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ABSTRACT

The primary cohabiting species of the southern pine bark beetle guild consists of the following scolytids: the southern pine beetle, *Dendroctonus frontalis*, the black turpentine beetle, *D. terebrans*, the four-spined engraver, *Ips avulsus*, the eastern five-spined engraver, *I. grandicollis*, and the six-spined engraver, *I. calligraphus*. They inhabit the phloem tissue of all native southern pines, often with three or more species in the same tree.

The pheromonal systems of each species have been investigated to various degrees in at least three areas: including pheromonal biosynthesis and release; semiochemical perception and sensory coding; and semiochemical-mediated behavior. Furthermore, the semiochemical interactions among the species are thought to govern many of the processes that result in cohabitation of southern pines.

The purpose of this paper is to provide a comprehensive review of the research carried out to date on the olfactory communication systems of these five scolytid species.

INTRODUCTION

The southern pine bark beetle guild include the following scolytids: the southern pine beetle, *Dendroctonus frontalis* Zimmerman, the black turpentine beetle, *D. terebrans* (Oliver), the four-spined engraver, *Ips avulsus* (Eichhoff), the eastern five-spined engraver, *I. grandicollis* (Eichhoff), and the six-spined engraver, *I. calligraphus* (Germar). As the term implies, this guild is comprised of species which exploit the same resource in a similar manner and whose niche requirements overlap significantly (Root 1973). All of the five principal species require fresh pine phloem tissue for their reproduction and development. And it is not unusual to find all five species co-habiting the same host tree. As one of the most destructive groups of forest insects known, the member species of this guild co-exist in pine forests across southeastern and southcentral United States. These hosts include: loblolly pine, *Pinus taeda* L.; shortleaf pine, *Pinus echinata* Mill.; pitch pine, *Pinus rigida* Mill; Virginia pine, *Pinus virginiana* Mill.; slash pine, *Pinus elliotti* Engel,; and longleaf pine, *Pinus palustris* Mill. Guild members have been found to colonize other conifer species as well (see Thatcher et al. 1980).

In the monogynous *Dendroctonus* species, females are responsible for host selection, initial attack, and gallery construction in new host trees. Male *Dendroctonus* enter the host only after females have selected and successfully attacked a host and pheromone production has begun. Once extensive feeding and defecation commences, the frass is not dislodged but is tightly packed in the galleries.

In contrast, males of the polygynous *Ips* species select hosts, prepare nuptial chambers, and produce pheromones. Female beetles locate the entrance holes of established males via pheromones, and/or acoustic emissions, enter, mate, and then construct galleries along which they lay eggs. Continuous ejection of frass from the galleries provides for sustained release of the semiochemicals with the male frass. In both genera, as more beetles arrive at the tree and produce and release pheromones, the attraction of the host increases until the whole tree is colonized. Termination of beetle arrival is also apparently under pheromonal control. Hypothetical schematic representations of these processes have been published by Renwick and Vité (1969), Payne and Coulson (1985), and Payne (1986).

The pheromonal systems of each species have been investigated to various degrees and in at least three areas for each species. These areas include the following: pheromonal biosynthesis and release, semiochemical perception and sensory coding, and semiochemical-mediated behavior. These investigations have included studies of both intra- and interspecific semiochemical-based interactions and have ranged from the very basic to the very applied aspects of the olfactory communication systems. Furthermore, the interactions of semiochemical-based behaviors among the species comprising the guild may explain many of the processes that result in cohabitation of southern pines.

The purpose of this paper is to provide a comprehensive review of past research studies on the semiochemical-based communication systems of the five scolytid species comprising the southern pine bark beetle guild. We believe it will be a useful source of information for investigators in this area of research and serve as an educational tool for students of bark beetle chemical ecology. Note, however, this paper does not attempt to extend beyond the boundaries of this. A generalized synthesis and review of the evolution of bark beetle semiochemical-based behavior can be found in other papers (see Alcock 1982; Raffa and Berryman 1983; Raffa et al. 1993).

TEMPORAL ARRIVAL

In Texas, *D. frontalis*, *I. calligraphus* and *I. avulsus* generally initiate colonization within a short period of time (ca. 1-3 days), with their arrvial appearing synchronus (Birch and Svihra 1979; Dixon and Payne 1979; Svihra et al. 1980). The first species to arrive was most often *D. frontalis*, followed soon afterwards by *I. avulsus* and *I. calligraphus* (Birch and Svihra 1979; Svihra et al. 1980). Birch et al. (1980) reported that the first species to colonize hosts were *D. frontalis*, *I. avulsus*, and *I. calligraphus* at 76%, 20% and 4% of the colonized trees, respectively. Conflicting reports of *I. grandicollis* arrival have been presented, in which arrival of *I. grandicollis* has been demonstrated to coincide with (Dixon and Payne 1979) or occur later than (Svihra et al., 1980) the other three scolytid species.

Changes in the density of arriving beetles over time further differentiates the arrival and attack characteristics of the cohabiting species (Coster et al 1977a; Fargo et al. 1978; Dixon and Payne 1979). Peak arrivals of *D. frontalis* occurred 3-5 days following initiation of arrival, after which the density of arriving beetles declined sharply. Peak arrival of *I. avulsus* and *I. calligraphus* occurred 12 and 21 days, respectively, following initiation of attack and then declined thereafter. In contrast, attacking *I. grandicollis* gradually increased in density for 18 days following initial of arrival and then maintained an intermediate attack rate until at least day 30.

SPATIAL DISTRIBUTION

Brood development in all five species is dependent on phloem tissue, which can be a scarce resource within trees where colonization has been initiated by more than one species. The beetle species, thus, compete for the limited amount of phloem tissue used as a site for reproduction. A thorough investigation of available data concerning the ecological relationships among these species should help explain their behavioral interactions and provide a basis for a more realistic interpretation of infestations by this complex of bark beetle species.

Dixon and Payne (1979) have reported on the spatial distribution of the five species. Peak densities of *D. frontalis* occurred at 2-6 m above ground level, but ranged from 1-12 m. Only 3% of the total *D. frontalis* were caught at heights of 11 and 12 m. Coster et al. (1977b) reported similar results; the maximum catch of *D. frontalis* at 3 m, and 53.7% of the total catch was on the lower 5 m of attacked trees. This observation is also in agreement with Gara et al. (1965), who found maximum densities of *D. frontalis* at 3 m above ground level on infested trees. By comparison, Dixon and Payne (1979) reported that *I. calligraphus, I. avulsus,* and *I. grandicollis* were most abundant on the upper half of the tree bole. The fifth species, *D. terebrans,* is often found in the base of living trees, including areas of the roots and root collar, and is not generally in close association with mass colonization of southern pines by the other species.

Birch et al. (1980) reported that *D. frontalis, I. calligraphus,* and *I. avulsus* have broadly overlapping distributions within infested trees. Both Svihra et al. (1980) and Paine et al. (1981) have reported that each species occupies a distinct area of the available tree surface, but an area that broadly overlaps that occupied by the other species. The lower bole region was predominantly occupied by *D. frontalis,* the middle and upper bole by *I. calligraphus,* and *I. avulsus* extended continuously from the lower bole to the crown (Birch and Svihra 1979). However, the least interactive species, *I. grandicollis,* rarely attacks the trunk of standing trees and was more frequently found in the larger branches of the crown (Birch et al. 1980).

Paine et al. (1981) utilized the niche breadth index as a measure of exploitation of the available resource by each species at each height level, and the niche overlap index to reflect the potential for competition among co-existing species. Basically, *I. avulsus* exhibited the broadest niche breadth, while *I. grandicollis* had the narrowest. *D. frontalis* dominated the lower bole and overlapped primarily with *I. calligraphus.* The upper bole was similarly dominated by *I. avulsus,* which overlapped only slightly with *D. frontalis,* but overlapped extensively with *I. calligraphus.* However, neither *D. frontalis* nor *I. avulsus* had an advantage over *I. calligraphus* in the mid-bole. *I. grandicollis* exhibited the highest niche breadth in the lower branches, with only a small peak in the middle levels of the main trunk. Furthermore, there was no overlap between *I. avulsus* and *I. grandicollis* in the higher levels or in the branches.

Finally, Wagner et al. (1985) examined the nature of intraspecific competition within the southern pine bark beetle guild, excluding *D. terebrans*, and described some of the adaptations employed by each species that enable them to minimize primarily intraspecific competition. Therefore, the resource allocation processes addressed were those operating only after the guild species had selected and entered the host tree. Wagner et al. (1985) reported that gallery construction and oviposition behaviors of the adult of each species, together with their respective larval feed behavior, enable each species to optimize the number of individuals in an area by spatially allocating gallery and eggs in a way that minimizes competition among developing brood. They hypothesized that chemicals originating from beetle galleries strongly influence the efficient placement of galleries and eggs via formation of a concentration gradient adjacent to the galleries. Furthermore, they hypothesized that these beetle-derived compounds are involved in terminating reproduction or egg deposition in females, which in turn initiates re-emergence. Thus, these chemicals would help insure possession of minimum space for developing brood. These hypotheses await verification.

PHEROMONE PRODUCTION

Production of pheromone by the five species has been investigated over the past 25 years, but most thoroughly for *D. frontalis*. The beetle-produced compounds have been collected from extracts of hindguts, feces or frass, and the volatiles from beetle-infested host material, followed by repeated fractionation. Biological activity of individual fractions and recombined mixtures of fractions has been determined in laboratory bioassays, thereby minimizing the probability of overlooking components of the pheromone system. Nevertheless, since the pheromone systems are usually composed of more than one pheromone and since some pheromones can be multifunctional, description of the precise chemical nature and behavioral function of some pheromones and pheromone mixtures awaits further investigation. The following discussion concerning pheromone production by each of the five scolytid species should be reviewed in concert with Appendices 1 through 5.

Site of Production and Mechanism of Release:

Renwick (1967), citing Gara and Vité (personal communication), stated that excision of hindguts of both sexes of emerged *D. frontalis* revealed an oil-like liquid in the rectum and ileum. Pitman et al. (1968) reported the presence of *trans*-verbenol and verbenone in the hindguts of *D. frontalis* females and males, respectively. These compounds were detected by gas chromatography analysis of oil-like droplets that were visible in the hindgut when viewed under a dissecting microscope. Vité and Pitman (1967) reported that the attractive components inducing mass attack originate from the hindgut of female *Dendroctonus* and male *Ips* species. Pitman et al. (1968) stated that in both *Dendroctonus* and *Ips* species, the mechanism of pheromone release is defecation and the probable sites of elaboration and concentration are the malpighian tubules and hindgut area.

Pitman et al. (1969), in their study of specificity of population-aggregating pheromones in *Dendroctonus*, showed that scolytid pheromones are associated with the alimentary system as are most true sex pheromones. Vité et al. (1972), in their study of the occurrence and production of pheromones in *Ips*, reported the presence of host terpenes in the foregut and midgut, and pheromones in the hindgut and feces of feeding *I. calligraphus*.

Hughes (1973) reported that although the precise site of pheromone production remains unknown, all known bark beetle pheromones are concentrated in the hindgut and released upon defecation. Furthermore, detection of the oxidation products of *alpha*- and *beta*- pinene in the hemolymph of *Dendroctonus*, coupled with the fact that ingestion of *alpha*-pinene is not necessary for production of these oxidation products, indicates they are formed outside the alimentary canal. The products may be secreted into the hindgut and concentrated by reabsorption of water.

Biosynthesis and Effects of Terpene and Non-terpene Vapor Exposure on Production:

Knowledge of bark beetle pheromone biosynthesis, although largely conjectural, is based upon simple host terpene metabolism. Vité and Pitman (1967) classified attractants that facilitate bark beetle aggregation according to their origin, ie. host-produced or insect-produced. They stressed the lack of discrete boundaries between these categories and suggested that these categories may be viewed as an evolutionary continuum in the process of host selection and colonization. Hughes (1973) expanded their suggestion by applying the hypothesis that some *Dendroctonus* aggregation pheromones arose from products of terpene metabolism or detoxification.

Vité et al. (1972) delineated contact and frass type pheromones. Contact pheromones are those released upon contact with host oleoresin vapors, while frass pheromones are released only after feeding. This nomenclature appears to be somewhat ambiguous since both pheromone types are released in the frass. Furthermore, since host terpenes serve as precursors for both contact type (Vité et al. 1972; Hughes 1973, 1974; Renwick et al. 1973) and frass type (Hughes 1974) pheromones, the biological implications of this nomenclature and its ability to clarify function appears questionable.

Later, White et al. (1980) proposed a more precise, biochemically-based division of bark beetle pheromones. In their classification system there are two pheromone types: 1. those produced de novo via synthetic or other endogenous pathways (constructed pheromones) and 2. those produced directly as waste pheromones from xenobiotic host terpenes. In other words, one type of pheromones are terpenoids that are probably microsomal cytochrome P-450 metabolites of host terpenes or the result of direct synthesis from aliphatic short carbon precursors, while the second type are terpenoid pheromones that are the result of xenobiotic detoxification mechanisms, most notably the cytochrome P-450, epoxide hydrase, and conjugating enzyme systems. Frontalin, *exo*-brevicomin, and *endo*-brevicomin would represent products of a specific metabolic system, possibly that of the steroid or hormone metabolism. Conversely, the rest of the pheromones, which are primarily alcohols and ketones, are produced from host-supplied terpenes. These terpene substrates would be available to beetles via contact, feeding, and vapor, while precursors for frontalin and the brevicomins would require feeding for their formation and release. It should be noted that in some cases certain microorganisms such as yeasts contribute to terpene pheromone production (Hunt and Borden 1990).

Upon emergence, individuals of *Dendroctonus* species generally possess their primary pheromones, whereas individuals of *Ips* species generally lack their primary pheromones. Although recent reports support this generalization (Payne et al. 1987; Phillips et al. 1989), Hughes (1973) demonstrated that *D. terebrans* generally had little or no detectable terpene oxidation products in their hindgut upon emergence. However, it should also be noted that the amount of terpene oxidation products in emergent beetles can vary both among species and among individuals within a species.

Gas liquid chromatography (GLC) analysis of adult *D. frontalis* hindguts (Renwick et al. 1973; Hughes 1973, 1975; Renwick and Hughes 1975; Renwick et al. 1976) revealed the presence of a number of volatile compounds after exposure of the adult beetles to host oleoresin or various host terpenes. Although the studies are more limited, similar results were obtained for adult *D. terebrans* (Hughes 1973, 1975). These volatile compounds, not found in the host and apparently oxidation products of monoterpenes, are produced when adult beetles are exposed to oleoresin or individual monoterpene vapors or when terpenes are topically applied. However, Renwick and Hughes (1975) demonstrated that oxidation of unsaturated cyclic hydrocarbons by *D. frontalis* is not restricted to terpenes. He reported the production of a number of volatile compounds in adult beetles following exposure to 1-methyl cyclohexene, a non-terpenoid hydrocarbon not known to be a component of host trees.

Interestingly enough, Hughes (1975) investigated the effects of *alpha*-pinene vapor exposure on the production of *trans*-verbenol and verbenone in larvae, pupae, and male adult *D. frontalis* and *D. terebrans*. First and foremost, Hughes (1975) found detectable quantities of *trans*-verbenol in each life stage of both species when the insects were excised from the host tree. Following exposure to *alpha*-pinene vapors, larvae and male adults of both species showed significant increases in *trans*-verbenol, while no such change was detected in pupae of either species. However, adults reared from pupae that had been exposed to *alpha*-pinene vapors showed a significant increase in *trans*-verbenol levels in both species. Hughes (1975) further reported that verbenone was detectable only in male adult *D. frontalis*, not in pupal *D. frontalis*, and its presence in larval *D. frontalis* apparently still remains in question. However, adult male *D. frontalis* reared from pupae that had been exposed to *alpha*-pinene vapors possessed significantly more verbenone than did adults reared from unexposed pupae or normal emergent adults. Although Hughes (1975) found no verbenone in any *D. terebrans* life stage, Phillips et al. (1989) recently showed the presence of verbenone in adult *D. terebrans*, males more so than females, following feeding. Hughes (1975) concluded that both larvae and adult *D. frontalis* and *D. terebrans* are capable of metabolizing *alpha*-pinene to *trans*-verbenol, whereas the pupae cannot. However, their data also indicate that pupae are capable of forming an intermediate compound(s) from *alpha*-penene, which are later metabolized by adult *D. frontalis* and *D. terebrans* to yield *trans*-verbenol and verbenone, and *trans*-verbenol only, respectively. *Dendroctonus frontalis* males are also capable of producing verbenone from *alpha*-pinene taken up in the adult stage.

