Ecology, 20, 2513-21.

Campos, M., & Pena, A. 1995. Response of *Phloeotribus scarabaeoides* (Coleoptera, Scolytidae) to ethylene in an olfactometer. Experientia, 51, 77-9.

Cates, R.G. 1981. Host plant predictability and the feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores. Oecologia, 48, 319-26.

Chapman, J.A. 1972. Ommatidia numbers and eyes in scolytid beetles. Annals of the Entomological Society of America, 65, 550-3.

Chararas, C., Katoulas, M., & Koutroumpas, A. 1982. Feeding preference of *Ruguloscolytus rugulosus* bark beetle parasite of fruit trees. Comptes Rendus de l Academie des Sciences Serie III, Sciences de la Vie, 294, 763-6.

Chénier, J.V.R., & Philogène, B.J.R. 1989. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. Journal of Chemical Ecology, 15, 1729-46.

Choudhury, J.H., & Kennedy, J.S. 1980. Light versus pheromone-bearing wind in the control of flight direction by bark beetles, *Scolytus multistriatus*. Physiological Entomology, 5, 207-14.

Claydon, N., Grove, J.F., & Pople, M. 1985. Elm bark beetle boring and feeding deterrents from *Phomopsis oblonga*. Phytochemistry, 24, 937-44.

Conn, J.E., Borden, J.H., Hunt, D.W.A., Holman, J., Whitney, H.S., Spanier, O.J., Pierce, H.D.Jr., & Oehlschlager, A.C. 1984. Pheromone production by axenically reared *Dendroctonus ponderosae* and *Ips paraconfusus* (Coleoptera: Scolytidae). Journal of Chemical Ecology, 10, 281-90.

Dahlsten, D.L., & Stephen, F.M. 1974. Natural enemies and insect associates of the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in sugar pine. Canadian Entomologist, 106, 1211-17.

David, C.T., Kennedy, J.S., Ludlow, A.R., Perry, J.N., & Wall, C. 1982. A reappraisal of insect flight towards a distant point source of wind-borne odor. Journal of Chemical Ecology, 8, 1207-15.

Deglow, E.K., & Borden, J.H. 1998. Green leaf volatiles disrupt and enhance response to aggregation pheromones by the ambrosia beetle, *Gnathotrichus sulcatus* (LeConte) (Coleoptera: Scolytidae). Canadian Journal of Forest Research, 28, 1697-1705.

DeMars, C.J., Slaughter, G.W., Bedard, W.D., Norick, N.X., & Roettgering, B. 1980. Estimating western pine beetle-caused tree mortality for evaluating an attractive pheromone treatment. Journal of Chemical Ecology, 6, 853-66.

Dethier, V.G. 1982. Mechanisms of host-plant recognition. Entomologia Experimentalis et Applicata, 31, 49-56.

Dickens, J.C. 1986. Specificity in perception of pheromones and host odours in Coleoptera. In. *Mechanisms in insect olfaction*, T.L. Payne, M.C. Birch, C.E.J. Kennedy (Eds.). Clarendon Press, Oxford.

Dickens, J.C., Payne, T.L., Ryker, L.C., & Rudinsky, J.A. 1985. Multiple acceptors for pheromonal enantiomers on single olfactory cells in the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae. Journal of Chemical Ecology, 11, 1359-70.

Dickens, J.C., Billings, R.F., & Payne, T.L. 1992. Green leaf volatiles interrupt aggregation pheromone response in bark beetles infesting southern pines. Experientia, 48, 523-4.

Doskotch, R.W., Mikhail, A.A., & Chatterji, S.K. 1973. Structure of the water soluble feeding stimulant for *Scolytus multistriatus*: a revision. Phytochemistry, 12, 1153-55.

Du, J.W., Löfstedt, C., & Löfqvist, J. 1987. Repeatability of pheromone emissions from individual female ermine moths *Yponomeuta padellus* and *Yponomeuta rorellus*. Journal of Chemical Ecology, 13, 1431-42.

Duelli, P., Zahradnik, P., Knizek, M., & Kalinova, B. 1997. Migration in spruce bark beetles (*Ips typographus* L.) and the efficiency of pheromone traps. Journal of Applied Entomology, 121, 297-303.

El-Sayed, A.M., & Byers, J.A. 2000. Inhibitory effect of monoterpenes on response of *Pityogenes bidentatus* to aggregation pheromone released by piezoelectric sprayer for precision release of semiochemicals. Journal of Chemical Ecology, 26, 1795-1809.

Elkinton, J.S., & Wood, D.L. 1980. Feeding and boring behavior of the bark beetle *Ips paraconfusus* (Coleoptera: Scolytidae) on the bark of a host and non-host tree species. Canadian Entomologist, 112, 797-809.

Elkinton, J.S., Wood, D.L., & Browne, L.E. 1981. Feeding and boring behavior of the bark beetle, *Ips paraconfusus*, in extracts of ponderosa pine phloem. Journal of Chemical Ecology, 7, 209-20.

Ehrlich, P.R., & Raven, P.H. 1965. Butterflies and plants: a study in coevolution. Evolution, 8, 586-608.

Faucheux, M.J. 1989. Morphology of the antennal club in the male and female bark beetles *Ips sexdentatus* (Boem.) and *Ips typographus* L. (Coleoptera: Scolytidae). Annales des Sciences Naturelles Zoologie et Biologie Animale, 10, 231-43.

Feeny, P. 1975. Biochemical coevolution between plants and their insect herbivores. In. *Coevolution of Animals and Plants*, L.E. Gilbert, P.H. Raven (Eds.). Austin: University of Texas Press.

Fisher, M.E., Van Den Driessche, P., & Barclay, H.J. 1985. A density dependent model of pheromone trapping. Theoretical Population Biology, 27, 91-104.

Flint, H.M., & Merkle, J.R. 1984. Studies on disruption of sexual communication in the pink bollworm, *Pectinophora gossypiella*, (Lepidoptera: Gelechidae) with micro encapsulated gossyplure or its component Z,Z isomer. Bulletin of Entomological Research, 74, 25-32.

Forsse, E. 1991. Flight propensity and diapause incidence in five populations of the bark beetle *Ips typographus* in Scandinavia. Entomologia Experimentalis et Applicata, 61, 53-57.

Forsse, E., & Solbreck, C. 1985. Migration in the bark beetle *Ips typographus* L.: duration, timing and height of flight. Zeitschrift für angewandte Entomologie, 100, 47-57.

Francke, W, Heemann, V, Gerken, B, Renwick, JAA, & Vité, JP 1977. 2-Ethyl-1-6-dioxaspiro[4.4]nonane, principal aggregation pheromone of *Pityogenes chalcographus* (L.). Naturwissenschaften, 64,590-1

Funk, A. 1970. Fungal symbionts of the ambrosia beetle, *Gnathotrichus sulcatus*. Canadian Journal of Botany, 48, 1445-8.

Furniss, M.M., Woo, J.Y., Deyrup, M.A., & Atkinson, T.H. 1987. Prothoracic mycangium on pine-infesting *Pityoborus* spp. (Coleoptera: Scolytidae). Annals of the Entomological Society of America, 80, 692-6.

Gara, R.I. 1963. Studies on the flight behavior of *Ips confusus* (LeC.)(Coleoptera: Scolytidae) in response to attractive material. Contributions of the Boyce Thompson Institute, 22, 51-66.

Gilbert, B.L., Baker, J.E., & Norris, D.M. 1967. Juglone (5-hydroxy- 1,4-napthoquinone) from *Carya ovata*, a deterrent to feeding by *Scolytus multistriatus*. Journal of Insect Physiology, 13, 1453-9.

Goeden, R.D., & Norris, D.M. 1964. Attraction of *Scolytus quadrispinosus* (Coleoptera: Scolytidae) to *Carya* spp. for oviposition. Annals of the Entomological Society of America, 57, 141-6.

Goeden, R.D., & Norris, D.M. 1965. The behavior of *Scolytus quadrispinosus* (Coleoptera: Scolytidae) during the dispersal flight as related to its host specificities. Annals of the Entomological Society of America, 58, 249-52.

Goldhammer, D.S., Stephen, F.M., & Paine, T.D. 1991. The effect of the fungi *Ceratocystis minor* Hedgecock-Hunt, *Ceratocystis minor* var. *barrasii* Taylor, and SJB 122 on reproduction of the southern pine beetle *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). Canadian Entomologist, 122, 407-18.

Gonzalez, R., & Campos, M. 1995. A preliminary study of the use of trap-trees baited with ethylene for the integrated management of the olive beetle, *Phloeotribus scarabaeoides* (Bern.) (Col., Scolytidae). Journal of Applied Entomology, 119, 601-5.

Gonzalez, R., & Campos, M. 1996. The influence of ethylene on primary attraction of the olive beetle, *Phloeotribus scarabaeoides* (Bern.) (Col., Scolytidae). Experientia, 52, 723-6.

Graham, K. 1959. Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. Nature, 184, 283-4.

Graham, K. 1968. Anaerobic induction of primary chemical attractancy for ambrosia beetles. Canadian Journal of Zoology, 46, 905-8.

Gries, G., Nolte, R., & Sanders, W. 1989. Computer simulated host selection in *Ips typographus*. Entomologia Experimentalis et Applicata, 53, 211-17.

Gries, G., Bowers, W.W., Gries, R., Noble, M., & Borden, J.H. 1990. Pheromone production by the pine engraver *Ips pini* following flight and starvation. Journal of Insect Physiology, 36, 819-24.

Groberman, L.J., & Borden, H.J. 1982. Electrophysiological response of *Dendroctonus pseudotsugae* and *Ips paraconfusus* (Coleoptera: Scolytidae) to selected wave length regions of the visible spectrum. Canadian Journal of Zoology, 60, 2180-9.

Guerrero, A, Feixas, J, Pajares, J, Wadhams, LJ, Pickett, JA, & Woodcock, CM 1997. Semiochemically induced inhibition of behaviour of *Tomicus destruens* (Woll.) (Coleoptera: Scolytidae). Naturwissenschaften, 84, 155-7.

Hagen, B.W., & Atkins, M.D. 1975. Between generation variability in the fat content and behaviour of *Ips paraconfusus* Lanier. Zeitschrift für angewandte Entomologie, 79, 169-72.

Hallberg, E. 1982. Sensory organs in *Ips typographus* (Insecta: Coleoptera) - fine structure of the sensilla of the maxillary and labial palps. Acta Zoologica, 63, 191-8.

Haniotakis, G., Kozyrakis, M., Fitsakis, T., & Antonidaki. A. 1991. An effective mass trapping method for the control of *Dacus oleae* (Diptera: Tephritidae). Journal of Economic Entomology, 84, 564-9.

Happ, G.M., Happ, C.M., & French, J.R.J. 1976. Ultrastructure of the mesonotal mycangium of an ambrosia beetle *Xyleborus dispar* (Coleoptera: Scolytidae). International Journal of Insect Morphology and Embryology, 5, 381-92.

Himejima, M., Hobson, K.R., Otsuka, T., Wood, D.L., & Kubo, I. 1992. Antimicrobial terpenes from oleoresin of ponderosa pine tree *Pinus ponderosa*: a defense mechanism against microbial invasion. Journal of Chemical Ecology, 18, 1809-18.

Hobson, K.R., Wood, D.L., Cool, L.G., White, P.R., Ohtsuka, T., Kubo, I., & Zavarin, E. 1993. Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. Journal of Chemical Ecology, 19, 1837-46.

Hodges, J.D., & Lorio, Jr., P.L. 1975. Moisture stress and composition of xylem oleoresin in loblolly pine. Forest Science, 21, 283-90.