As previously mentioned, individuals of *Ips* species generally lack their pheromones upon emergence from their host tree. However, Vité et al. (1972) first demonstrated the appearance of *trans*-verbenol and *cis*-verbenol in *I. calligraphus* following exposure to oleoresin vapor. Hughes (1974) clearly demonstrated that among the three *Ips* species, only male *I. avulsus* produces its pheromone, ipsdienol, upon simple exposure to myrcene vapors. Therefore, myrcene may serve as a precursor of ipsdienol in *I. avulsus*. On the other hand, both *I. calligraphus* and *I. grandicollis* males produce their respective pheromones, ipsdienol and ipsenol, only after feeding.

Although the precise mechanism of oxidation and rearrangement is still unknown, the pattern of products resulting from exposure to hydrocarbons suggests that general metabolic systems for oxidation of these potentially toxic compounds exist within these *Dendroctonus* and *Ips* species. Hughes (1973) hypothesized that terpene metabolism developed primarily as a detoxification mechanism, detoxifying the terpenes that Smith (1959, 1965) has reported are toxic to bark beetles. Furthermore, some of these oxidation products, eliminated by excretion, may have only secondarily become utilized as pheromones (Hughes 1973). These conclusions are consistent with the association of the malpighian tubule-hindgut region with the concentration and release of pheromones in scolytids, and provide one explanation for the ubiquity of these compounds serving as chemical messengers in *Dendroctonus* and *Ips*.

Effects of Feeding Upon Pheromone Production:

In general, extensive feeding in new host material by *Dendroctonus* species soon inhibits the release of attractants. Investigating *D. frontalis*, Vité and Pitman (1968) reported a depletion of the oil-like droplets and *trans*-verbenol within 12-16 hours after feeding commenced. Coster (1970a) then demonstrated that the pheromone content of female *D. frontalis* hindguts decline rapidly as feeding and gallery construction progress. Coster and Vité (1972), in GLC analysis of female *D. frontalis* hindguts, found that feeding, independent of mating activity, resulted in a decrease of the frontalin and *trans*-verbenol content. However, both pheromones were still present, yet at low levels, after 48 hours of feeding. Although the comment is ambiguous, it should be noted that Hughes (1973) reported that frontalin levels remained "about the same" after feeding. Hughes (1973) also reported that myrtenol and verbenone declined after feeding by *D. frontalis* males and females, and males, respectively. On the other hand, he reported that *trans*-verbenol increased in male *D. frontalis* after feeding. And while only after feeding did *cis*-verbenol appear in both sexes, feeding apparently resulted in the disappearance of *cis*-3-pinen-2-ol in female *D. frontalis*.

This was supported by Vité and Pitman (1968) and Coster and Vité (1972) when they reported that the attractiveness of *D. frontalis*-infested host material remained strong for several days during the initial attack phase, but ceased as gallery establishment progressed. The decline in pheromone content following feeding initiation (while field attractancy to infested material increased for up to 48 hours) is thought to be due to the capture of the pheromones in frass particles, thus slowing their rate of release (Coster and Vité 1972). Therefore, the general decline or disappearance of pheromones in feeding adult *D. frontalis* may be due to both a loss of the oxidation products by defecation (Hughes 1975) and/or a slowing or cessation of pheromone production.

In contrast to most other *Dendroctonus* species and particularly *D. frontalis*, in which pheromones generally decline after feeding, Hughes (1973) found that in *D. terebrans*, terpene oxidation products generally first appeared or increased following feeding on host material. This phenomenon is consistent with the report that *D. terebrans*, like *D. valens*, generally had little or no detectable oxidation products in its hindgut upon emergence (Hughes 1975). More recently, Phillips et al. (1989) reported the appearance of *trans*-verbenol, *cis*-verbenol, verbenone, myrtenol, myrtenal, and *trans*-pinocarveol in *D. terebrans* after feeding. As previously discussed herein, *D. terebrans* clearly possesses the appropriate metabolic pathway for terpene oxidation. Therefore, the apparent absence or near absence of terpene oxidation products in emergent *D. terebrans* adults may be due in part to factors relating to terpene exposure and uptake. *Dendroctonus terebrans* oxidation products may be released upon defecation, as they are in *D. frontalis*. The rate of terpene oxidation in feeding *D. terebrans* would therefore increase to a level that exceeds that of newly emerged adults and that exceeds oxidation product loss via defecation.

In sharp contrast to *Dendroctonus* species in general, feeding clearly triggers and sustains the generation of pheromones in the *Ips* species. However, it should be noted that Hughes (1974) demonstrated that the mean pheromone content in individuals of all three *Ips* species significantly diminishes within 48 hours after feeding. Thus, pheromone production either progressed at a slower rate than did pheromone volatilization or ceased entirely within 48 hours after feeding. However, Hughes (1974) also reported that exposure to myrcene vapors 48 hours following feeding significantly slowed the decline in pheromone content by maintaining some level of pheromone production in *I. calligraphus* and *I. grandicollis*, while in *I. avulsus* pheromone content actually increased. Therefore, all three *Ips* species possess the biological framework for producing their respective pheromones via the two distinct biosynthetic pathways described above. However, while both pathways are independently functional in *I. avulsus*, the pathway that utilizes vaporous precursors in *I. calligraphus* and *I. grandicollis* becomes operational only after ingestion. Neither the precise source of the stimulus nor the stimulus associated with this phenomen on itself is known, but the stimulus is certainly associated with feeding in these two species.

In support of this conclusion, Hughes (1974) showed that topical application of fed male *I. grandicollis* with ipsdienol significantly enhanced ipsenol biosynthesis compared to that of untreated fed males. More important, however, similarly treated unfed male *I. grandicollis* did not show this ability to reduce ipsdienol to ipsenol. Thus, again, pheromone biosynthesis in *I. grandicollis* is clearly associated with ingestion.

In an interesting study, Vité et al. (1972) demonstrated that *I. calligraphus* males produce large amounts of *trans*-verbenol and little ipsdienol upon encountering resin in the lower trunk of longleaf pine, *Pinus palustris* Mill. Male beetles found in the most attractive portion of the crown bole contain large amounts of both the verbenols and ipsdienol. Transfer of these beetles from the crown bole to the resinous lower bole of the same host tree resulted, within a few hours, in the cessation of ipsdienol production and continual production of large amounts of *trans*-verbenol. By comparison, males found in the thin phloem of branches produced only traces of the verbenols and very little ipsdienol. No explanation was provided for this most interesting phenomenon.

Effects of Mating Upon Pheromone Production:

Tsao and Yu (1967) found, in laboratory bioassays of *D. frontalis* pheromones, that extracts of mated females were only slightly less attractive than those of virgin females. However, Coster (1970b) reported in GLC studies of female *D. frontalis* hindguts that virgin females contained 4.1 and 1.9 times as much frontalin and *trans*-verbenol, respectively, as re-emerged beetles. Likewise, live feeding virgin female *D. frontalis* were 4.5 times more attractive than live feeding re-emergent females. Coster and Vité (1972) later reported that hindguts of feeding virgin female *D. frontalis* contained 2.8 - 3.5 and 1.4 - 3.4 times as much frontalin and *trans*-verbenol, respectively, as feeding mated females. Coster (1970b) also reported that while pheromone content of female *D. frontalis* declines to a low level following mating, gallery construction, and egg deposition, females are again capable of producing significant attraction upon re-emergence. Thus, mating and these subsequent reproductive activities apparently do not irreversibly inhibit pheromone production in female *D. frontalis*.

Since a second mating is not required by re-emerged *D. frontalis* females for deposition of viable eggs (Tsao and Yu 1967), production of a sex pheromone by such females would appear to be superfluous (Coster 1970b). But, because mass attack of a host is essential for overcoming its oleoresin resistance mechanism, aggregation obviously has a high survival value for *D. frontalis*. Therefore, the evolutionary value of the pheromone as an aggregation pheromone is at least as important as its value as a sex pheromone. Coster (1970b) suggested that sexual behavior in the aggregations may have, in fact, been a secondary development. However, Raffa et al (1993) present a convincing argument that scolytid pheromones may have evolved in the sexual context of courtship and male-male competition, and were elaborated further into cooperative attack messages in tree killing species where both senders and responders benefit.

In reference to the *Ips* species, Vité et al. (1972) reported that in the presence of a single female or no female, *I. calligraphus* males produce increasing amounts of ipsdienol for a few days, which then declines as the beetles age. However, when joined by three or more females, *I. calligraphus* males cease to synthesize ipsdienol. Therefore, although the data are quite limited, decline of pheromone production after mating is one example of the commonality among species of these two genera.

Hormonal Effects on Pheromone Biosynthesis:

There have been few investigations of the involvement of the endocrine system in pheromone biosynthesis for the southern pine beetle guild species. As previously discussed herein, Hughes (1975) found that *trans*-verbenol and verbenone are synthesized from *alpha*-pinene contacted by *D. frontalis* during the immature stage. And since these compounds are not present in pupal *D. frontalis*, but appear in callow adults prior to emergence, synthesis of these compounds must be under some form of control that delays their production until adult beetles are ready to emerge. Although external stimuli may be involved, it is quite likely that a hormonal system plays a significant role in regulating production of these pheromones.

Hughes (1973), in his discussion of pheromone production, suggested that pheromones that are produced primarily during feeding and are unaffected by simple oleoresin exposure, are under neural and/or hormonal control, and that pheromones whose production is both inversely related to feeding and greatly increased by oleoresin exposure are apparently not under neural or hormonal control. Confirmation of this hypothesis was not provided. It would seem that production of both pheromone types would require some form of hormonal involvement.

Finally, Bridges (1982), working with *D. frontalis* teneral adults, demonstrated that topical application with JH-II significantly increased levels of *trans*-verbenol in one-day-old male and female adults and of *endo*-brevicomin in five-day-old male adults. Bridges (1982) also evaluated the effects of methoprene, a juvenile hormone-like compound, on pheromone titres in one- and five-day-old teneral adults. He showed that *endo*-brevicomin increased in one- and five-day old *D. frontalis* adults, while *trans*-verbenol increased and decreased in one-day old and five-day old adults, respectively. These results suggest that not only does a hormone influence pheromone production, but that interactions among several physiological systems effect a degree of regulation over pheromone production.

Role of Microorganisms in Pheromone Production:

White et al. (1980), citing Brand et al. (1975, 1976, 1977), reported that both fungi and bacteria associated with certain bark beetles, including *D. frontalis*, contribute to pheromone production. Furthermore, yeast symbionts of *D. frontalis* produce, in vitro, a variety of alcohols and acetates that may enhance beetle response to known pheromone mixtures. Borden (1982) suggested that there are two systems involved in pheromone production: one an independent microorganism system and the other a hormonally-controlled beetle system. See Hunt and Borden (1989) and Vanderwel and Oehlschlager (1987) for recent reviews on the microbial role of pheromone production for other bark beetle species.

CHEMORECEPTION

The antennae of bark beetles have been shown to be the primary location of sensilla involved in the olfactory reception of behavior-releasing substances (Borden and Wood 1966; Payne 1970; Dickens and Payne 1978a; Smith et al. 1988). More specifically, the distal portion of antennae, the club, is composed of three or four fused segments and is the primary structure in pheromone and host odor reception.

Structure and function of the sensilla on the antennal club have been investigated to varying degrees among the five bark beetle species reported herein, but certainly most thoroughly in *D. frontalis*. Dickens (1979) briefly reviewed electrophysiological studies of olfactory perception of pheromones and host odors by bark beetles, including *D. frontalis*. Payne (1979) more thoroughly reviewed pheromone and host odor perception in bark beetles at both the electrophysiological and behavioral levels.

Chemoreceptor Morphology:

Both genera (*Dendroctonus* and *Ips*) have antennal clubs, but with distinctly different shapes and unique arrangements of sensilla (Payne et al. 1973). In both *Dendroctonus* species the antennae consist of seven segments each. The club is nearly round, and flattened on the anterior and posterior surfaces. Most sensilla are located on the distal 2/3 of the club on all surfaces. *D. terebrans* has two complete sensory bands and a near-complete third sensory band at the distal region of the club. *D. frontalis*, however, does not have a near complete third sensory band.

The antennae of the three *Ips* species are also seven segmented. However, unlike the *Dendroctonus* species, the antennal club is more oval in shape, proximal to distal, than rounded, and slightly convex on the anterior surface. The sensilla on the club occur primarily on the anterior surface, with a few occurring sporadically on the posterior surface. Most sensilla found on the anterior surface are located on the most distal 3/4 of the club, and are arranged in three serpentine-shaped sensory fields. These sensory fields do not encircle the antennal club, but extend only to the margins of the anterior surface.

Six morphologically different antennal sensilla are found on all five bark beetle species (Payne et al., 1973). Sensilla types, ranges in sensilla size, suggested sensilla functions, and a brief description of each type are shown for each species in Appendix 6. Later, Dickens and Payne (1978a) described the structure and function of the sensilla on the antennal club of *D. frontalis* (Appendix 7). For a more thorough review of the external and internal morphology of the antennae of bark beetles refer to Payne (1979) and the references cited therein.

Chemoreceptor Electrophysiology:

Payne (1971) presented the first report of the successful application of electrophysiological techniques to record electroantennograms (EAGs) from scolytids, in particular *D. frontalis*. Since that time, EAG analysis of *D. frontalis* (Payne 1970, 1971, 1974; Dickens and Payne 1977; Payne et al. 1982), *D. terebrans* (Payne et al. 1987; Delorme and Payne 1990), *I. calligraphus* (Smith et al. 1988), *I. avulsus* (Smith et al. 1988) and *I. grandicollis* (Smith et al. 1988) have been reported. Summaries of these analyses are shown in Appendices 8 - 10.

D. frontalis: Payne (1975) reported the intensity of EAG response was greater to higher concentrations of pheromones (*exo*-brevicomin and frontalin) than to the terpene hydrocarbons (3-carene and *alpha*-pinene), and suggested that more receptors[1] are present on the antennae of *D. frontalis* for pheromones than for terpene hydrocarbons (Appendix 8). Payne (1975) also demonstrated via adaptation experiments that frontalin and *exo*-brevicomin share the same receptors on the antennae of *D. frontalis*, which are distinct receptors from those specific for the terpene hydrocarbons, *alpha*-pinene and 3-carene. Furthermore, terpene hydrocarbons share some, but not all, of the same receptors.

Payne and Dickens (1976) and Dickens and Payne (1977), utilizing both EAG and single cell recording (SCR) analyses, reported that frontalin blocks response of receptors to all other compounds tested, including *endo*- and *exo*-brevicomin, verbenone, *trans*-verbenol, *alpha*-pinene and 3-carene, in both male and female *D. frontalis*. Therefore, all *D. frontalis* receptors can be occupied by frontalin. However, these six compounds do not interact with all frontalin receptors, and Smith and Payne (unpublished), utilizing SCR analyses, have shown that not all receptors of *D. frontalis* can be occupied by frontalin.

Dickens and Payne (1977) further demonstrated that the oxygen-containing compounds interacted with a larger percentage of the receptors of *D. frontalis* than did the hydrocarbon host terpenes. Among the bicyclic ketals tested, the percent interaction with the pheromone receptors followed the order frontalin > *endo*-brevicomin>>*exo*-brevicomin for both male and

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[1] The term receptor represents an olfactory cell. References dated after 1975 use the term acceptor which was defined by Kaissling (1969) as the site on the receptor where the odorant binds. In this paper, only the term receptor is used to avoid confusion.

female beetles. Furthermore, while *endo*-brevicomin blocked response to *exo*-brevicomin, *exo*-brevicomin did not block response to *endo*-brevicomin.