Hodges, J.D., Elam, W.W., Watson, W.R., & Nebeker, T.E. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. Canadian Entomologist, 111, 889-96.

Hodges, J.D., Nebeker, T.E., DeAngelis, J.D., Karr, B.L., & Blanche, C.A. 1985. Host resistance and mortality: a hypothesis based on the southern pine beetle-microorganism-host interactions. Bulletin of the Entomological Society of America, 31, 31-5.

Hodges, R.J., Benton, F.P., Hall, D.R., & Dos, S.S.R. 1984. Control of *Ephestia cautella* (Lepidoptera: Phycitidae) by synthetic sex pheromones in the laboratory and store. Journal of Stored Product Research, 20, 191-8.

Horntvedt, R.E., Christiansen, H., Solheim, H., & Wang, S. 1983. Artificial inoculation with *Ips typographus*-associated bluestain fungi can kill healthy Norway spruce trees. Meddelelser fra Norsk Institutt for Skogforskning, 38, 1-20.

Huber, D.P.W., & Borden, J.H. 2001a. Angiosperm bark volatiles disrupt response of Douglas-fir beetle, *Dendroctonus pseudotsugae*, to attractant-baited traps. Journal of Chemical Ecology, 27, 217-33.

Huber, D.P.W., & Borden, J.H. 2001b. Protection of lodgepole pines from mass attack by mountain pine beetle, *Dendroctonus ponderosae*, with nonhost angiosperm volatiles and verbenone. Entomologia Experimentalis et Applicata, 99, 131-41.

Huber, D.P.W., Gries, R., Borden, J.H., & Pierce, H.D. Jr. 1999. Two pheromones of coniferophagous bark beetles found in the bark of non-host angiosperms. Journal of Chemical Ecology, 25, 805-16.

Huber, D.P.W., Borden, J.H., Jeans-Williams, N.L., & Gries, R. 2000. Differential bioactivity of conophthorin on four species of North American bark beetles (Coleoptera: Scolytidae). Canadian Entomologist, 132, 649-53.

Huber, D.P.W., Borden, J.H., & Stastny, M. 2001. Response of the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), to conophthorin and other angiosperm bark volatiles in the avoidance of non-hosts. Agricultural and Forest Entomology, 3, 225-32.

Hughes, P.R. 1973. *Dendroctonus*: production of pheromones and related compounds in response to host monoterpenes. Zeitschrift für angewandte Entomologie, 73, 294-312.

Hynum, B.G., & Berryman, A.A. 1980. *Dendroctonus ponderosae* (Coleoptera: Scolytidae) pre-aggregation landing and gallery initiation on lodgepole pine. Canadian Entomologist, 112, 185-92.

Jakus, R. 1998. A method for the protection of spruce stands against *Ips typographus* by the use of barriers of pheromone traps in north-eastern Slovakia. Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz, 71, 152-8

Jactel, H. 1991. Dispersal and flight behavior of *Ips sexdentatus* (Coleoptera: Scolytidae) in pine forest. Annales des Sciences Forestières, 48, 417-28.

Jactel, H., & Gaillard, J. 1991. A preliminary study of the dispersal potential of *Ips sexdentatus* Boern (Coleoptera: Scolytidae) with an automatically recording flight mill. Journal of Applied Entomology, 112, 138-45.

Jones, R.G., & Brindley, W.A. 1970. Tests of eight rearing media for the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), from lodgepole pine. Annals of the Entomological Society of America, 63, 313-16.

Jones, O.T., Lisk, J.C., Howse, P.E., Baker, R., Bueno, A.M., & Ramos, P. 1982. Mating disruption of the olive fruit fly *Dacus oleae* with the major component of its sex pheromone, In. *Fruit Flies of Economic Importance*. R. Cavalloro (ed.). Proceedings of the CEC/IOBC International Symposium, Athens, Greece.

Kajimura, H., & Hijii, N. 1992. Dynamics of the fungal symbionts in the gallery system and the mycangia of the ambrosia beetle *Xylosandrus mutilatus* Blandford (Coleoptera: Scolytidae) in relation to its life history. Ecological Research, 7, 107-17.

Kelsey, R.G. 1994. Ethanol synthesis in Douglas-fir logs felled in November, January, and March, and its relationship to ambrosia beetle attack. Canadian Journal of Forest Research, 24, 2096-2104.

Kelsey, R.G. 1996. Anaerobic induced ethanol synthesis in the stems of greenhouse-grown conifer seedlings. Trees, 10, 183-8.

Kelsey, R.G., & Joseph, G. 1997. Ambrosia beetle host selection among logs of Douglas fir, western hemlock, and western red cedar with different ethanol and α-pinene concentrations. Journal of Chemical Ecology, 23, 1035-51.

Kelsey, R.G., & Joseph, G. 1999. Ethanol and water in *Pseudotsuga menziesii* and *Pinus ponderosa* stumps. Journal of Chemical Ecology, 25, 2779-92.

Kimmerer, T.W., & Kozlowski, T.T. 1982. Ethylene, ethane, acetaldehyde and ethanol production by plants under stress. Plant Physiology, 69, 840-7.

Kinzer, G.W., Fentiman, Jr., A.F., Page, T.F., Foltz, R.L., Vité, J.P., & Pitman, G.B. 1969. Bark beetle attractants: identification, synthesis and field bioassay of a new compound isolated from *Dendroctonus*. Nature, 211, 475-6.

Klimetzek, D., Köhler, J., Vité, J.P., & Kohnle, U. 1986. Dosage response to ethanol mediates host selection by `secondary' bark beetles. Naturwissenschaften, 73, 270-2.

Knipling, E.F., & McGuire, J.U., Jr. 1966. Population models to test theoretical effects of sex attractants used for insect control. USDA Information Bulletin, 308, 2-4.

Kohnle, U. 1985. Investigations of chemical communication systems in secondary bark beetles. Zeitschrift für angewandte Entomologie, 100, 197-218.

Långström, B. 1983. Within tree development of *Tomicus minor* (Coleoptera: Scolytidae) in wind thrown scotch pine. Acta Entomologica Fennica, 42, 42-6.

Långström, B., & Hellqvist, C. 1991. Shoot damage and growth losses following three years of *Tomicus* attacks in scots pine stands close to a timber storage site. Silva Fennica, 25, 133-45.

Lanier, G.N. 1983. Integration of visual stimuli, host odorants, and pheromones by bark beetles and weevils in locating and colonizing host trees. In. *Herbivorous Insects: Host-Seeking Behavior and Mechanisms*, S. Ahmad (Ed.). Academic Press, New York.

Lanier, G.N., Classon, A., Stewart, T., Piston, J.J., & Silverstein, R.M. 1980. *Ips pini*: the basis for interpopulational differences in pheromone biology. Journal of Chemical Ecology, 6, 677-87.

Lanne, B.S., Schlyter, F., Byers, J.A., Löfqvist, J., Leufvén, A., Bergström, G., Van Der Pers, J.N.C., Unelius, R., Baeckström, P., & Norin, T. 1987. Differences in attraction to semiochemicals present in sympatric pine shoot beetles, *Tomicus minor* and *T. piniperda*. Journal of Chemical Ecology, 13, 1045-67.

Leufvén, A., Bergström, G., & Falsen, E. 1984. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. Journal of Chemical Ecology, 10, 1349-61.

Leufvén, A., Bergström, G., & Falsen, E. 1988. Oxygenated monoterpenes produced by yeasts isolated from *Ips typographus* (Coleoptera: Scolytidae) and grown in phloem medium. Journal of Chemical Ecology, 14, 353-62.

Levieux, J., Cassier, P., Guillaumin, D., & Roques, A. 1991. Structures implicated in the transportation of pathogenic fungi by the European bark beetle *Ips sexdentatus* Boerner: ultrastructure of a mycangium. Canadian Entomologist, 123, 245-54.

Lindelöw, A., & Weslien, J. 1986. Sex-specific emergence of *Ips typographus* L. (Coleoptera: Scolytidae) and flight behavior in response to pheromone sources following hibernation. Canadian Entomologist, 118, 59-67.

Lindelöw, A., Risberg, B., & Sjodin, K. 1992. Attraction during flight of scolytids and other bark and wood-dwelling beetles to volatiles from fresh and stored spruce wood. Canadian Journal of Forest Research, 22, 224-8.

Lindgren, B.S., Borden, J.H., Chong, L., Friskie, L.M., & Orr, D.B. 1983. Factors influencing the efficiency of pheromone baited traps for three species of ambrosia beetles (Coleoptera: Scolytidae). Canadian Entomologist, 115, 303-14.

Löyttyniemi, K., Heliovaara, K., & Repo, S. 1988. No evidence of a population pheromone in *Tomicus piniperda* (Coleoptera: Scolytidae): a field experiment. Annales Entomologici Fennici, 54, 93-5.

Macias-Samano, J.E., Borden, J.H., Gries, R., Pierce, H.D.Jr., Gries, G., & King, G.G.S. 1998. Primary attraction of the fir engraver, *Scolytus ventralis*. Journal of Chemical Ecology, 24, 1049-75.

Magema, N., Gaspar, C., & Séverin, M. 1982. Efficacité de l'éthanol dans le piégeage du scolyte *Trypodendron lineatum* (Olivier, 1795)(Coleoptera, Scolytidae) et role des constituants terpeniques de l'epicea. Annales de la Societe Royale Zoologique de Belgique, 112, 49-60.

Mathre, D.E. 1964. Pathenogenicity of *Ceratocystis ips* and *Ceratocystis minor* to *Pinus ponderosa*. Contributions of the Boyce Thompson Institute, 22, 363-88.

McLean, J.A., & Borden, J.H. 1977. Attack by *Gnathotrichus sulcatus* (Coleoptera: Scolytidae) on stumps and felled trees baited with sulcatol and ethanol. Canadian Entomologist, 109, 675-86.

McMullen, L.H., & Atkins, M.D. 1962. On the flight and host selection of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae). Canadian Entomologist, 94, 1309-25.

Meyer, H.J., & Norris, D.M. 1967a. Behavioral responses by *Scolytus multistriatus* (Coleoptera: Scolytidae) to host- (*Ulmus*) and beetle-associated chemotactic stimuli. Annals of the Entomological Society of America, 60, 642-6.

Meyer, H.J., & Norris, D.M. 1967b. Vanillin and syringaldehyde as attractants for *Scolytus multistriatus* (Coleoptera: Scolytidae). Annals of the Entomological Society of America, 60, 858-9.

Meyer, H.J., & Norris, D.M. 1974. Lignin intermediates and simple phenolics as feeding stimulants for *Scolytus multistriatus*. Journal of Insect Physiology, 20, 2015-21.

Miller, D.R., & Borden, J.H. 1990. ß-Phellandrene: kairomone for pine engraver *Ips pini* (Say)(Coleoptera: Scolytidae). Journal of Chemical Ecology, 16, 2519-31.

Miller, J.M., & Keen, F.P. 1960. *Biology and Control of the Western Pine Beetle*. USDA miscellaneous publication # 800,.

Miller, J.R., & Strickler, K.L. 1984. Finding and accepting host plants. In: *Chemical Ecology, of Insects*, W.J. Bell, R.T. Cardé (Eds.). London: Chapman and Hall.

Mirov, N.T. 1961. Composition of gum turpentines of pines. USDA Forest Service Technical Bulletin, No. 1239.

Moeck, H.A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). Canadian Entomologist, 102, 985-94.

Moeck, H.A. 1981. Ethanol induces attack on trees by spruce beetles *Dendroctonus rufipennis* (Coleoptera: Scolytidae). Canadian Entomologist, 113, 939-42.