In regard to chiral receptors, Dickens and Payne (1977) first demonstrated a phenomenon similar to the one described above for the (+)- and (-)- enantiomers of *exo*-brevicomin. Although their data were limited, they reported that the latency period before response of single units to the (-)- enantiomer was shorter than that required for the (+)- enantiomer. Payne et al. (1982) reported SCR analyses that showed that both (+)- frontalin and (-)- frontalin elicit response from the same olfactory cell. However, spike frequency elicited by (-)- frontalin was consistently greater than that elicited by (+)- frontalin, and response to (-)- frontalin adapted within 300-400 msec, while a prolonged tonic response was elicited by (+)- frontalin. Based upon EAG adaptation studies, they also demonstrated the presence of some receptors specific for the (+)- and (-)- frontalin enantiomers. Furthermore, based upon response intentsity, EAGs indicated the presence of significantly more receptors for (-)- frontalin than for (+)- frontalin. Thus, Payne et al. (1982) showed that frontalin enantiomers can elicit response from common receptor cells as well as from chiral-specific cells.

Payne et al. (1988) recorded EAG responses to frontalin analogs in order to gain insight into the structural activity relationships of frontalin. They reported that EAG response to frontalin was significantly greater than response to its analogs and that both the number and position of the methyl groups appear to be critical in the structural activity of frontalin.

Payne (1974) also recorded muscle potentials from EAG preparations of *D. frontalis* in response to frontalin, *exo*-brevicomin, *alpha*-pinene, and 3-carene. Muscle potential activity was considerably greater in response to pheromone stimulation than to stimulation by the host terpenes. Subsequently, Dickens and Payne (1978b) investigated these muscle potentials and demonstrated that frontalin-induced potentials in *D. frontalis* (male and female) could be reduced by verbenone or *trans*-verbenol stimulation.

The broad area of receptor specificity, particularly as it relates to compounds sharing common receptors, is unresolved. Adequate specificity and sensitivity data have yet to be developed on receptor response to all the key insect- and host-produced compounds shown to have behavioral significance within the chemical ecology of *D. frontalis*. Smith and Payne (in preparation), utilizing SCR to analyze receptor response to biologically relevant dosages of behavioral chemical stimuli, should begin to provide answers to these basic questions.

D. terebrans: Payne et al. (1987) investigated, to a limited extent, the antennal olfactory responsiveness of *D. terebrans* to frontalin, *trans*-verbenol, *endo*-brevicomin, and turpentine (Appendix 9). Male and female *D.*

terebrans were clearly more responsive to frontalin and *endo*-brevicomin than to *trans*-verbenol and *alpha*-pinene. Delorme and Payne (1990) subsequently investigated the ability of male and female *D. terebrans* to detect *endo*-brevicomin, frontalin, ipsenol, ipsdienol, *alpha*-pinene, *beta*-pinene, verbenone, *trans*-verbenol, and turpentine. Response thresholds were lowest for *endo*-brevicomin.

Ips species: Smith et al. (1988) reported EAG analysis of *I. avulsus, I calligraphus*, and *I. grandicollis* responsiveness to their pheromones, selected *D. frontalis* pheromones, and host odors (Appendix 10). They verified the presence, in both sexes of each species, of antennal olfactory receptors capable of detecting ipsdienol, ipsenol, *cis*- and *trans*-verbenol, *endo*-brevicomin, *alpha*-pinene, frontalin and verbenone. Using SCR analysis on *I. grandicollis*, Ascoli-Christensen et al. (1993) determined that when compared with males, females had a greater percentage of cells responsive to primary pheromones of *D. frontalis*, frontalin and *trans*-verbenol, and of *Ips* spp., ipsdienol and ipsenol. Among females, more cells responded to *trans*-verbenol and *Ips* -produced volatiles than to host or other *D. frontalis*-produced compounds. Olfactory cells of males responded mostly to *cis*-verbenol, followed by *alpha*-pinene, verbenone, *trans*-verbenol, and *endo*-brevicomin. Of those cells responsive primarily to one compound, the greatest percentage were responsive to *trans*-verbenol in females and to verbenone in males.

In conclusion, electrophysiological analysis of the peripheral receptor systems in these five bark beetle species is clearly not complete. However, it is apparent that the versatility of the receptor system in *D. frontalis* is probably due in part to the apparent lack of "labelled lines" for behaviorally significant chemicals, with the possible exception of frontalin. Overlapping receptor specificities may provide the insect with the genetic plasticity necessary to code both qualitative and quantitative information for several behaviorally significant odors that might permeate the insect's environment. Thus, compounds that attract or arrest, enhance attraction, or inhibit attraction may be perceived by the same neuron and acceptor.

SEMIOCHEMICAL-MEDIATED BEHAVIOR

In conducting bioassays to ascertain beetle response patterns to behavioral chemicals, researchers have utilized a number of methods, particularly for stimulus presentation. In the most common laboratory bioassay, the pedestrian bioassay, walking behavior is generally observed in response to behavioral chemicals of known concentration and purity or to extracts of beetle-produced frass or body parts. In field tests, the number of beetles caught in baited traps is generally utilized as a measure of chemically-mediated attraction and/or arrestment. The most common methods for presenting the chemical stimuli include elution of natural pheromonal/kairomonal mixtures from beetle-infested pine bolts, elution of chemical stimuli from crushed beetles or beetle body parts, and elution of the behavioral chemicals from various devices.

Each method has limitations in its ability to accurately stimulate the context in which the beetles naturally encounter the stimuli, whether the stimuli be chemical and/or visual. The limitations may be in the form of the lack of the entire bouquet of insect- and host-produced chemical stimuli, lack of the proper ratio and/or elution rates of chemical stimuli, lack of the proper visual cues, or any combination of these. Therefore, analysis and interpretation of results are presented here within the context of the methods utilized.

Behavioral Analysis of *Dendroctonus frontalis*

Response to Beetle-Produced Frass and Body Parts, and to Pheromones Under Controlled Laboratory Conditions:

Behavior of *D. frontalis* has been investigated to a limited extent in laboratory bioassays (Appendices 11 and 12). Tsao and Yu (1967) first measured attractancy and repellency of *D. frontalis* to *D. frontalis*-produced frass (boring dust and fecal material) and crushed body parts. Although male and female *D. frontalis* were each attracted to both male and female *D. frontalis* frass, each sex was more attracted to its conspecific's frass than to its own frass. A small percentage of each sex was in fact repelled by its own frass. When female frass extract was assayed, both sexes displayed an attractive response, although more so in male than in female beetles.

Tsao and Yu (1967) also reported that both anterior (head and prothorax) and posterior (mesothorax, metathorax, and abdomen) body regions of male and female *D. frontalis* were attractive to both sexes. However, the posterior body region of male and female beetles repelled some male and female beetles, and some female beetles, respectively. Bioassay of extracts of the two body regions showed, most notably, that male beetles were highly attracted to extracts of the posterior body region of female beetles. However, both sexes were strongly repelled by extracts of the posterior body region of male beetles. Tsao and Yu (1967) concluded that there are at least two pheromones in *D. frontalis*, a male-attracting pheromone in the female, and a male- and female-repelling pheromone in both sexes, but most notably in male beetles. These results also provide supportive evidence in regard to the site of pheromone production previously discussed herein.

Subsequently, Rudinsky (1973) and Rudinsky et al. (1974) measured arrestment as an indication of attraction. Most notably, both verbenone and myrtenol appeared to be multifunctional. Low concentrations of either compound, as found in female *D. frontalis*, enhanced *D. frontalis* attraction to mixtures of frontalin, *trans*-verbenol and *alpha*-pinene, and frontalin, *trans*-verbenol and turpentine (Rudinsky 1973, Rudinsky et al. 1974; McCarty et al. 1980). Conversely, high concentrations of either compound, as found in male *D. frontalis*, reduced *D. frontalis* attraction to the same attractive mixtures. Furthermore, male beetles responded to intermediate concentrations of verbenone by performing the "rivalry" stridulation and fighting, rather than by the typical stridulation evoked by the female attractants (Rudinsky 1973). Higher verbenone concentrations (0.01%) elicited considerable "rivalry" stridulation (Rudinsky et al. 1974). Multifunctional pheromones may allow economy in the insect receptor system without sacrificing behavioral diversity (Blum 1970).

Rudinsky et al. (1974) also reported that *endo*-brevicomin, regardless of concentration, significantly reduced male beetle arrestment or attraction elicited by a mixture of frontalin, *trans*-verbenol, and *alpha*-pinene. *Endo*-brevicomin also evoked considerable "rivalry" stridulation. These three "rivalry" or "antiaggregation" pheromones (verbenone, myrtenol and *endo*-brevicomin) appear to affect intra-sex male response and may be important in terminating aggregation. Rudinsky et al. (1974) suggested that, to be effective, it is essential that an "antiaggregative" pheromone be released and act rapidly during mass attack, as overcrowding would result if such a pheromone was released more slowly and less flexibly than are the attractant pheromones.

Payne et al. (1982) later demonstrated that male *D. frontalis* were significantly more attracted to treatments containing (-)- frontalin than to treatments containing only (+)- frontalin. Finally, Payne et al. (1988), investigating *D. frontalis* behavioral response to frontalin analogs in a pedestrian bioassay, demonstrated significantly greater response to frontalin than to any of the frontalin analogs. However, lack of significant difference in response among the frontalin analogs indicated that the position and number of methyl groups are not critical to the walking response in the laboratory bioassay, yet are critical to EAG's (see p. 20).

Response to Beetle-Infested Pine Under Natural Field Conditions :

Behavioral responses of *D. frontalis* to beetle-infested pine clearly demonstrate *D. frontalis* attraction to female *D. frontalis*-infested bolts, while *D. frontalis* are apparently not attracted to male *D. frontalis*-infested bolts (Appendix 13). These results certainly support the concept that it is the female of the species that produces and releases the aggregation pheromone. Attraction of both sexes of *D. frontalis* to female-infested bolts may be explained primarily by the attraction of male beetles to female-produced pheromones, and of both male and female beetles to host odors. It should be noted that *D. frontalis* attraction to female *D. frontalis*-infested bolts was not affected by the addition of male *D. frontalis* (Svihra 1982). It should also be noted that Gara et al. (1965) reported that *D. frontalis* was more attracted to beetle-infested bolts wired to vertical trees than to those wired to horizontal trees. These results are supportive of the conceptual model proposed by Payne and Coulson (1985), which describes the role of visual and olfactory stimuli in host selection and aggregation behavior by *D. frontalis*.

Studies reported to date provide no evidence of *D. frontalis* attraction to bolts infested with only *I calligraphus*, *I. avulsus*, or *I. grandicollis*. In fact, male *I. grandicollis*-infested bolts tend to significantly reduce *D. frontalis* attraction to *D. frontalis*-infested bolts (Svihra et al. 1980). No explanation has been provided for this phenomenon.

Response to Crushed Bodies of *Dendroctonus* Species Under Natural Field Conditions :

Analyses of *D. frontalis* behavioral response under natural field conditions to the crushed bodies of *D. frontalis*, *D. brevicomis* and *D. pseudotsugae* has been limited to but four published studies (Vité and Renwick 1968; Renwick and Vité 1968; Pitman et al. 1969; Kinzer et al. 1969) (Appendix 14). It is apparent from these studies that *D. frontalis* contains compounds which, when concentrated, elicit an attractive and/or arresting response in *D. frontalis*. More specifically, active compounds are concentrated in the hindgut and malpighian tubules of female *D. frontalis*. In addition, both *D. brevicomis* and *D. pseudotsugae* contain compounds that attract *D. frontalis*. Male and female *D. brevicomis* are known to produce frontalin and verbenone, and *exo*-brevicomin, *trans*-verbenol and myrcene, respectively (Bordon 1985). Female *D. pseudotsugae* produce frontalin, *trans*-verbenol, verbenone, seudenol, *trans*-pentenol and 3,2-MCH (3-methylcyclohex-2-en-1-one); males produce 3,2-MCH, 3,3-MCH and methylheptenone (Borden 1985). Therefore, given the fact that both male *D. brevicomis* and female *D. pseudotsugae* produce frontalin, it is not surprising to find that both elicit an attractive response from *D. frontalis*.

Response to Pheromones Under Natural Field Conditions:

Behavioral response of *D. frontalis* to behavioral chemicals has been researched extensively under natural field conditions. As a whole, it has been very difficult to directly compare data from the large number of studies, due in part to the varying environmental conditions, *D. frontalis* population characteristics, tree and forest characteristics, and experimental methods. However, these data have been compiled into a single table (Appendix 15) so that meaningful generalizations may be made with regard to the function of specific behavioral chemicals within the chemical ecology of *D. frontalis*.

Dendroctonus frontalis were neither attracted to nor arrested on traps baited with any of the behavioral chemicals tested individually, including frontalin, *trans*-verbenol, turpentine, *endo*-brevicomin, *exo*-brevicomin, verbenone, oleoresin, or *Ips* pheromone paste. *D. frontalis* was generally attracted to frontalin alone, but in low numbers. However, what little attractancy *D. frontalis* displayed may have resulted from the simultaneous presence of host volatiles in the air in the test areas (Payne et al. 1978; Billings 1985). More specifically with regard to frontalin, Payne et al. (1982) demonstrated that significantly greater numbers of *D. frontalis* were attracted to treatments containing (-)- frontalin than to treatments in which (-)-frontalin was absent. Release rates of 10-100 mg/h appeared to maximize *D. frontalis* attractancy (Vité 1971).

Although both enhanced frontalin attractiveness to *D. frontalis*, *alpha*-pinene enhanced attractancy of frontalin more than did *trans*-verbenol (Renwick and Vité 1970). In combination with frontalin plus *trans*-verbenol, *alpha*-pinene was significantly more attractive to *D. frontalis* than were the other host terpenes tested (Renwick and Vité 1969).

Endo-brevicomin, *exo*-brevicomin, and verbenone generally reduced *D. frontalis* attractancy to attractive compounds or compound mixtures. Although both reduced attraction of *D. frontalis* to frontalin plus *alpha*-pinene (Vité and Renwick 1971a; Payne et al. 1978), *endo*-brevicomin reduced attraction more than did *exo*-brevicomin (Vité and Renwick 1971a). In addition, Payne et al. (1978) reported that *exo*-brevicomin had no effect on the attractancy of frontalin plus turpentine, with or without the addition of *trans*-verbenol. However, *endo*-brevicomin did reduce the attractancy of frontalin plus turpentine, with or without the addition of *trans*-verbenol. More specifically, (-)- *endo*-brevicomin significantly reduced *D. frontalis* attractancy to frontalure plus turpentine-baited traps to the level of attractancy of turpentine alone (Vité et al. 1985). It should also be noted that the reducing effect of *endo*-brevicomin on *D. frontalis* attractancy to frontalin plus turpentine, with or without *trans*-verbenol, was not affected by the addition of *exo*-brevicomin. Finally, *endo*- plus *exo*-brevicomin (50:50), at a release rate of 600 mg/ha/24 h, significantly reduced both male and female *D. frontalis* landings on traps placed on host trees on an area-wide basis in a natural infestation (Payne et al. 1977).