Moeck, H.A., Wood, D.L., & Lindahl, Jr., K.Q. 1981. Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. Journal of Chemical Ecology, 7, 49-83.

Montgomery, M.E., & Wargo, P.M. 1983. Ethanol and other host derived volatiles as attractants to beetles that bore into hardwoods. Journal of Chemical Ecology, 9, 181-90.

Moser, J.C., & Browne, L.E. 1978. A nondestructive trap for *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae). Journal of Chemical Ecology, 4, 1-7.

Mustaparta, H. 1984. Olfaction. In. *Chemical Ecology, of Insects*, W.J. Bell, R.T. Cardé (Eds.). London: Chapman and Hall.

Mustaparta, H., Angst, M.E., & Lanier, G.N. 1980. Receptor discrimination of enantiomers of the aggregation pheromone ipsdienol, in two species of *Ips*. Journal of Chemical Ecology, 6, 689-701.

Nakamura, K. 1982. Competition between females and pheromone traps: Time lag between female mating activity and male trap captures. Applied Entomology and Zoology, 17, 292-300.

Nakasuji, F., & Fujita, K. 1980. A population model to assess the effect of sex pheromones on population suppression. Applied Entomology and Zoology, 15, 27-35.

Nijholt, W.W., & Shönherr, J. 1976. Chemical response behavior of scolytids in West Germany and western Canada. Canadian Forest Service Bi-monthly Research Notes, 32, 31-2.

Nilssen, A.C. 1978. Development of a bark fauna in plantations of spruce (Picea abies [L.] Karst.) in north Norway. Astarta, 11, 151-69.

Paine, T.D. 1984. Influence of the mycangial fungi of the western pine beetle *Dendroctonus brevicomis* on water conduction through ponderosa pine seedlings. Canadian Journal of Botany, 62, 556-8.

Paine, T.D., & Stephen, F.M. 1987. Fungi associated with the southern pine beetle: avoidance of induced defense response in loblolly pine. Oecologia, 74, 377-9.

Paine, T.D., Stephen, F.M., & Cates, R.G. 1988. Moisture stress, tree suitability, and southern pine beetle population dynamics. In. *Integrated Control of Scolytid Bark Beetles*, T.L. Payne, H. Saarenmaa (Eds.). Blacksburg (USA): Virginia Polytechnical Institute and State University.

Paiva, M.R., & Kiesel, K. 1985. Field responses of *Trypodendron* spp. (Col., Scolytidae) to different concentrations of lineatin and α-pinene. Zeitschrift für angewandte Entomologie, 99, 442-8.

Payne, T.L. 1979. Pheromone and host odor perception in bark beetles. In. *Neurotoxicology of Insecticides and Pheromones*, T. Narahashi (ed.). New York: Plenum Publishing Company.

Payne, T.L., Moeck, H.A., Willson, C.D., Coulson, R.N., & Humphreys, W.J. 1973. Bark beetle olfaction - II. antennal morphology of sixteen species of Scolytidae (Coleoptera). International Journal of Insect Morphology and Embryology, 2, 177-92.

Payne, T.L., Richerson, J.V., Dickens, J.C., West, J.R., Mori, K., Berisford, C.W., Hedden, R.L., Vité, J.P., & Blum, M.S. 1982. Southern pine beetle: olfactory receptor and behavior discrimination of enantiomers of the attractant pheromone frontalin. Journal of Chemical Ecology, 8, 873-81.

Phillips, T.W. 1990. Responses of *Hylastes salebrosus* to turpentine, ethanol and pheromones of *Dendroctonus* (Coleoptera: Scolytidae). Florida Entomologist, 73, 286-92.

Phillips, T.W., Wilkening, A.J., Atkinson, T.H., Nation, J.L., Wilkinson, R.C., & Foltz, J.L. 1988. Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera). Environmental Entomology, 17, 456-62.

Pierce, Jr., H.D., Conn, J.E., Oehlschlager, A.C., & Borden, J.H. 1987. Monoterpene metabolism in female mountain pine beetles, *Dendroctonus ponderosae* Hopkins attacking ponderosa pine. Journal of Chemical Ecology, 13, 1455-80.

Pitman, G.B., Renwick, J.A.A., & Vité, J.P. 1966. Studies on the pheromone of *Ips confusus* (LeConte). IV. Isolation of the attractive substance by gas-liquid chromatography. Contributions of the Boyce Thompson Institute, 23, 243-50.

Pitman, G.B., & Vité, J.P. 1969. Aggregation behavior of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in response to chemical messengers. Canadian Entomologist, 101, 143-9.

Pitman, G.B., Hedden, R.L., & Gara, R.I. 1975. Synergistic effects of ethyl alcohol on the aggregation of *Dendroctonus pseudotsugae* (Col., Scolytidae) in response to pheromones. Zeitschrift für angewandte Entomologie, 78, 203-8.

Poland, T.M., Borden, J.H., Stock, A.J., & Chong, L.J. 1998. Green leaf volatiles disrupt responses by the spruce beetle, *Dendroctonus rufipennis*, and the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae) to attractant-baited traps. Journal of the Entomological Society of British Columbia, 95, 17-24.

Poland T.M., & Haack R.A. 2000. Pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae), responses to common green leaf volatiles. Journal of Applied Entomology, 124, 63-70

Popp, M.P., Johnson, J.D., & Lesney, M.S. 1995. Changes in ethylene production and monoterpene concentration in slash pine and loblolly pine following inoculations with bark beetle vectored fungi. Tree Physiology, 15, 807-12.

Raffa, K.F., & Berryman, A.A. 1979. Flight responses and host selection by bark beetles. In. *Dispersal of Forest Insects: Evaluation, Theory and Management Implications,* A.A. Berryman, L. Safranyik (Eds.). Proc. second IUFRO conf., Canadian and USDA Forest Service.

Raffa, K.F., & Berryman, A.A. 1982. Gustatory cues in the orientation of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) to host trees. Canadian Entomologist, 114, 97-104.

Raffa, K.F., & Berryman, A.A. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? American Naturalist, 129, 234-62.

Raffa, K.F., Phillips, T.W., & Salom, S.M. 1993. Strategies and mechanisms of host colonization by bark beetles. In. *Beetle-Pathogen Interactions in Conifer Forests* T.D. Schowalter, G.M. Filip (Eds.). London: Academic Press.

Ramaswamy, S.B., & Cardé, R.T. 1984. Rate of release of spruce budworm *Choristoneura fumiferana* pheromone from virgin females and synthetic lures. Journal of Chemical Ecology, 10, 1-8.

Ramisch, H. 1986. Host location by *Trypodendron domesticum* and *Trypodendron lineatum* (Coleoptera: Scolytidae). Zeitschrift für angewandte Zoologie, 73, 159-98.

Raulston, J.R., Lingren, P.D., Sparks, A.N., & Martin, D.F. 1979. Mating interaction between native tobacco budworms and released backcross adults. Environmental Entomology, 8, 349-53.

Renwick, J.A.A., & Vité, J.P. 1968. Isolation of the population aggregating pheromone of the southern pine beetle. Contributions of the Boyce Thompson Institute, 24, 65-8.

Renwick, J.A.A., & Vité, J.P. 1969. Bark beetle attractants: mechanisms of colonization by *Dendroctonus frontalis*. Nature, 224, 1222-3.

Renwick, J.A.A., & Vité, J.P. 1970. Systems of chemical communication in *Dendroctonus*. Contributions of the Boyce Thompson Institute, 24, 283-92.

Richeson, J.S., Wilkinson, R.C., & Nation, J.L. 1970. Development of *Ips calligraphus* on foliage based diets. Journal of Economic Entomology, 63, 1797-9.

Richter, D. 1991. Control of bark beetles in the five new states of the Federal Republic of Germany, In. A. Wulf and R. Kehr (Eds.). *Bark Beetle Hazards Following Storm Damage: Possibilities and Limits of Integrated Control*. Colloquium, Braunschweig, Germany. Communications from the Federal Biological Institute for Agriculture and Forestry, Berlin-Dahlem, No. 267.

Ricklefs, R.E. 1990. Evolution, social behavior, and population regulation. In. *Ecology*. New York: W.H. Freeman and Company.

Roelofs, W.L., Glass, E.H., Tette, J., & Comeau, A. 1970. Sex pheromone trapping for red-banded leaf roller control: Theoretical and actual. Journal of Economic Entomology, 63, 1162-7.

Rose, W.F., Billings, R.F., & Vité, J.P. 1981. Southern pine bark beetles *Ips calligraphus*: evaluation of nonsticky pheromone trap designs for survey and research. Southwest Entomologist, 6, 1-9.

Rudinsky, J.A. 1966. Host selection and invasion by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. Canadian Entomologist, 98, 98-111.

Rudinsky, J.A., Novak, V., & Svihra, P. 1971. Attraction of the bark beetle *Ips typographus* L. to terpenes and a male-produced pheromone. Zeitschrift für angewandte Entomologie, 67, 179-88.

Rudinsky, J.A., Morgan, M.E., Libbey, L.M., & Putnam, T.B. 1974. Antiaggregative-rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. Environmental Entomology, 3, 90-8.

Salom, S.M., & Mclean, J.A. 1989. Influence of wind on the spring flight of *Trypodendron lineatum* Olivier (Coleoptera: Scolytidae) in a second-growth coniferous forest. Canadian Entomologist, 121, 109-20.

Salonen, K. 1973. On the life cycle, especially on the reproduction biology of *Blastophagus piniperda* L. (Col., Scolytidae). Acta Forestalia Fennica, 127, 1-72.

Schlyter, F. 1992. Sampling range, attraction range, and effective attraction radius: Estimates of trap efficiency and communication distance in coleopteran pheromone and host attractant systems. Journal of Applied Entomology, 114, 439-54.

Schlyter, F., & Birgersson, G. 1999. Forest Beetles. In. J. Hardie, J., A.K. Minks (Eds.). *Pheromone in Non-Lepidopteran Insects Associated with Agricultural Plants*, Oxford: CAB International.

Schlyter, F., Birgersson, G., Byers, J.A., Löfqvist, J., & Bergström, G. 1987a. Field response of spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates. Journal of Chemical Ecology, 13, 701-16.

Schlyter, F., Byers, J.A., & Löfqvist, J.. 1987b. Attraction to pheromone sources of different quantity, quality, and spacing: density-regulation mechanisms in bark beetle *Ips typographus*. Journal of Chemical Ecology, 13, 1503-23.

Schlyter, F., Löfqvist, J., & Byers, J.A. 1987c. Behavioural sequence in the attraction of the bark beetle *Ips typographus* to pheromone sources. Physiological Entomology, 12, 185-96.

Schlyter, F., Byers, J.A., Löfqvist, J., Leufvén, A., & Birgersson, G. 1988. Reduction of attack density of the bark beetles *Ips typographus* and *Tomicus piniperda* on host bark by verbenone inhibition of attraction to pheromone and host kairomone. In. *Integrated Control of Scolytid Bark Beetles*, T.L. Payne, H. Saarenmaa (Eds.). Blacksburg (USA): Virginia Tech. Press.

Schlyter, F., Birgersson, G., & Leufven, A. 1989. Inhibition of attraction to aggregation pheromone by verbenone and ipsenol: density regulation mechanisms in bark beetle *Ips typographus*. Journal of Chemical Ecology, 15, 2263-77.

Schlyter, F., Birgersson, G., Byers, J.A., & Bakke, A. 1992. The aggregation pheromone of *Ips duplicatus* and its role in competitive interactions with *I. typographus* (Coleoptera: Scolytidae). Chemoecology, 3, 103-12.