Verbenone, at a release rate of 0.5 mg/h, reduced *D. frontalis* attraction to the combination of frontalin, *alpha*-pinene, and *trans*-verbenol (Renwick and Vité 1969). At 5 and 10 mg/h, verbenone reduced *D. frontalis* attraction to frontalin plus *alpha*-pinene, and to frontalin plus turpentine (Payne et al. 1978). However, lower verbenone release rates of 0.5 mg/h and 2.5 mg/h each had no effect on *D. frontalis* attractancy to frontalin plus *alpha*-pinene or frontalin plus turpentine (Payne et al. 1978a). Renwick and Vité (1969) also showed that verbenone released at 0.5 mg/h had no effect on *D. frontalis* attraction to frontalin alone. Although release rates were not specified, small quantities of verbenone reduced male *D. frontalis* attraction to frontalin, while higher quantities reduced attractancy of both males and females (Renwick and Vité 1970). Therefore, the behavioral effects of verbenone on *D. frontalis* attraction to other attractive compounds are release-rate dependent. An exception to these results found that verbenone, released at 10 mg/h, had no effect on *D. frontalis* attractancy to frontalin plus *alpha*-pinene (Payne et al. 1978). No explanation was provided for these mixed results. In the only investigation of its kind, Salom et al. (1992) evaluated the effects of different enantiomeric ratios and elution rates of verbenone on the numerical response of *D. frontalis* to frontalin plus turpentine-baited Lindgren funnel traps (Lindgren 1983). They reported that the greatest reduction in *D. frontalis* catch occurred with verbenone baits containing 34 - 50% (+) enantiomer, at a release rate of 2.9 mg/h. Evaluation of release rates using vebenone 34%(+):66%(-) showed that a reduction in male *D. frontalis* catch decreased continuously between 4.2 to 12.5 mg/h. No response to release rates was observed for females.

Richerson and Payne (1979) demonstrated that mixtures of *endo-* and *exo*-brevicomin, with and without verbenone, significantly reduced the number of *D. frontalis* landing on host trees, and also greatly reduced the estimated *D. frontalis* oviposition by significantly reducing *D. frontalis* gallery density. Verbenone alone, however, failed to reduce either *D. frontalis* landings on host trees or gallery density, but it generally resulted in an increase in the estimated oviposition. This failure of verbenone to reduce *D. frontalis* landings on host trees may be due to the low elution rate of 80 mg/24 h/tree. Watterson et al. (1982) subsequently demonstrated that a 1:1 mixture of 85:15 *endo- :exo*-brevicomin and verbenone (eluted at 160 and 80 mg/24 h/tree, respectively) significantly reduced *D. frontalis* re-emergence, gallery density, and brood emergence. It should be noted that in both studies, while *D. frontalis* landings, re-emergence, emergence, and gallery density decreased on the brevicomin isomers plus verbenone treated trees, evaluation of the same population characteristics for *I. avulsus* showed a significant increase. Therefore, it was not possible to determine conclusively if the reduction in *D. frontalis* population characteristics was due strictly to the effects of the applied behavioral chemicals, or was due in part to interspecific competition with *I. avulsus*. Payne and Richerson (1985) subsequently reviewed the data by Richerson and Payne (1979) and Watterson et al. (1982). They concluded that the brevicomin isomers plus verbenone may have potential for use in suppressing *D. frontalis* infestations by facilitating replacement of the more aggressive species (*D. frontalis*) by a less aggressive species (i.e., *I. avulsus*). Their conclusion remains to be verified.

Although *endo*-brevicomin, *exo*-brevicomin, and verbenone generally reduced *D. frontalis* attraction to compounds or compound mixtures, these three behavioral chemicals appear to be multifunctional. In contrast to their reducing effects on *D. frontalis* attractancy, Billings (1985) demonstrated that *endo*-brevicomin plus verbenone, at low release rates, significantly enhanced *D. frontalis* attractancy to frontalure (a 1:2 mixture of frontalin plus *alpha*-pinene). However, although both enhanced *D. frontalis* attractancy to frontalure, turpentine enhanced attractancy significantly more than did the *endo*-brevicomin plus verbenone mixture. Vité et al. (1985) also reported that while both (±)- *endo*-brevicomin and (+)- *endo*-brevicomin significantly enhanced *D. frontalis* attractancy to frontalure plus turpentine, (+)- *endo*-brevicomin enhancement was significantly greater than that of (±)- *endo*-brevicomin. The addition of (-)- *endo*-brevicomin to (+)- *endo*-brevicomin, in fact, significantly reduced the (+)- *endo*-brevicomin enhancement of *D. frontalis* attractancy.

The nature of this multifunctionality of these behavioral chemicals appears to be dependent on release-rate and enantiomeric ratio. These results are also supported, at least for verbenone, by laboratory bioassays discussed previously in this review (Rudinsky 1973; Rudinsky et al. 1974; McCarty 1980).

Behavioral Analyses of *Dendroctonus terebrans*

Response to Pheromones Under Controlled Laboratory Conditions :

Analysis of *D. terebrans* behavior in laboratory bioassays is limited to a single study by Payne et al. (1987) (Appendix 16). They reported that both male and female beetles were significantly attracted to frontalin and *endo*-brevicomin, while only males were significantly attracted to *trans*-verbenol and turpentine. Male and female beetles were significantly more attracted to frontalin and *endo*-brevicomin, respectively, than to the other compounds tested. They also reported that male beetles were significantly more attracted to frontalin and turpentine, individually, than were female beetles.

Response to Beetle-Infested Pine Under Natural Field Conditions:

Analysis of *D. terebrans* behavioral responsiveness to host material under natural field conditions is limited to but a few studies (Appendix 17). *Dendroctonus terebrans* was reported to kill healthy pine trees (*Pinus* spp.) that are mechanically injured, as well as those trees that are stressed or severely weakened (Kowal and Coyne, 1951; Smith and Lee, 1957; Merkel, 1981). Smith (1963) first reported that *D. terebrans* are attracted to *D. terebrans*-infested trees. Godbee and Franklin (1976) later demonstrated *D. terebrans* attraction, females more than males, to unattacked bolts and trees, thus indicating that female beetles may be the host-finding, gallery-initiating sex. Phillips et al. (1989) have recently reported *D. terebrans* attraction to mechanically injured and paraquat-treated trees, suggesting that host odors emanating from stressed trees may function in primary attraction of this host-finding sex.

Godbee and Franklin (1976) also demonstrated *D. terebrans* attraction (males more than females) to male only, female only, and male and female *D. terebrans*-infested bolts. Bolts infested with only males or only females were, in fact, significantly more attractive than were male- and female-infested bolts and unattacked bolts. Phillips et al. (1989) reported that although female *D. terebrans* were not significantly attracted to male only, female only, or male and female *D. terebrans*-infested bolts, male *D. terebrans* were significantly attracted to female only and to male- and female-infested bolts. These data from both studies clearly indicate that female *D. terebrans* adults produce secondary attractants and that males are the responding sex.

Vité et al. (1964) reported some slight attraction of *D. terebrans* to *D. frontalis*-infested bolts. However, *D. terebrans* were not attracted to *I. avulsus*-, *I. calligraphus*-, or *I. grandicollis*-infested bolts.

Response to Pheromones Under Natural Field Conditions :

Hopkins (1909) reported turpentine to be a potent attractant for *D. terebrans*. Fatzinger (1985) reported that ethanol, which is produced by stressed or cut conifers, significantly enhanced attraction of *D. terebrans* to turpentine-baited traps (Appendix 18). Siegfried et al. (1986) reported that individual monoterpene constituents of gum turpentine, in ethanol, did not elicit an attractive response in *D. terebrans*. Although a mixture of these monoterpenes did attract *D. terebrans*, response was less than that to whole gum turpentine plus ethanol. Therefore, the monoterpenes within the mixture were only partially responsible for the attractiveness of whole gum turpentine. Other constituents of gum turpentine include *alpha*-phellandrene, sesquiterpenes, and non-terpene compounds (Mirov 1961). Some evidence indicates that *D. terebrans* is actually attracted to certain terpenoid oxidation products rather than to the terpenes themselves (Krawielitzki et al. 1983).

Phillips et al. (1990), in an assay of *D. terebrans* response to turpentine and synthetic enantiomers of frontalin, *exo*-brevicomin and *endo*-brevicomin, found male *D. terebrans* attraction to turpentine was enhanced by the presence of (-)- frontalin more so than the presence of (+)- frontalin; was not enhanced by the presence of (+)-, (-)-, and (±)- *exo*-brevicomin; and was enhanced by the presence of (+)- *endo*-brevicomin, but not (-)- *endo*-brevicomin. Female *D. terebrans* attraction to turpentine was also enhanced by the presence of (-)- frontalin, yet not to (+)- frontalin. Attraction by female *D. terebrans* to turpentine was enhanced by the presence of (+)-, (-)-, and (±)- *exo*-brevicomin, as well as, (+)- *endo*-brevicomin, yet not (-)- *endo*-brevicomin.

Phillips et al. (1988) demonstrated that *D. terebrans* was more attracted to a turpentine:ethanol solution (1:1 mixture) than to undiluted turpentine or to turpentine and ethanol deployed in separate, but side by side, dispensers. Fatzinger et al. (1987) also reported that by the presence of both ethanol and ethanol-plus-*trans*-verbenol, male and female *D. terebrans* attraction to turpentine was enhanced. However, ethanol plus *trans*-verbenol enhancement of male and female attractancy was significantly greater than that for ethanol only when *trans*-verbenol was released at 50 ul/day and 50 ul/3-4 days, respectively.

Male and female *D. terebrans* were unresponsive to frontalin, frontalure, *trans*-verbenol, *endo*-brevicomin, *exo*-brevicomin, myrtenol, and verbenone when tested individually (Payne et al. 1987, Phillips et al. 1989). However, the elution of turpentine at high rates in combination with frontalin, frontalure, or *endo*-brevicomin rendered these compounds attractive to *D. terebrans* (Payne et al. 1987). In addition, although turpentine alone was attractive to primarily male *D. terebrans*, female and male attraction was enhanced significantly when *endo*-brevicomin and frontalure were added to the blend (Payne et al. 1987). While male *D. terebrans* were very attracted to frontalin plus turpentine, the addition of *endo*-brevicomin and/or *exo*-brevicomin or verbenone significantly reduced male beetle attraction. Phillips et al. (1989) subsequently proposed that the *D. terebrans* aggregation pheromone is composed of frontalin and *exo*-brevicomin, since both affect the behavior of males only.

Therefore, it is apparent that host-produced kairomones present in turpentine can, in concert, serve as primary attractants for *D. terebrans*. However, these kairomones do not appear to be the only semiochemicals involved in the host selection and colonization processes. Male *D. terebrans* appear also to aggregate in response to frontalin plus host odors. Finally, the brevicomins, both *endo-* and *exo-*, and verbenone clearly function to reduce male *D. terebrans* aggregation behavior.

Behavioral Analysis of *Ips calligraphus*

Response to Beetle-Infested Pine Under Natural Field Conditions:

Behavioral analysis of *I. calligraphus* to beetle-infested pine clearly demonstrates *I. calligraphus* attraction, particularly females to male *I. calligraphus*-infested bolts (Vité et al. 1964; Renwick and Vité 1972; Birch et al. 1980; Svihra et al. 1980; Svihra 1982) (Appendix 19). Female *I. calligraphus*-infested bolts elicited no attractive response from conspecifics (Vité et al. 1964), and in fact, reduced attractiveness of male *I. calligraphus* infested bolts (Svihra 1982). These results support the concept that males of this species produce and release the aggregation pheromone. It should be noted that *I. calligraphus* attraction to male *I. calligraphus*-infested bolts was significantly reduced by the presence of female *I. calligraphus* (Svihra 1982).

Ips calligraphus responses to bolts infested by the other cohabiting *Ips* and *Dendroctonus* species were quite variable and thus difficult to interpret (Vité et al. 1964; Birch et al. 1980; Svihra 1982). *I. grandicollis*-infested bolts either did not attract *I. calligraphus* or enhanced attractiveness of *I. calligraphus*-infested bolts to *I. calligraphus* during low *I. calligraphus* population levels (Birch et al. 1980). However, during high *I. calligraphus* population levels, *I. grandicollis*-infested bolts were either attractive to *I. calligraphus* or reduced *I. calligraphus* attraction to *I. calligraphus*-infested bolts (Birch et al. 1980).

Although *I. calligraphus* were attracted in low numbers to *I. avulsus*-infested bolts in one study, *I. avulsus*-infested bolts were generally not attractive or reduced attraction of *I. calligraphus* to *I. calligraphus*-infested bolts (Birch et al. 1980; Svihra 1982). *I. calligraphus* were also attracted to *I. paraconfusus*-infested bolts, a species known to produce ipsenol, ipsdienol, *cis*-verbenol, and 2-phenylethanol (Borden 1985). Furthermore, *I. calligraphus* were either not attracted to or were attracted to *D. frontalis*-infested bolts (Vité et al. 1964; Birch et al. 1980; Dixon and Payne 1980; Svihra 1982).

Response to Pheromones Under Natural Field Conditions:

Renwick and Vité (1972) demonstrated that ipsdienol plus *cis*-verbenol was much more attractive than ipsdienol plus *trans*-verbenol (Appendix 20). Additionally, they reported that while *I. calligraphus* male (40 males)-infested bolts were significantly more attractive than ipsdienol plus *cis*-verbenol, the former was equally as attractive as a combination of ipsdienol, *cis*-verbenol, and uninfested pine bolts. Vité et al. (1976b) later reported that the inactive enantiomer of *cis*-verbenol, (*R*)-*cis*-verbenol, appeared to require a higher saturation level at the receptor sites than did (*S*)-*cis*-verbenol, in order to reduce the attractiveness of ipsdienol plus (*S*)-*cis*-verbenol. Vité et al. (1978) subsequently demonstrated that (*R*)-(-)-ipsdienol is the active isomer of ipsdienol, as is the case for *I. avulsus*. Therefore, the olfactory guidance of mass aggregation of *I. calligraphus* depends on a combination of (*R*)-(-)-ipsdienol, (*S*)-*cis*-verbenol, and host odors.

Behavioral Analysis of *Ips avulsus*

Response to Beetle-Infested Pine Under Natural Field Conditions:

Behavioral analysis of *I. avulsus* to beetle-infested pine clearly demonstrates *I. avulsus* attraction to male *I. avulsus*-infested bolts (Vité et al. 1964; Birch et al. 1980; Svihra et al. 1980; Svihra 1982) (Appendix 21). These results support the concept that males of this species produce and release the aggregation pheromone. ISurprisingly, *I. avulsus* attraction to male *I. avulsus*-infested bolts was not affected by the addition of female *I. avulsus* (Svihra 1982).

Ips avulsus were highly attracted to *I. calligraphus*-infested bolts (Vité et al. 1964; Birch et al. 1980; Svihra et al. 1980; Svihra 1982). These results support the findings that *I. avulsus* utilizes (*R*)-(-)- ipsdienol, also a pheromone of *I. calligraphus*, as a pheromone during aggregation. However, both bolts infested with either female *D. frontalis* (Birch et al. 1980) or female *I. calligraphus* (Svihra et al. 1980) reduced *I. avulsus* attraction to male *I. calligraphus*-infested bolts.

Although *I. avulsus* displayed little or no attraction to *I. grandicollis*-infested bolts, *I. grandicollis*-infested bolts certainly enhanced *I. avulsus* attraction to both male *I. avulsus*-infested bolts, and male *I. calligraphus*-infested bolts (Birch et al. 1980; Svihra 1982) These results support the findings that *I. avulsus* may utilize (*S*)-(-)- ipsenol, a pheromone of *I. grandicollis*, as a kairomone during aggregation. Finally, although *I. avulsus* behavioral responses to female *D. frontalis*-infested bolts were mixed, *I. avulsus* were generally attracted to *D. frontalis*-infested bolts (Vité et al. 1964; Svihra et al. 1980).

Response to Pheromones Under Natural Field Conditions:

Renwick and Vité (1972) noted that synthetic mixtures containing ipsdienol were slightly attractive to *I. avulsus*. (Appendix 22). Vité et al. (1978) subsequently demonstrated that (*R*)-(-)- ipsdienol is the active isomer of ipsdienol, as is the case for *I. calligraphus*. Hedden et al. (1976) reported that *I. avulsus* are attracted to (*S*)-(-)- ipsenol, the same isomer utilized by *I. grandicollis* for aggregation. This response may represent the evolution of secondary attraction to a cohabiting sympatric species. It should be noted that *I. avulsus* males were generally more responsive to the pheromones and pheromone mixtures than were females. This responsiveness is particularly interesting since it is the male beetle which initiates attack and produces the aggregation pheromones.