Schlyter, F, Löfqvist, J, & Jakus, R 1995. Green leaf volatiles and verbenone modify attraction of European Tomicus, Hylurgops, and Ips bark beetles. In. *Behavior, Population Dynamics, and Control of Forest Insects*, F.P. Hain, S.M. Salom, W.F. Ravlin, T.L. Payne, K.F. Raffa, KF (Eds.). Proceedings IUFRO Working Party Conference. Ohio State Univ.

Schlyter, F., Zhang, Q.H., Anderson, P.A., Byers, J.A., Wadhams, L.J., Löfqvist, J., & Birgersson, G. 2000. Electrophysiological and behavioural responses of *Tomicus piniperda* and *T. minor* (Coleoptera: Scolytidae), to non-host leaf and bark volatiles. Canadian Entomologist, 132, 965-81.

Schroeder, L.M. 1987. Attraction of the bark beetle *Tomicus piniperda* to Scots pine trees in relation to tree vigor and attack density. Entomologia Experimentalis et Applicata, 44, 53-8.

Schroeder, L.M. 1988. Attraction of the bark beetle *Tomicus piniperda* and some other bark- and wood-living beetles to the host volatiles α-pinene and ethanol. Entomologia Experimentalis et Applicata, 46, 203-10.

Schroeder, L.M. 1992. Olfactory recognition of nonhosts aspen and birch by conifer bark beetles *Tomicus piniperda* and *Hylurgops palliatus*. Journal of Chemical Ecology, 18, 1583-93.

Schroeder, L.M., & Eidmann, H.H. 1987. Gallery initiation by *Tomicus piniperda* (Coleoptera: Scolytidae) on Scots pine trees baited with host volatiles. Journal of Chemical Ecology, 13, 1591-9.

Schroeder, L.M., & Lindelöw, A. 1989. Attraction of scolytids and associated beetles by different absolute amounts and proportions of α-pinene and ethanol. Journal of Chemical Ecology, 15, 807-18.

Schuh, B.A., & Benjamin, D.M. 1984. The chemical feeding ecology of *Neodipron dubiosus* Schedl, *N. rugifrons* Midd., and *N. lecontei* (Fitch) on Jack pine (*Pinus banksiana* Lamb.). Journal of Chemical Ecology, 10, 1071-9.

Scriber, J.M. 1984. Host-plant suitability. In. *Chemical Ecology, of Insects*, W.J. Bell, R.T. Cardé (Eds.). London: Chapman and Hall.

Seybold, S.J., & Tittiger, C. 2003. Biochemistry and molecular biology of *de novo* isoprenoid pheromone production in the Scolytidae. Annual Review of Entomology, 48, 425-53.

Seybold, S.J., Bohlmann, J., & Raffa, K.F. 2000. The biosynthesis of coniferophagous bark beetle pheromones and conifer isoprenoids: evolutionary perspective and synthesis. Canadian Entomologist, 132, 697-753.

Silverstein, R.M., Brownlee, R.G., Bellas, T.E., Wood, D.L., & Browne, L.E. 1968. Brevicomin: principal sex attractant in the frass of the female western pine beetle. Science, 159, 889-91.

Smith, L.V., & Zavarin, E. 1960. Free mono- and oligosaccharides of some California conifers. TAPPI Journal, 43, 218-21.

Städler, E. 1984. Contact chemoreception. In. *Chemical Ecology, of Insects*, W.J. Bell, R.T. Cardé (Eds.). Londong: Chapman and Hall.

Sternlicht, M., Barzakay, I., & Tamim, M. 1990. Management of Prays citri in lemon orchards by mass trapping of males. Entomologia Experimentalis et Applicata, 55, 59-68.

Struble, G.R. 1957. The fir engraver, a serious enemy of western true firs. US Agricultural Product Research Report II.

Teale, S.A., Webster, F.X., Zhang, A., & Lanier, G.N. 1991. Lanierone: a new pheromone component from *Ips pini* (Coleoptera: Scolytidae) in New York. Journal of Chemical Ecology, 17, 1159-76.

Thompson, S.N., & Bennett, R.B. 1971. Oxidation of fat during flight of male Douglas-fir beetles, *Dendroctonus pseudotsugae*. Insect Physiology, 17, 1555-63.

Tilden, P.E., Bedard, W.D., Lindahl, Jr., K.Q., & Wood, D.L. 1983. Trapping *Dendroctonus brevicomis*: changes in attractant release rate, dispersion of attractant, and silhouette. Journal of Chemical Ecology, 9, 311-21.

Tommeräs, B.A., Mustaparta, H., & Gregoire, J.C. 1984. Receptor cells in *Ips typographus* and *Dendroctonus micans* specific to pheromones of the reciprocal genus. Journal of Chemical Ecology, 10, 759-69.

Villavaso, E.J. 1982. Boll weevil, Anthonomus grandis, isolated field plot studies of disruption of pheromone communication. Journal of the Georgia Entomological Society, 17, 347-50.

Villavaso, E.J., & McGovern, W.L. 1981. Boll weevil, *Anthonomus grandis grandis*, disruption of pheromonal communication in the laboratory and small field plots. Journal of Georgia Entomological Society, 16, 306-10.

Vité, J.P. 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. Contributions of the Boyce Thompson Institute, 21, 37-66.

Vité, J.P. 1989. The European struggle to control *Ips typographus*: Past present and future. Holarctic Ecology, 12, 520-5.

Vité, J.P., & Pitman, G.B. 1969. Insect and host odors in the aggregation of the western pine beetle. Canadian Entomologist, 101, 113-17.

Vité, J.P., & Bakke, A. 1979. Synergism between chemical and physical stimuli in host selection by an ambrosia beetle. Naturwissenschaften, 66, 528-9.

Vité, J.P., Volz, H.A., Paiva, M.R., & Bakke, A. 1986. Semiochemicals in host selection and colonization of pine trees by the pine shoot beetle *Tomicus piniperda*. Naturwissenschaften, 73, 39-40.