Richerson and Payne (1979) demonstrated that mixtures of *endo*- and *exo*-brevicomin, with and without verbenone, significantly increased *I. avulsus* landings on host trees. Brevicomin isomer mixtures plus verbenone also significantly increased *I. avulsus* gallery density. Verbenone, however, failed to reduce *I. avulsus* landings on host trees. Watterson et al. (1982) subsequently demonstrated that a 1:1 mixture of 85:15 endo-:*exo*-brevicomin and verbenone (eluted at 160 and 80 mg/24 h/tree, respectively) significantly increased *I. avulsus* re-emergence, brood emergence, and gallery density. As mentioned above, in both studies, while *I. avulsus* landings, re-emergence, emergence, and gallery density increased on trees treated with brevicomin isomers plus verbenone, the same population characteristics for *D. frontalis* significantly decreased. Therefore, it was not possible to determine conclusively if the increases in *I. avulsus* population characteristics were due strictly to the effects of the applied behavioral chemicals, or were due to a decrease in interspecific competition with *D. frontalis*.

Payne and Richerson (1985) subsequently reviewed the data by Richerson and Payne (1979) and Watterson et al. (1982). They concluded that it is unlikely that the increases in *I. avulsus* population characteristics were a direct result of a kairomonal response. This conclusion was based upon the fact that *I. avulsus* were not significantly attracted to *D. frontalis*-infested bolts (Birch et al. 1980; Svihra 1982) nor to *D. frontalis* pheromone (including the brevicomin isomers and verbenone) baited traps (Dixon and Payne 1980; Billings and Cameron 1984). However, since *I. avulsus* landings significantly increased on brevicomin isomer plus verbenone-treated trees (Richerson and Payne 1979), we believe that *I. avulsus* is in fact utilizing these behavioral chemicals together with host tree volatiles to locate suitable hosts. Increased gallery density and brood emergence may have subsequently resulted from the increased resource availability due to a decline in *D. frontalis* density.

Behavioral Analysis of *Ips grandicollis*

Response to Behavioral Chemicals Under Controlled Laboratory Conditions:

In laboratory bioassays conducted to determine host species preference, *I. grandicollis* showed a preference for loblolly pine> eastern white pine> Norway spruce> Frasier fir> eastern red cedar> eastern hemlock (Werner 1972a). *I. grandicollis* also showed response to raw phloem tissue and petroleum ether extracts of phloem, but not to bark or xylem tissues (Werner 1972a). Werner (1972a) also showed that male *I. grandicollis* were most responsive to geraniol, myrcene, methyl chavicol, and limonene, while female beetles were most responsive to myrcene and camphene (Appendix 23). Werner (1972c) also demonstrated that frontalin, *trans*-verbenol, and *Dendroctonus* spp. pheromones generally masked the activity of pine terpenes, reducing or eliminating their attractiveness to *I. grandicollis*. The only exception was the enhancement of geraniol attraction by the addition of frontalin plus *trans*-verbenol. Thus, Werner (1972c) suggests that the combined effect of frontalin plus *trans*-verbenol with host terpenes may provide the stimulus whereby *I. grandicollis* avoids host trees attacked by *D. frontalis*. However, it appears that *I. grandicollis* may utilize host volatiles, with or without frontalin plus *trans*-verbenol, to locate suitable hosts. Thereafter, *I. grandicollis* may utilize these three compounds together to avoid *D. frontalis*-colonized areas of the suitable host. It should also be noted that geraniol, myrcene and D-limonene enhance male *I. grandicollis* attraction, while D, L-camphene enhances female *I. grandicollis* attraction to male *I. grandicollis* frass extract.

Response to Beetle-Infested Pine Under Natural Field Conditions:

Behavioral analysis of *I. grandicollis* to beetle-infested pine clearly demonstrated *I. grandicollis* attraction, particularly females, to male *I. grandicollis*-infested bolts (Vité et al. 1964; Vité and Renwick 1971b; Hain and Anderson 1976a,b; Birch and Svihra 1979; Birch et al. 1980; Svihra et al. 1980; Svihra 1982) (Appendix 24). In addition, *I. grandicollis* attraction to male *I. grandicollis*-infested bolts was significantly reduced by the presence of female *I. grandicollis* (Svihra 1982). These results support the concept that males of this species produce and release the aggregation pheromone.

Hain and Anderson (1976a) investigated the effects of age, flight exercise, and feeding on *I. grandicollis* attraction to male *I. grandicollis*-infested bolts. They reported that although response was too low to differentiate age-dependent attraction, flight exercise did not increase response but did reduce the beetles' ability to disperse from the release sites. In addition, beetles that had fed on inner-bark delayed taking flight but eventually responded to attraction centers in a greater proportion than did unfed beetles. Hain and Anderson (1976b) also reported that *I. grandicollis* attraction was inversely related to the distance from the source of attraction, i.e. male *I. grandicollis*-infested bolts. Utilizing marked beetles, they found that *I. grandicollis* attraction was rather low and the variability between tests was high. They speculated that *I. grandicollis* have a tendency to fly and disperse before initiating attack in new hosts. This would prevent beetles from overcrowding in small areas with limited resources.

Ips grandicollis were generally attracted to *I. calligraphus*-infested bolts (Vité et al. 1964; Birch et al. 1980; Svihra 1982). However, *I. calligraphus*-infested bolts also reduced *I. grandicollis* attraction to *I. grandicollis*-infested bolts (Birch et al 1980; Svihra et al. 1980). Similarly, *I. grandicollis*, particularly males, were generally attracted to female *D. frontalis*- infested bolts (Vité et al. 1964; Birch and Svihra 1979; Birch et al. 1980; Svihra et al. 1980; Dixon and Payne 1980), yet reduced *I. grandicollis* attraction to *I. grandicollis*-infested bolts (Birch and Svihra 1979; Birch et al. 1980). Therefore, initial host selection by *I. grandicollis* may be enhanced by the presence of *I. calligraphus* and/or *D. frontalis*. However, later in the colonization process, the presence of *D. frontalis*, *I. calligraphus*, and *I. grandicollis* may signal incoming *I. grandicollis* that the micro-habitats on the infested host tree are fully colonized. *Ips grandicollis* behavioral responses to *I. avulsus*-infested bolts were mixed, and *I. avulsus*-infested bolts apparently had no effect on *I. grandicollis* attraction to *I. grandicollis*-infested bolts (Birch et al. 1980).

Response to Pheromones Under Natural Field Conditions:

Werner (1972a,c) showed that male *I. grandicollis* were generally more attracted than were female *I. grandicollis* to various host terpenes (Appendix 25). This result suggests that the initial attacking sex, males, might utilize host terpenes as primary attractants in the host selection process. Werner (1972c) also demonstrated that male *I. grandicollis* frass extract enhanced attraction of both male and female *I. grandicollis* to various host terpenes. This observation would indicate that the combination of host terpenes and constituents of male *I. grandicollis* frass is likely one of the primary mechanisms involved in *I. grandicollis* aggregation.

The (*S*)-(-)- ipsenol, with and without ipsdienol, was significantly more attractive than racemic ipsenol plus ipsdienol, and racemic ipsenol or (*R*)-(+)-ipsenol, respectively (Vité et al. 1976a). The (*R*)-(+)- ipsenol enantiomer, in fact, significantly reduced the attraction of *I. grandicollis* to the (*S*)-(-)- ipsenol. Therefore, while *I. grandicollis* appears to be less selective in its use of behavioral chemicals (host terpenes, *Dendroctonus* spp. pheromones), the proposed components of its aggregation semiochemicals are (*S*)-(-)- ipsenol and host terpenes.

Based upon their laboratory studies, Werner (1972c) suggested that frontalin and *trans*-verbenol may provide the stimulus that is the mechanism whereby *I. grandicollis* avoids trees attacked by *D. frontalis*. However, under natural field conditions, although results are mixed, *I. grandicollis* was generally attracted to frontalin plus *trans*-verbenol, with and without turpentine (Dixon and Payne 1980). Thus, *I. grandicollis* may use these compounds to aid in locating a temporary host, while avoiding micro-habitats occupied by *D. frontalis* once a suitable host has been selected.

SUMMARY OF INTERSPECIFIC BEHAVIORAL INTERACTIONS AMONG MEMBER SPECIES OF THE SOUTHERN PINE BARK BEETLE GUILD

The preceding discussions of beetle behavioral responses to infested pine under natural field conditions allows an assessment of the possible role of interspecific semiochemical-based communication in host selection, colonization, and resource partitionment. This is summarized in Appendix 26.

In conjunction with their sequence of arrival studies, Svihra et al. (1980) investigated the role of olfactory perception in isolating mechanisms and in modifying the pattern of the host-tree utilization among *D. frontalis, I. calligraphus, I. avulsus,* and *I. grandicollis*. Birch et al. (1980), in an extensive investigation of the behavioral interactions of these four cohabiting species, summarized the response of these species when each one in turn was hypothetically considered as the initial attacking species. Both studies confirmed the hypothesis that semiochemical-based communication does occur among these four species. Their results also support the hypothesis that chemically mediated behavioral interactions among the species play a significant role in defining the patterns of colonization of host trees. Furthermore, these chemically-mediated behavioral interactions also appear to limit species colonization to certain areas of the tree, and, by specific enhancement or reduction of response, they may also affect the sequence of colonization. Therefore, these interactions may partially explain the temporal and spatial patterns of colonization by all species at the heights characterized by Svihra et al. (1980).

Birch et al. (1980) suggested that any mechanism that delineates spatial distribution and that is effective before energy is expended in penetrating the bark would be intrinsically a more efficient system than one that operated below the surface. Furthermore, the observed rapid attack, facilitated by pheromonal and interspecific attraction, appears to be a strategy in which each species benefits and takes advantage of by overwhelming the trees' resistance mechanisms as quickly as possible. Birch et al. (1980) concluded that the semiochemical-based interactions that occur between species arriving at trees undergoing colonization are potentially a very important mechanism in determining the pattern of exploitation by each species of this temporary habitat. They further concluded that the resulting sequence of arrival and resource partitioning between the cohabiting species represents the coevolution of a highly interactive behavioral system whereby host trees are colonized in a very short space of time while disadvantageous interactions in the breeding sites are minimized.

BEHAVIORAL CHEMICALS AND PEST MANAGEMENT

Although there exists a wealth of knowledge about chemically-mediated behavior within this bark beetle guild, particularly for *D. frontalis*, research and development efforts directed at utilizing chemicals in pest management systems have been limited. Research into alternative methods for *D. frontalis* control utilizing pheromones began in 1962 and resulted in the formulation of the attractant frontalure®, consisting of frontalin and *alpha*-pinene. Efforts have been carried out to evaluate the effectiveness of frontalure in a trap-tree application incorporating the herbicide cacodylic acid (Vité 1971), with little success. In an aerial application, frontalure was also evaluated for its effectiveness in suppressing an infestation through disruption of communication among the flying beetles, thereby hindering host tree colonization. This treatment failed to reduce attack of new host trees by *D. frontalis* and actually increased aggregation on host trees.

Richerson et al. (1980) subsequently conducted field tests to determine the effects of frontalure on *D. frontalis* in a combination of these bait-tree and interruption methods. They sought to protect uninfested trees in the area of active colonization within an infestation from mass attack. They also attempted to contain flying adult brood populations within the infestation on trees no longer naturally attractive nor suitable for brood production. Test results showed that no previously uninfested trees came under successful mass attack during the frontalure treatment periods. Frontalure treatment randomly redistributed brood adults within the infestation and, consequently, insufficient numbers of beetles were present at the active front of the infestation to successfully overcome host resistance. Richerson and Payne (1980) speculated that the normal synchrony of re-emergent parent adults and brood adults necessary to maintain infestation spot growth had been disrupted. Tests are still necessary to determine if the frontalure treatment can disrupt normal beetle activity in treated infestations over a period of time long enough to cause sufficient beetle mortality to permanently halt spot growth.

The knowledge that other behavioral chemicals, particularly *endo*- and *exo*-brevicomin and verbenone, reduce *D. frontalis* attraction to frontalin, prompted additional research to evaluate the usefulness of these compounds to protect individual trees from *D. frontalis* attack, as well as to slow or stop the spread of *D. frontalis* infestations. In addition, these compounds, known as inhibitors, would appear to offer potential use by increasing dispersal flight and, therefore, in-flight beetle mortality.

Payne et al. (1977) evaluated the effects of the continual presence of *endo*- and *exo*-brevicomin on the flight and landing activity of *D. frontalis* in a natural infestation. Their tests showed that although the intra-plot flight activity of *D. frontalis* was not significantly affected by the presence of the compounds, *D. frontalis* landings on host trees were interrupted or inhibited by these compounds. Thus, their results suggest the potential for development of these behavioral chemicals for *D. frontalis* population control on an area-wide basis.

Richerson and Payne (1979) attempted to demonstrate the potential of known *D. frontalis* pheromones that reduce attraction and/or arrestment to protect individual trees within an active infestation from *D. frontalis* attack. Although the brevicomin isomers and brevicomin isomers plus verbenone significantly reduced *D. frontalis* landings, the compounds failed to prevent the treated trees from succumbing to *D. frontalis* and/or *Ips* attack. However, a reduction in the number and length of *D. frontalis* galleries indicated that the compounds could cause significant reduction in brood production.

Southern pine beetle suppression tactics using verbenone and cutting strategies, alone or in combination, have been quite successful (Payne and Billings 1989; Payne et al. 1992). Payne and Billings (1989) applied (*S*) (-)-verbenone, as a liquid polymer, to trees freshly attacked by *D. frontalis*, as well as to a buffer strip of unattacked trees (ahead of the infestation) . The most effective treatment was to treat trees with verbenone and cut freshly attacked trees. However, treating trees with verbenone only was effective in slowing rates of spot growth in small to moderated-sized infestations. In a similar study reported by Payne et al. (1992), the verbenone-only treatment was as effective as verbenone plus cutting. In the 1989 - 1990 experiments from this study, verbenone was eluted from sealed polyethylene bags that contained a 4.5 x 7 cm piece of dense foam rubber. Two bags were placed on each of the treated trees at a height of 3 m. In addition, verbenone 34%(+):66%(-) was used instead of 11%(+):89%(-), because the former enantiomeric ratio was found to be more effective than the latter in reducing *D. frontalis* catch in frontalin plus turpentine-baited traps (Salom et al. 1992).

COMPARATIVE ECOLOGICAL PERSPECTIVE

Birch et al. (1980) reported that *D. frontalis* and *I. avulsus* were the initial attacking species in 76% and 20% of the trees attacked, respectively. Conversely, *I. calligraphus* was the initial attacking species in only 4% of the trees attacked, while *I. grandicollis* was never the first species to attack a tree. Species that are most often the initial attackers must obviously possess certain traits that enable them to overcome a host's natural defense mechanisms.

Degree of Aggregation:

Mason (1970) suggested that the degree of aggregation may be an index of aggressiveness. He showed that *I. avulsus* have a more highly aggregated flight than *I. grandicollis*.

Both *D. frontalis* and *I. avulsus* have concentrated attack periods, with peak arrival occurring 3-5 days and 12 days, respectively, following the initiation of attack. Afterwards, attack rates decline sharply. Also, both *D. frontalis* and *I. avulsus* have a more synchronous reemergence period of a shorter duration than *D. terebrans, I. calligraphus,* and *I. grandicollis*. This synchronous emergence may aid each species in rapidly assembling large numbers for attack. This attack pattern, known as "mass attack," is characteristic of more aggressive species that must rapidly overwhelm the natural defense mechanisms of their hosts. Interestingly enough, this attack pattern coincides with the higher numbers of expendable female *D. frontalis* and male *I. avulsus*, as reflected in their sex ratios.

Conversely, *I. calligraphus* have a less concentrated attack period, with peak arrival occurring approximately 21 days following *I. calligraphus* attack initiation. Attack rate declines thereafter. *Ips calligraphus* reemergence is also less synchronous and more protracted, extending over a greater time period than those of *D. frontalis* and *I. avulsus*. *Ips grandicollis,* which lacks a concentrated attack pattern, gradually increases in attack density for 18 days following attack initiation. Afterwards, *I. grandicollis* maintains an intermediate attack rate, for an extended total arrival period of 30-50 days. Berisford and Franklin (1971) suggest that this extended attack period enables *I. grandicollis* to succeed, since this species normally attacks logging slash or very weakened trees that have little or no remaining natural resistance mechanisms. *Ips grandicollis* also have a higher percentage of female beetles than do *I. avulsus*, and fewer male *I. grandicollis* are killed during host attack.

It should be noted that response to odors of a sympatric and more aggressive bark beetle species would be advantageous to a less aggressive species for the location of suitable host trees for colonization. As discussed previously herein, *I. grandicollis* is attracted to trees undergoing attack by the more aggressive *D. frontalis*, although once such a host is located, *I.*

grandicollis attraction is significantly reduced. This may aid *I. grandicollis* in locating a suitable host, and at the same time, minimize competition once they have landed.

Reproductive and Developmental Strategies:

Wagner et al. (1985) reported that among the three *Ips* species discussed herein, the reproductive and developmental strategies of *I. avulsus* are most similar to those of *D. frontalis*. For example: (1) *I. avulsus* and *D. frontalis* uniformly deposit eggs alternately on opposite sides of egg gallery, while *I. calligraphus* concentrate eggs on one side of the gallery and *I. grandicollis* irregularly deposit eggs on alternate sides of the gallery; (2) *I. avulsus* and *D. frontalis* respectively space eggs 3-6 mm and 2-5 mm apart, while *I. calligraphus* and *I. grandicollis* space eggs 1-3 mm and 1-5 mm apart, respectively; (3) *I. avulsus* and *D. frontalis* excavate short galleries of 4-8 mm and 5-10 mm, respectively, during the first two larval stages, while *I. calligraphus* and *I. grandicollis* excavate galleries of 100-200 mm and 50-70 mm, respectively, during the larval stage; and (4) *I. avulsus* and *D. frontalis* form broad feeding "cells" at the end of the short excavated galleries during the third larval stage, while neither *I. calligraphus* nor *I. grandicollis* form such cells. These reproductive and developmental strategies enable *I. avulsus* and *D. frontalis* to pack more individuals into a given area than can *I. calligraphus* or *I. grandicollis*; thus the two former species require smaller feeding areas. Therefore, *I. avulsus* and *D. frontalis* have a greater capacity for population growth than do *I. calligraphus* and *I. grandicollis*. It should be noted, however, that in an effort to differentiate *D. frontalis* and *I. avulsus*, Paine et al. (1981) reported that while *D. frontalis* exclusively colonized areas closest to the stump and *I. avulsus* dominated colonization in the upper levels of the trunk, the degree of exploitation by *I. avulsus* was not as great as that measured for *D. frontalis*.

Pheromone Production and Release:

Differences in production and release of population-aggregating pheromones may reflect distinct evolutionary trends in the establishment of the two bark beetle genera discussed herein.

In *Dendroctonus*, chemical messengers serve primarily as a signal for mutual invasion of more resistant hosts. *Ips avulsus* also may utilize chemical messengers in this way. Pheromone production in *D. frontalis* continues as long as the host resists extensive feeding and gallery construction. In contrast, *Ips* utilize chemical messengers of comparable function as a means of locating and colonizing scattered and temporary habitats (Atkins 1966). Host suitability is assured by the feeding requirements for pheromone production, particularly in *I. calligraphus* and *I. grandicollis.*

Their production stimulated by resin flow, pheromones are likely to supplement host odors in signaling mass attack. More aggressive species, such as *D. frontalis* and *I. avulsus,* utilize pheromones to orchestrate mass invasion of resistant hosts. *D. frontalis,* the more aggressive of these two species, possesses frontalin within its hindgut upon emergence, and feeding actually results in a decline of frontalin levels. In contrast, the *I. avulsus* pheromone, ipsdienol, is not present upon emergence but is produced upon exposure to myrcene host vapors.

Frass pheromones, conversely, likely mark suitable hosts for colonization. Less aggressive species, such as *I. grandicollis,* must first feed to determine host susceptibility. Once a suitable host is located, feeding stimulates production of their respective frass pheromones to insure host colonization. *Ips calligraphus* employs a combination of frass (ipsdienol) and contact (*cis*-verbenol) pheromones in the host-selection process. Therefore, *I. calligraphus* may be more aggressive than *I. grandicollis,* which depends on a frass pheromone exclusively.

Influence of the Second Sex on Attraction:

In results previously discussed herein, Svihra (1982) determined the influence of the opposite sex on attraction produced by the initial attacking sex. Interestingly, for the more aggressive species of *D. frontalis* and *I. avulsus,* the simultaneous presence of the second sex has no effect on attraction. Conversely, in the less aggressive species of *I. calligraphus* and *I. grandicollis,* attraction is significantly reduced by the simultaneous presence of the second sex. This correlation may have evolutionary implications and warrants further investigation.

ADDITIONAL RESEARCH NEEDS AND CONCLUSIONS

This treatise is evidence that much is known about the olfactory communication systems of the five sympatric cohabiting scolytid species which comprise the southern pine bark beetle guild. However, many of the mechanisms involved at all three levels of this communication system--pheromone biosynthesis, perception, and mediated behavior--are not well understood.

With respect to pheromone biosynthesis and perception, the mechanisms related to the endocrine system and its functional relationships to feeding, flight, and mating are not understood. These are of particular interest given the differences among the two scolytid genera discussed herein. Additionally, with what is known about the mechanisms of oxidation and rearrangement of terpenes to yield pheromones, the role of microorganisms in pheromone biosynthesis may be critical. In the specific area of pheromone perception, the mechanisms involved in transduction are crucial to our understanding of sensory coding. And intertwined among the three levels of this communication system is the question of multifunctional pheromones and their mechanisms of sensory coding and behavioral mediation.

Much is also known behaviorally about the intra- and interspecific semiochemical-based communication among the guild species, particularly during host colonization and resource partitioning. However, selected pheromones or host tree volatiles and beetle-infested pine logs have been utilized in most behavioral investigations conducted under natural field conditions. The independent roles played in host selection by the defined beetle-produced pheromonal blends and the host tree-produced compounds remains to be investigated. In addition, the process of host selection (what triggers the first beetle to select a particular host tree) and its relation to direct versus random flight, attraction versus arrestment, and primary versus secondary attraction, must be resolved. The reader is referred to Person (1931), Moeck et al. (1981), Hines and Heikkenen (1977), Heikkenen (1977), Wood (1972, 1982), and Hynum and Berryman (1980) for reviews of this topic. This area of research may be that weak link in bark beetle ecology that we can ultimately directly or indirectly exploit. While many of these questions appear basic in nature, they also have ecological significance. Answers to these questions should provide not only a more thorough understanding of a complex olfactory communication system within an insect guild of sympatric species but, just as important, an intelligible approach to their management within our southern pine forests.

In conclusion, it appears that adaptation of guild members that cue into hosts colonized by other guild members results in increased resource available to each species. Furthermore, the beneficial effects of their adaptation to the presence of each species appears to outweigh any of the negative effects resulting from competition. The interspecific, chemically-mediated behavior by the guild species in colonization and resource partitioning results in reduced intensity of inter- and intraspecific competition at all population density levels and allow the species to more fully exploit their southern pine hosts.

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REFERENCES

Alcock, J. 1982. Natural selection and communication among bark beetles. Fla. Entomol. 65:17-32

Andryszak, N.A., Payne, T.L., Billings, P.M., and Benenati, J.M. 1982. Effect of flight activity on laboratory response of the southern pine beetle to attractivity. J. Ga. Entomol. Soc. 17: 456-560.

Ascoli-Christensen, A., Salom, S.M., and Payne, T.L. 1993. Olfactory receptor cell reponses of *Ips grandicollis* (Eichoff) (Coleoptera: Scolytidae) to intra- and interspecific behavioral chemicals. J. Chem. Ecol. 19:699-712.

Atkins, M.D. 1966. Behavioral variation among scolytids in relation to their habitat. Can. Entomol. 98: 285-288.

Berisford, C.W., and Franklin, R.T. 1971. Attack patterns of *Ips avulsus* and *Ips grandicollis* (Coleoptera: Scolytidae) on four species of southern pines. Ann. Entomol. Soc. Am. 64: 894-897.

Billings, R.F. 1985. Southern pine bark beetles and associated insects: Effects of rapidly-released host volatiles on response to aggregation pheromones. Sonderdruck aus Bd. 99: 483-491.

Billings, R.F. and Cameron, R.S. 1984. Kairomonal responses of Coleoptera, *Monochamus titillator* (Cerambycidae), *Thanasimus dubius* (Cleridae), and *Temnochila virescens* (Trogosotidae), to behavioral chemicals of the southern pine bark beetles. Environ. Entomol. 13:1542-1548.

Birch, M.C., and Svihra, P. 1979. Novel approaches to forest insect control: Exploiting olfactory interactions between species of Scolytidae. pp 135-138. *In*: W. E. Waters (ed.), Current Topics in Forest Entomology. New York: John Wiley and Sons, Inc. 179 pp.

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

Blum, M.S. 1970. The chemical basis of insect sociality. pp. 61-90. *In*: M. Beroza (ed.), Chemicals Controlling Insect Behavior. Academic Press, New York. 170 pp.

Borden, J.H. 1982. Aggregation Pheromones. pp. 74-139. *In*: J.B. Mitton and K.B. Sturgeon (eds.), Bark Beetles of North American Conifers: A System for the Study of Evolutionary Biology. Univ. of Texas Press, Austin, Texas. 527 pp.

Borden, J.H. 1985. Aggregation Pheromones. pp. 257-285. *In*: G. A. Kerkut and L. I. Gilbert (eds.), Comprehensive Insect Physiology, Biochemistry and Pharmacology: Behavior (Vol. 9). Pergamon Press, New York, N. Y. 735 pp.

Borden, J.H., and Wood, D.L. 1966. The antennal receptors and olfactory response of *Ips confusus* (Coleoptera: Scolytidae) to male sex attractant in the laboratory. Ann. Entomol. Soc. Am. 59: 253-261.

Brand, J.M., Bracke, J.W., Markovetz, A.J., Wood, D., Browne L.E. 1975. Production of verbenol pheromone by a bacterium isolated from bark beetles. Nature 254: 136-137.

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*. J. Chem. Ecol. 2: 195-199.

Brand, J.M., Schultz, J., Barras, S.J., Edson, L.J., Payne, T.L., and Hedden, R.L. 1977. Bark beetle pheromones: Enhancement of *Dendroctonus frontalis* (Coleoptera: Scolytidae) aggregation pheromone by yeast metabolites in laboratory bioassays. J. Chem. Ecol. 3: 657-666.

Bridges, J.H. 1982. Effects of juvenile hormone on pheromone synthesis in *Dendroctonus frontalis*. Environ. Entomol. 11: 417-420.

Clements, R.W., and Williams, H.G. 1981. Attractants, techniques, and devices for trapping bark beetles. USDA For. Serv. Res. Note SE-309, 3 p. Southeast. For. Expt. Stn., Asheville, N. C.

Coster, J.E. 1970a. Certain aspects of pheromone release and aggregation behavior in the southern pine beetle (Coleoptera: Scolytidae). Ph.D. dissertation, Texas A&M University. 129 pp.

Coster, J.E. 1970b. Production of aggregating pheromones in re-emerged parent females of the southern pine beetle. Ann. Entomol. Soc. Am. 63: 1186-1187.

Coster, J.E., and Gara, R.I. 1968. Studies on the attack behavior of the southern pine beetle. II. Response to attractive host material. Contrib. Boyce Thompson Inst. 24: 69-75.

Coster, J.E., and Vité, J.P. 1972. Effects of feeding and mating on pheromone release in the southern pine beetle. Ann. Entomol. Soc. Am. 65: 263-266.

Coster, J.E., Payne, T.L., Hart, E.R., and Edson, L.J. 1977a. Seasonal variation in mass attack behavior of southern pine beetle. J. Ga. Entomol. Soc. 12: 204-211.

Coster, J.E., Payne, T.L., Hart, E.R., and Edson, L.J. 1977b. Aggregation of the southern pine beetle in response to attractive host trees. Environ. Entomol. 6: 725-731.

Delorme, J.D. and Payne, T.L. 1990. Antennal olfactory responses of the black turpentine beetle, *Dendroctonus terebrans* (Olivier), to bark beetle pheromones and host odors. J. Chem. Ecol. 16:1321-1329.

Dickens, J.C. 1979. Electrophysiological investigations of olfaction in bark beetles. Bull. Soc. Entomol Suisse 52: 203-216.

Dickens, J.C., and Payne, T.L. 1977. Bark Beetle Olfaction: Pheromone receptor system in *Dendroctonus frontalis*. J. Insect. Physiol. 23: 481-489.

Dickens, J.C., and Payne, T.L. 1978a. Structure and function of the sensilla on the antennal club of the southern pine beetle, *Dendroctonus frontalis* (Zimmerman) (Coleoptera: Scolytidae). Int. J. Insect. Morphol. and Embryol. 7: 251-265.

Dickens, J.C., and Payne, T.L. 1978b. Olfactory-induced muscle potentials in *Dendroctonus frontalis*: Effects of *trans*-verbenol and verbenone. Experentia 34: 463-464.

Dixon, W.N., and Payne, T.L. 1979. Sequence of arrival and spatial distribution of entomophagous and associate insects of southern pine beetle-infested trees. Texas Agric. Exp. Stn. Misc. Publ. 1432. 28 pp.

Dixon, W.N., and Payne, T.L. 1980. Attraction of entomophagous and associate insects of the southern pine beetle to beetle- and host tree-produced volatiles. J. Ga. Entomol. Soc. 15: 378-389.

Fargo, W.S., Coulson, R.N., Pulley, P.E., Pope, D.N., and Kelley, C.L. 1978. Spatial and temporal patterns of within-tree colonization by *Dendroctonus frontalis* (Coleoptera: Scolytidae). Can. Entomol. 110: 1213-1232.

Fatzinger, C.W. 1975. Turpentine-baited traps capture black turpentine beetles and other Forest Coleoptera but do not prevent attacks on pines. pp. 26-31. *In*: S. J. Branham and R. C. Thatcher (eds.), Integrated Pest Management Research Symposium: The Proceedings. U.S.D.A. - For. Serv., So. For. Exper. Sta., N.O., LA., General Tech. Rep. S0-56. 383 pp.

Fatzinger, C.W. 1984. Development and evaluation of a trapping system, using host produced behavioral chemicals, for preventing attacks by the black turpentine beetle, *Dendroctonus terebrans* (Oliv.), and engraver beetles, *Ips*. spp., in naval stores areas. USDA For. Serv. 101 pp. SE-2252.

Fatzinger, C.W. 1985. Attraction of the black turpentine beetle. (Coleoptera: Scolytidae) and other forest Coleoptera to turpentine-baited traps. Environ. Entomol. 14: 768-775.

Fatzinger, C.W., Siegfried, B.D., Wilkenson, R.C., and Nation, J.L. 1987. *Trans*-verbenol, turpentine, and ethanol as trap baits for the black turpentine beetle, *Dendroctonus terebrans*, and other forest Coleoptera in north Florida. J. Entomol. Sci. 22: 201-209.

Gara, R.I., Vité, J.P., and Cramer, H.H. 1965. Manipulation of *Dendroctonus frontalis* by use of a population aggregation pheromone. Contrib. Boyce Thompson Inst. 23: 55-66.

Godbee Jr., J.F., and Franklin, R.T. 1976. Attraction, attack patterns and seasonal activity of the black turpentine beetle. Ann. Entomol. Soc. Am. 69: 653-655.

Hain, F.P., and Anderson, R.F. 1976a. Effect of age, flight exercise and feeding on the field attractant response of *Ips grandicollis*. J. GA Entomol. Soc. 11: 30-34.

Hain, F.P., and Anderson, R.F. 1976b. Some response and attack behaviors of *Ips grandicollis*. J. GA Entomol. Soc. 11: 157-162.