Volz, H.A. 1988. Monoterpenes governing host selection in the bark beetles *Hylurgops palliatus* and *Tomicus piniperda*. Entomologia Experimentalis et Applicata, 47, 31-6.

Vrkoc, J. 1989. Use of insect pheromone in integrated pest management examples from Czechoslovakia. Chem Scripta, 29, 407-10.

Wagner, M.R., Benjamin, D.M., Clancy, K.L., & Schuh, B.A. 1983. Influence of diterpene resin acids on feeding and growth of larch sawfly, *Pristphora erichsonii* (Hartig). Journal of Chemical Ecology, 9, 119-27.

Webb, J.L. 1906. The western pine destroying bark beetle. USDA Bureau of Entomology Bulletin, 58, Pt. II.

Webb, J.W., & Franklin, R.T. 1978. Influence of phloem moisture on brood development of the southern pine beetle (Coleoptera: Scolytidae). Environmental Entomology, 7, 405-10.

Weber, T. 1987. Can bark beetles be controlled efficiently by application of pheromone traps. Allgemeine Forstzeitschrift, 42, 87-9.

White, J.D. 1981. A bioassay for tunneling responses of southern pine beetles to host extractives. Journal of the Georgia Entomological Society, 16, 484-92.

Whitehead, A.T. 1981. Ultrastructure of sensilla of the female mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae). International Journal of Insect Morphology and Embryology, 10, 19-28.

Whitney, H.S. 1982. Relationships between bark beetles and symbiotic organisms. In. *Bark Beetles in North American Conifers: a System for the Study of Evolutionary Biology*, J.B. Mitton, J.B., K.B. Sturgeon (Eds.). Austin: University of Texas Press.

Whitney, H.S., & Spanier, O.J. 1982. An improved method for rearing axenic mountain pine beetles *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Canadian Entomologist, 114, 1095-1100.

Wilson, I.M., Borden, J.H., Gries, R., & Gries, G. 1996. Green leaf volatiles as antiaggregants for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Journal of Chemical Ecology, 22, 1861-75.

Witanachchi, J.P., & Morgan, F.D. 1981. Behavior of the bark beetle, *Ips grandicollis*, during host selection. Physiological Entomology, 6, 219-23.

Witz, J.A., Lopez, J.D., Jr., & Latheef, M.A. 1992. Field density estimates of *Heliothis virescens* (Lepidoptera: Noctuidae) from catches in sex pheromone-baited traps. Bulletin of Entomological Research, 82, 281-6.

Wood, D.L. 1962. Experiments on the interrelationship between oleoresin exudation pressure in *Pinus ponderosa* and attack by *Ips confusus* (LeC.)(Coleoptera: Scolytidae). Canadian Entomologist, 94, 473-7.

Wood, D.L. 1980. Approach to research and forest management for western pine beetle control. In. *New Technology of Pest Control*. C.B. Huffaker (ed.), New York: John Wiley and Sons.

Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology, 27, 411-46.

Wood, D.L., & Bushing, R.W. 1963. The olfactory response of *Ips confuses* (LeConte) (Coleoptera: Scolytidae) to the secondary attraction in the laboratory. Canadian Entomologist, 95, 1066-78.

Wood, D.L., & Vité, J.P. 1961. Studies on the host selection behavior of *Ips confusus* (LeConte)(Coleoptera: Scolytidae) attacking *Pinus ponderosa*. Contributions of the Boyce Thompson Institute, 21, 79-96.

Wood, S.L. 1982. *The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph*. Great basin naturalist memoirs, Brigham Young Univ., Provo, Utah.

Zhang, Q.H. 2003. Interruption of aggregation pheromone in *Ips typographus* (L.) (Col.: Scolytidae) by non-host bark volatiles. Agricultural and Forest Entomology, 5, 145-53.

Zhang, Q.H., & Schlyter, F. 2003. Olfactory recognition and behavioural avoidance of angiosperm non-host volatiles by conifer-inhabiting bark beetles. Agricultural and Forest Entomology, *In press*

Zhang, Q.H., Birgersson, G., Zhu, J., Löfstedt, C., Löfqvist, J., & Schlyter, F. 1999a. Leaf volatiles from nonhost deciduous trees: Variation by tree species, season, and temperature, and electrophysiological activity in *Ips typographus*. Journal of Chemical Ecology, 25, 1923-43.

Zhang, Q.H., Schlyter, F., & Anderson, P. 1999b. Green leaf volatiles interrupt pheromone response of spruce bark beetle, *Ips typographus*. Journal of Chemical Ecology, 25, 2847-61.

Zhang, Q.H., Schlyter, F., & Birgersson, G. 2000. Bark volatiles from nonhost angiosperm trees of spruce bark beetle, *Ips typographus* (L.) (Coleoptera: Scolytidae): Chemical and electrophysiological analysis. Chemoecology, 10, 69-80.

Zhang, Q.H., Liu, G.T., Schlyter, F., Birgersson, G., Anderson, P., & Valeur, P. 2001. Olfactory response of *Ips duplicatus* to nonhost leaf and bark volatiles in inner Mongolia, China. Journal of Chemical Ecology, 27, 955-1009.

Zolubas, P., & Byers, J.A. 1995. Recapture of dispersing bark beetles, *Ips typographus* L. (Col., Scolytidae) in pheromone-baited traps: regression models. Journal of Applied Entomology, 19, 285-89.

Zumr, V. 1992. Dispersal of the spruce bark beetle *Ips typographus* (L.)(Col., Scolytidae) in spruce woods. Journal of Applied Entomology, 114, 348-52.

Zvirgzdins, A., Lingren, P.D., Henneberry, T.J., Nowell, C.E., & Gillespie, J.M. 1984. Mating Disruption of a wild population of tobacco budworm, *Heliothis virescens*, (Lepidoptera: Noctuidae) with virelure. Journal of Economic Entomology, 77, 1464-69.