Hedden, R., Vité, J.P., and Mori, K. 1976. Synergistic effect of a pheromone and a kairomone on host selection and colonization by *Ips avulsus*. Nature 261: 696-697.

Heikkenen, H.J. 1977. Southern pine beetle: a hypothesis regarding its primary attractant. J. For. 75: 412-413.

Hertel, G.D., Hain, F.P., and Anderson, R.F. 1969. Response of *Ips grandicollis* (Coleoptera: Scyolytidae) to the attractant produced by attacking male beetles. Can. Entomol. 101: 1084-1091.

Hines, J.W., and Heikkenen, H.J. 1977. Beetles attracted to severed Virginia pine (*Pinus virginiana* Mill.) Environ. Entomol. 6: 123-127.

Hopkins, A.D. 1909. The genus *Dendroctonus*. U. S. Department of Agriculture Bureau of Entomology Technical Series 17, Part 1.

Hughes, P.R. 1973. *Dendroctonus*: Production of pheromones and related compounds in response to host monoterpenes. Z. Angew. Entomol. 73: 294-312.

Hughes, P.R. 1974. Myrcene: A precursor of pheromones in *Ips* beetles. J. Insect Physiol. 20: 1271-1275.

Hughes, P.R. 1975. Pheromones of *Dendroctonus*: Origin of *alpha*-pinene oxidation products present in emergent adults. J. Insect Physiol. 21: 687-691.

Hunt, D.W.A. and Borden, J.H. 1989. Terpene alcohol pheromone production by *Dendroctonus ponderosae* and *Ips paraconfusus* (Coleoptera: Scolytidae) in the absence of readily culturable microorganisms. J. Chem. Ecol. 15:1433-1463.

Hunt, D.W.A. and Borden, J.H. 1990. Conversion of verbenols to verbenone by yeasts isolated from *Dendroctonus ponderosae* (Coleoptera: Scolytidae). J. Chem. Ecol. 16:1385-1397.

Hynum, B.G. and Berryman, A.A. 1980. *Dendroctonus ponderosae* (Coleoptera: Scolytidae): Pre-aggregation landing and gallery initiation on lodgepole pine. Can. Entomol. 112: 185-191.

Kaissling, K.A. 1969. Kinetics of olfactory receptor potentials pp. 52-70. *In:* Pfaffmann, C. (ed.). Olfaction and Taste. III. Rockerfeller Univ. Press. N.Y., N.Y.

Kinzer, G. W., Fentiman Jr., A.F., Page Jr., T.E., Foltz, R.L., Vité, J.P., and Pitman Jr., G.B. 1969. Bark beetle attractants: Identification, synthesis and field bioassay of a new compound isolated from *Dendroctonus*. Nature 221: 477-478.

Kowal, R.J., and Coyne, J.F. 1951. The black turpentine beetle can kill trees. *Am. Turpentine-Farmers Assoc. J.* 13:14-15.

Krawielitzki, V.S., Vité, J.P., Sturm, V., and Franke, W. 1983. Interactions between resin flow and subcortically feeding Coleoptera. Z. Angew. Entomol. 96: 140-146.

Lindgren, B.S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Ent. 115:299-302.

Mason, R.R. 1970. Comparison of flight aggregation in two species of southern *Ips* (Coleoptera: Scolytidae). Can. Entomol. 102: 1036-1041.

McCarty, F.A., Billings, P.M., Richerson, J.V., Payne, T.L., and Edson, L.J. 1980. Response of the southern pine beetle to behavioral chemicals in the laboratory. J. Ga. Entomol. Soc. 15: 307-317.

Merkel, E.P. 1981. Control of the black turpentine beetle. Georgia Forest Research Paper 15. Georgia Forestry Commission.

Mirov, N.T. 1961. Composition of gum turpentines of pines. U.S. Dep. Agric. Tech. Bull. No. 1239.

Moeck, H.A., Wood, D.L., and 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*. J. Chem. Ecol. 7: 49-83.

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

Payne, T.L. 1970. Electrophysiological investigations on response to pheromones in bark beetles. Contrib. Boyce Thompson Inst. 24: 275-282.

Payne, T.L. 1971. Bark Beetle Olfaction 1. Electroantennogram responses of the southern pine beetle (Coleoptera: Scolytidae) to its aggregation pheromone frontalin. Ann. Entomol. Soc. Am. 64: 266-268.

Payne, T.L. 1974. Pheromone and host odor-stimulated potentials in *Dendroctonus*. Experientia 30: 509-510.

Payne, T.L. 1975. Bark Beetle Olfaction. III. Antennal olfactory responsiveness of *Dendroctonus frontalis* Zimmerman and *D. brevicomis* LeConte (Coleoptera: Scolytidae) to aggregation pheromones and host tree terpene hydrocarbons. J. Chem. Ecol. 1: 233-242.

Payne, T.L. 1979. Pheromone and host odor perception in bark beetles. pp. 27-57. *In*: T. Narahashi (ed.), Neurotoxicology of Insecticides and Pheromones. Plenum Publ. Co., New York.

Payne, T.L. 1986. Olfaction and vision in host finding by a bark beetle. pp. 111-116. *In*: T. L. Payne, M. C. Birch and C. E. J. Kennedy (eds.), Mechanisms in Insect Olfaction. Oxford: Clarendon Press. 364 pp.

Payne, T.L. and Billings, R.F. 1989. Evaluation of (S)-verbenone applications for suppressing southern pine beetle (Coleoptera: Scolytidae) infestations. Environ. Entomol. 82:1702-1708

Payne, T.L. and Coulson, R.N. 1985. Role of visual and olfactory stimuli in host selection and aggregation behavior by *Dendroctonus frontalis*. pp. 73-82. L. Safranyik (ed.), Proceedings of the IUFRO Conference on the Role of the Host in the Population Dynamics of Forest Insects. Pacific Forest Research Center of the Canadian Forestry Service, Victoria, B.C.

Payne, T.L., and Dickens, J C. 1976. Adaptation to determine receptor system specificity in insect olfactory communication. J. Insect. Physiol. 22: 1569-1572.

Payne, T.L. and Richerson, J.V. 1979. Management implications of inhibitors for *Dendroctonus frontalis* (Coleoptera: Scolytidae). Bull .de. la Societe Entomol. Suisse. 52:323-331.

Payne, T.L., and Richerson, J.V. 1985. Pheromone-mediated competitive replacement between two bark beetle populations: Influence on infestation suppression. Sonderdruck avs Bd. 99, H. 2,5. 131-138.

Payne, T.L., Moeck, H.A., Wilson, C.D., Coulson, R.N., and Humphreys, W.J. 1973. Bark beetle olfaction. II. Antennal morphology of sixteen species of Scolytidae (Coleoptera). Int. J. Insect. Morphol. Embryol. 2: 177-192.

Payne, T.L., Hart, E.R., Edson, L.J., McCarty, F.A., Billings, P.M., and Coster, J.E. 1976. Olfactometer for assay of behavioral chemicals for the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae) J. Chem. Ecol. 2: 411-419.

Payne, T.L., Coster, J.E., and Johnson, P.C. 1977. Effects of slow-release formulation of synthetic *endo-* and *exo*-brevicomin on southern pine beetle flight and landing behavior. J. Chem. Ecol. 3: 133-141.

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

Payne, T.L., Richerson, J.V., Dickens, J.C., West, J.R., Mori, K., Berisford, C.W., Hedden, R.L., Vité, J.P., and Blum, M.S. 1982. Southern Pine Beetle: Olfactory receptor and behavior discrimitation of enantiomers of the attractant pheromone frontalin. J. Chem Ecol. 8: 873-881.

Payne, T.L., Billings, R.F., Delorme, J.D., Andryszak, N.A., Bartels, J., Francke, W., and Vité, J.P. 1987. Kairomonal-Pheromonal system in the black turpentine beetle, *Dendroctonus terebans* (Ol.). J. Appl. Entomol. 103: 15-22.

Payne, T.L., Andryszak, N.A., Wieser, H., Dixon, E.A., Ibrahim, N., and Coers, J. 1988. Antennal olfactory and behavioral response of southern pine beetle, *Dendroctonus frontalis,* to analogs of its aggregation pheromone frontalin. J. Chem. Ecol. 14: 1217-1225.

Payne, T.L., Billings, R.F., Berisford, C.W., Salom, S.M., Grosman, D.M., Dalusky, M.J., and Upton, W.W. 1992. Disruption of *Dendroctonus frontalis* (Col., Scolytidae) infestations with an inhibitor pheromone. J. Appl. Ent. 114:341-347.

Person, H.L. 1931. Theory in explanation of the selection of certain trees by the western pine beetle. J. For. 29: 696-699.

Phillips, T.W., Wilkening, A.J., Atkinson, T.H., Nation, S.L., Wilkinson, R.C., and Foltz, J.L. 1988. Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera) Environ. Entomol. 17:456-462.

Phillips, T.W., Nation, J.L., Wilkinson, R.C., and Foltz, J.L. 1989. Secondary attraction and field activity of beetle-produced volatiles in *Dendroctonus terebrans.* J. Chem. Ecol. 15:1513-1533.

Phillips, T.W., Nation, J.L., Wilkinson, R.C., and Foltz, J.L., Pierce, H.D., and Ochlschlager, A.C. 1990. Response specificity of *Dendroctonus terebrans* (Coleoptera: Scolytidue) to enantiomers of its sex pheromone. Ann. Entomol. Soc. Am. 83:251-257.

Pitman, G.B. and Vité, J.P. 1969. Aggregation behavior of Dendroctonus ponderosae (Coleoptera: Scolytidae) in response to chemical mesengers. Can. Ent. 101:143-149.

Pitman, G B., Vité, J.P., Kinzer, G.W., and Fentiman Jr., A.F. 1968. Bark beetle attractants: *Trans*-verbenol isolated from *Dendroctonus.* Nature 218: 168-169.

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

Raffa, K.F. and Berryman, A.A. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol. Monogr. 53:27-49.

Raffa, K.F. ,Phillips, T.W., and Salom, S.M. 1993. Strategies and mechanisms of host colonization by bark beetles. pp. 103-128. In: Schowalter, T.D. and Filip, G.M. (eds.). Beetle-Pathogen Interactions in Conifer Forests. Academic Press, London.

Redlich, H. Bruns, W., Francke, W., Schurig, V., Payne T.L., and Vité, J.P. 1987. Chiral building units from carbohydrates - XIII. Identification of the absolute configuration of *endo*-brevicomin from *Dendroctonus frontalis* and synthesis of both enantiomers from D-ribose. Tetrahedron 43: 2029-2034.

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

Renwick, J.A.A., and Hughes, P.R. 1975. Oxidation of unsaturated cyclic hydrocarbons by *Dendroctonus frontalis*. Insect Biochem 5: 459-463.

Renwick, J.A.A., and Vité, J.P. 1968. Isolation of the population aggregating pheromone of the southern pine beetle. Contrib. Boyce Thompson Inst. 24: 65-68.

Renwick, J.A.A., and Vité, J.P. 1969. Bark beetle attractants: Mechanism of colonization by *Dendroctonus frontalis*. Nature 224:1222-1223.

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

Renwick, J.A.A., and Vité, J.P. 1972. Pheromones and host volatiles that govern aggregation of the six-spined engraver beetle, *Ips calligraphus*. J. Insect Physiol. 18: 1215-1219.

Renwick, J.A.A., Hughes, P.R., and Tanletin, D.T. 1973. Oxidation products of pinene in the bark beetle, *Dendroctonus frontalis*. J. Insect Physiol. 19: 1735-1740.

Renwick, J.A.A., Hughes, P.R., Pitman, G.B., and Vité, J.P. 1976. Oxidation products of terpenes identified from *Dendroctonus* and *Ips* bark beetles. Contrib. Boyce Thompson Inst. 22: 725-727.

Richerson, J.V., and Payne, T.L. 1979. Effects of bark beetle inhibitors on landing and attack behavior of the southern pine beetle and beetle associates. Environ. Entomol. 8: 360-364.

Richerson, J.V. and Payne, T.L. 1980. Management implications of attractants for *Dendroctonus frontalis* pp. 164-172. *In* Berryman, A.A. and Safranyik, L. (eds.). Proc. 2nd IUFRO Conference on Dispersal of Forest Insects: Evaluation, Theory and Management Implications. Sandpoint, ID.

Richerson, J.V., McCarty, F.A., and Payne, T.L. 1980. Disruption of southern pine beetle infestations with frontalure. Environ. Entomol. 9: 90-93.

Roberts, E.A., Billings, P.M., Payne, T.L., Richerson, C.W., Hedden, R.L., and Edson, L.J. 1982. Seasonal variation in laboratory response to behavioral chemicals of the southern pine beetle. J. Chem Ecol. 8: 641-652.

Root, R.B. 1973. Organization of plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecol. Monogr. 43:95-124.

Rose, W.F., Billings, R.F., and Vité, J.P. 1981. Southern Pine Bark Beetles: Evaluation of non-sticky pheromone trap designs for survey and research. Southwest. Entomol. 6: 1-9.

Rudinsky, J.A. 1973. Multiple functions of the southern pine beetle pheromone verbenone. Environ. Entomol. 2: 511-514.

Rudinsky, J.A., Morgan, M.E., Libbey, L.M., and Putman, T.B. 1974. Antiaggregative-rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. Environ. Entomol. 3: 90-98.

Salom, S.M., Billings, R.F., Upton, W.W., Dalusky, M.J., Grosman, D.M., Payne, T.L., Berisford, C.W., and Shaver, T.L. 1992. Effect of verbenone enatiomers and racemic *endo*-brevicomin on response of *Dendroctonus frontalis* (Coleoptera: Scolytidae) to attractant-baited traps. Can. J. For. Res. 22:925-931.

Siegfried, B.B., 1984. Attraction of the black turpentine beetle, *Dendroctonus terebrans*, to host- and insect- produced volatiles. M.S. Theses, Univ. of Florida.

Siegfried, B.D., Fatzinger, C.W., Wilkinson, R.C., and Nation, J.L. 1986. In-flight responses of the black turpentine beetle (Coleoptera: Scolytidae) to individual monoterpenes, turpentine, and paraquat-treated slash pines. Environ. Entomol. 15: 710-714.

Smith, M.T., Busch, G.R., Payne, T.L., and Dickens, J.C. 1988. Antennal olfactory responsiveness of three sympatric *Ips* species [*Ips avulsus* (Eichhoff), *Ips calligraphus* (Germar), *Ips grandicollis* (Eichhoff)], to intra- and interspecific behavioral chemicals. J. Chem. Ecol. 14:1289-1304.

Smith, R.H., and Lee, R.E., III. 1957. Black turpentine beetle. U. S. Forest Service Pest Leaflet 12.

Smith, R.H. 1959. Resistance of pines to bark beetles, studies of toxicity of resins. 1958. U.S. For. Serv., Pacific Southwest For., and Range Expt. Sta., Berkeley, Calif., 43 pp.

Smith, R.H. 1963. Preferential attack by *Dendroctonus terebrans* on *Pinus elliotti*. J. Econ. Entomol. 56: 817-819.

Smith, R.H. 1965. Effect of monoterpene vapors on the western pine beetle. J. Econ. Entomol. 58: 509-510.

Stewart, T.E., Plummer, E.L., McCandless, L.L., West, J.R., and Silverstein, R.M. 1977. Determination of enantiomer composition of several bicyclic ketal insect pheromone components. J. Chem. Ecol. 3: 27-43.

Svihra, P. 1982. Influence of opposite sex on attraction produced by pioneer sex of four bark beetle species cohabiting pine in the southern United States. J. Chem. Ecol. 8: 373-378.

Svihra, P., Paine, T.D., and Birch, M.C. 1980. Interspecific olfactory communications in southern pine beetles. Naturwiss. 67: 518-519.

Thatcher, R.C., Searcy, J.L., Coster, J.E., and Hertel, G.D. 1980. The southern pine beetle. USDA For. Serv. Tech. Bull. 1631. 266 pp.

Tsao, C.H., and Yu, C.C. 1967. Sex pheromones of the southern pine beetle, *Dendroctonus frontalis* Zimm. J. Ga. Entomol. Soc. 2: 13-20.

Vanderwel, D. and Oehlasclager,A.C. 1987. Biosynthesis of pheromones and endocrine regulation of pheromone production in Coleoptera. In: Prestwich, G.D. and Bloomquist (eds.). Pheromone Biochemistry. Academic Press. N.Y.

Vité, J.P. 1971. Pest management systems using synthetic pheromones. Contrib. Boyce Thompson Inst. 24: 343-350.

Vité, J.P., and Crozier, R.G. 1968. Studies on the attack behavior of the southern pine beetle. IV. Influence of host conditions on aggregation pattern. Contrib. Boyce Thompson Inst. 24: 87-93.

Vité, J.P., and Pitman, G.B. 1967. Concepts in research on bark beetle attraction and manipulation. XIV. Congress, Int. Union For. Res. Organ. (Munich). Sect. 24: 683-701.

Vité, J.P., and Pitman, G.B., 1968. Bark beetle aggregation: Effects of feeding on the release of pheromones in *Dendroctonus* and *Ips*. Nature 218: 169-170.

Vité, J.P., and Renwick, J.A.A. 1968. Insect and host factors in the aggregation of the southern pine beetle. Contrib Boyce Thompson Inst. 24: 61-63.

Vité, J.P., and Renwick, J.A.A. 1971a. Inhibition of *Dendroctonus frontalis* response to frontalin by isomers of brevicomin. Naturwiss 58:418-419.

Vité, J.P., and Renwick, J.A.A. 1971b. Population aggregating pheromone in the bark beetle, *Ips grandicollis*. J. Insect Physiol. 17: 1699-1704.

Vité, J.P., Gara, R.I., and von Scheller, H.D. 1964. Field observations on the response to attractants of bark beetles infesting southern pines. Contrib. Boyce Thompson Inst. 22: 461-470.

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

Vité, J.P., Hedden, R., and Mori, K. 1976a. *Ips grandicollis*: Field response to the optically pure pheromone. Naturwiss. 63: 43-33.

Vité, J.P., Klimetzek, D., Laskant, G. Hedden, R., and Mori, K. 1976b. Chirality of insect pheromones: Response interruption by inactive antipodes. Naturwiss. 63: 582-583.

Vité, J.P., Ohloff, G., and Billings, R.F. 1978. Pheromonal chirality and integrity of aggregation response in southern species of the bark beetle *Ips* sp. Nature 272: 817-818.

Vité, J.P., Billings, R.F., Ware, C.W., and Mori, K. 1985. Southern Pine Beetle: Enhancement or inhibition of aggregation response mediated by enantiomers of *endo*-brevicomin. Naturwiss 72: 99.

Wagner, T.L., Flamm, R.O., and Coulson, R.N. 1985. Strategies for cohabitation among the southern pine beetle species: Comparisons of life-process biologies. pp. 87-101. *In:* S. J. Branham and R. C. Thatcher (eds.), Integrated Pest Management Research Symposium: The Proceedings. U.S.D.A. - F.S., S. For. Expt. Stn., N.O., LA., General Tech. Rep. S0-56. 383 pp.

Ward, J.G.D. 1967. Investigations dealing with species attractant of *Ips grandicollis* (Eichh.) and the dispersal in different types of vegetation. A problem. Duke Univ., School of Forestry, Durham, N. C.

Watterson, G.P., Payne, T.L., and Richerson, J.V. 1982. The effects of verbenone and brevicomin on the within-tree populations of *Dendroctonus frontalis*. J. Ga. Entomol. Soc. 17: 118-126.

Werner, R.A. 1972a. Agregation behavior of the beetle *Ips grandicollis* in response to host- produced attractants. J. Insect Physiol. 18: 423-437.

Werner, R.A. 1972b. Aggregation behavior of the beetle *Ips grandicollis* in response to insect-produced attractants. J. Insect Physiol. 18: 1001-1013.

Werner, R.A. 1972c. Response of the beetle, *Ips grandicollis*, to combinations of host and insect produced attractants. J. Insect Physiol. 18: 1403-1412.

White, Jr., A., Agosin, M., Franklin, R.T., and Webb, J.W. 1980. Bark beetle pheromones: evidence for physiological synthesis mechanisms and their ecological implications. Z. ang. Entomol. 90: 255-274.

Wood, D.L. 1972. The selection and colonization of ponderosa pine by bark beetles. pp. 101-117. In: H. F. vanEmden (ed.), Insect/Plant Relationships. Blackwell Scientific Publications, London.

Wood, D.L. 1982. The role of pheromones, kairomones and allomones in the host selection and colonization behavior of bark beetles. Ann. Rev. Entomol. 27: 411-446.

Appendix 1. Pheromone Production by Dendroctonus frontalis.

	NEWLY EMERGED ADULTS		EFFECTS ON PHEROMONE PRODUCTION FOLLOWING EXPOSURE TO:								
			host resin vapor (oleoresin)			alpha - pinene			beta - pinene		
COMPOUND PRODUCT	Sex [1]	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]
frontalin	F M, F	1, 2, 3, 4, 5 [3] 6									
endo-brevicomin	M	6, 8, 9 [4]	M	appears	4 [5, 6]	M	appears	4 [5, 6]	M	appears	4 [5, 6]
exo-brevicomin	M	9 [4], 11									
trans-verbenol	F M M<<F	3, 6, 12, 13, 14, 15, 16 17 [7] 2, 4	M<<F	appears	4 [5, 6, 7]	M M F F M>>>F	appears increases appears increases increases	16 17 [7] 18 [9] 16 4 [5, 7]			
cis-verbenol	F	2, 16	M>F	appears	4 [6, 8]	M F F M>F	appears appears increases appears	16 18 [9] 16 4 [6, 8]			
verbenone	M M>F	4, 12, 15, 16, 18 [8] 2, 6[5]				M	increases	17 [7]			
myrtenol	M<F M, F	4 6, 16, 18	M>>>F	----	4 [6]	M>>>F	increases	4 [6, 8]	M>>>F	----	4 [6]
cis-3-pinen-2-ol	F	4				M>>>F F	increases appears	4 [5, 8] 18 [9, 12]			
myrtenal	M	16									
4-methyl-2-pentanol			----	appears	4 [5, 8]	M, F M>>>F	appears appears	16 4 [5, 8]			
trans-pinocarveol			----	appears	4 [5, 8]				M, F M>F	appears appears	16 4 [6, 8]
pinocarvone	M	6, 16	M	appears	4 [6, 8]	M	appears	4 [6]	M M	increases appears	16 4 [6, 8]
unknown									F	appears	4 [6]
2-methyl-2-cyclohexen-1-ol [13]											
3-methyl-2-cyclohexen-1-ol (seudenol) [13]											
3-methyl-2-cyclohexen-1-one (MCH) [13]											
1-methyl-2-cyclohexen-1-ol [14]											
1-cyclohexenemethanol [13]											
a methylene cyclohexanol											
6-hydroxy-camphene (camphenol)											

camphene			3-carene			myrcene			1-methyl - 1 cyclohexene [18]			EFFECTS OF FEEDING ON PHEROMONE PRODUCTION		
SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT [2]	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]
												F F	declines No effect	3 4
M	appears	4 [5, 6]				M F	appears appears	4 [4, 5] 4 [2, 4]						
												---- F M	decreases decreases increases	19 3, 4, 15 4
F	appears	4, [5, 6]	F	appears	4 [5, 6]	F	appears	4 [5, 6]				M, F	appears	4
						M	increases	4 [8]				M	declines	4, 15
												M=F	declines	4
												F	disappears	4
M, F	appears	4 [6, 8]	M, F	appears	4 [6, 8]	M, F	appears	4 [6, 8]						
									M, F	appears	18			
									M, F	appears	18			
									M, F	appears	18			
									M, F	appears	18			
									M, F	appears	18			
									M, F	appears	18			
M, F	appears	20												

EFFECTS OF MATING ON PHEROMONE PRODUCTION			HORMONAL EFFECTS ON PHEROMONE PRODUCTION					
			JH-II Treatment (1-5 day old adults)			methoprene treatment (1-5 day old adults)		
SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]
F	declines	3, 7						
			M	increases	10	M	increases	10
F	declines	3, 7	M<F	increases	10	M<<F M<F	increases decreases	10 [10] 10 [11]
			M	no effect	10	M	decreases	10
			M>F	no effect	10	F M	decreases no effect	10 10

Footnotes for SPB

[1] M = male; F = female; --- sex not indicated.

[2] 1 Kinzer et al. 1969; 2 Pitman et al. 1969; 3 Coster & Vité 1972; 4 Hughes 1973; 5 Stewart et al. 1977; 6 Rudinsky et al. 1974; 7 Coster 1970b; 8 Vité & Renwick 1971a; 9 Redlich et al. 1987; 10 Bridges 1982; 11 Pitman & Vité 1969; 12 Renwick 1967; 13 Pitman et al. 1968; 14 Renwick & Vité 1968; 15 Vité & Crozier 1968; 16 Renwick et al. 1973; 17 Hughes 1975; 18 Renwick & Hughes 1975; 19 Vité & Pitman 1968; 20 Renwick et al. 1976.

[3] frontalin enantiomers reported to be present in a ratio of 85% (-): 15% (+).

[4] brevicomin identified in *D. frontalis* males was a 97:3 mix of endo: exo - brevicomin; the endo-brevicomin was a 97:3 mix of +:-endo-brevicomin and exo-brevicomin enantiomers were not differentiated.

[5] discrepancy between text and chromatogram within a given publication.

[6] based upon chromatogram.

[7] only males tested and/or reported.

[8] based upon text.

[9] only females tested.

[10] one-day old adults.

[11] five-day old adults.

[12] results from acid-catalyzed rearrangement of seudenol.

[13] results directly from oxidation of 1-methyl cyclohexene.

[14] results from acid-catalyzed rearrangement of trans-verbenol.

[15] a non-terpenoid hydrocarbon.

Appendix 2. Pheromone Production by Dendroctonus terebrans

COMPOUND	NEWLY EMERGED ADULTS		EFFECTS ON PHEROMONE PRODUCTION FOLLOWING EXPOSURE TO:									EFFECTS OF FEEDING ON PHEROMONE PRODUCTION [3]		
			Alpha - pinene			Beta - pinene			Myrcene					
	SEX [1]	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]
frontalin	F	1, 2												
endo-brevicomin	M	1												
exo-brevicomin	M	1, 2												
trans-verbenol	M, F M	1 3 [4]	M F M	appears appears increases	4 [4, 5] 4 [4, 6] 3 [4]	M	appears	4 [4, 5]				M, F	appears	2, 4 [5]
cis-verbenol	F	4 [5]	M	appears	4 [4, 5]							M F	appears increases	2, 4 [5] 4 [5]
verbenone	NONE	3 [4]										M > F	appears	2
myrtenol	M, F	1	M	appears	4 [4, 5]	M	appears	4 [4, 5]				M, F	appears	2, 4 [5]
cis-3-pinen-2-ol			M	appears	4 [4, 5]							M	appears	4 [5]
myrtenal												M, F	appears	2
trans-pinocarveol						M	appears	4 [4, 5]				M, F	appears	2
pinocarvone						M	appears	4 [4, 5]						
unknown						M	appears	4 [4, 5]						
ipsdienol									M	appears	4 [5]			
alpha-pinene	M, F	2												
beta-pinene	F	2										M	appears	2

[1] M = male; F = female.

[2] 1 Payne et al. 1987; 2 Phillips et al. 1989; 3 Hughes 1975; 4 Hughes 1973.

[3] or effects of encountering resin, under natural conditions, on pheromone production.

[4] only males tested and/or reported.

[5] based upon results of D. valens as presented on chromatographic data of a given publication.

[6] based upon results of D. valens as presented in the test of the cited publication.

Appendix 3. Pheromone Production by Ips calligraphus

	CALLOW ADULT			NEWLY EMERGENT ADULT			EFFECTS ON PHEROMONE PRODUCTION FOLLOWING EXPOSURE TO:								
							oleoresin vapor			myrcene vapor			myrcene vapor after 48 hr feeding		
COMPOUND	SEX [1]	PHEROMONE	REF [2]	SEX [1]	PHEROMONE	REF [2]	SEX [1]	EFFECT	REF [2]	SEX [1]	EFFECT	REF [2]	SEX [1]	EFFECT	REF [2]
ipsdienol	M, F	none	1	M, F M	none none	1 2	M, F	none	1	M	none	2	M	appears	2
ipsenol	M, F	none	1	M, F M	none none	1 2	M, F	none	1	M	none	2	M	none	2
trans-verbenol	M, F	none	1	M, F	none	1	M >>> F	appears	1						
cis-verbenol	M, F	none	1	M, F	none	1	M [7]	appears	1						
host terpenes															
unknown															

[1] M = male; F = female.

[2] 1 Vité et al. 1972; 2 Hughes 1974; 3 Renwick & Vité 1972

[3] Florida and east Texas I. calligraphus frass volatiles were identical.

[4] also found in feces, but not in the midgut.

[5] mating not proven, but both males and females were present together in the host tree.

[6] produce primarily the trans-isomer.

[7] only a trace found in females.

EFFECTS OF FEEDING ON PHEROMONE PRODUCTION			EFFECTS OF MATING ON PHEROMONE PRODUCTION			EFFECT OF POSITION WITHIN A HOST TREE ON PHEROMONE PRODUCTION								
						Lower trunk			Attractive portion of crown bole			Branches		
SEX [1]	EFFECT	REF [2]	SEX [1]	EFFECT	REF [2]	SEX [1]	EFFECT	REF [2]	SEX [1]	EFFECT	REF [2]	SEX [1]	EFFECT	REF [2]
M	appears	1 [4], 2, 3 [3]	M	ceased	1 [5]	M	little	1	M	much	1	M	very little	1
M	none	1												
M	trace	2												
M > F	appears	3 [3, 6]				M	much	1	M	much	1	M	trace	1
---	present	1 [4]												
M > F	appears	3 [3, 6]							M	much	1	M	trace	1
---	present	1 [4]												
M = F	appears	1 [3]												

Appendix 4. Pheromone Production by Ips avulsus

	NEWLY EMERGENT ADULT			EFFECTS ON PHEROMONE PRODUCTION FOLLOWING EXPOSURE TO:						EFFECTS OF FEEDING ON PHEROMONE PRODUCTION		
				myrcene vapor			myrcene vapor after 48 hr feeding					
COMPOUND	SEX [1]	PHEROMONE	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]
ipsdienol	M	none	1	M	appears	1	M	appears	1	M M	present appears	2 1
ipsenol	M	none	1	M	none	1	M	none	1	M M	none none	2 1
trans-verbenol										M	present	2
cis-verbenol										M	present	2
host terpenes												
unknown										M	present	2

[1] M = male; F = female.

[2] 1 Hughes 1974; 2 Vité et al. 1972.

Appendix 5. Pheromone Production by *Ips grandicollis*

COMPOUND	BODY REGION	NEWLY EMERGENT ADULT			EFFECTS ON PHEROMONE PRODUCTION FOLLOWING EXPOSURE TO:					
					myrcene vapor			myrcene vapor after 48 hr feeding		
		SEX [1]	PHEROMONE	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]
ipsdienol	HG	M	none	1	M	none	1	M	trace	1
ipsenol	HG	M	none	1	M	none	1	M	appears	1
trans-verbenol	HG									
cis-verbenol	HG									
host terpenes	HG									
unknown	HG									

[1] M = male; F = female.

[2] 1 Hughes 1974; 2 Vité et al. 1972; 3 Vité & Renwick 1971b; 4 Hertel et al. 1969; 5 Ward 1967.

EFFECTS OF FEEDING ON PHEROMONE PRODUCTION			EFFECTS OF MATING ON PHEROMONE PRODUCTION			EFFECTS OF TOPICAL APPLICATION OF IPSDIENOL ON PHEROMONE PRODUCTION					
						Unfed			Fed		
SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]	SEX [1]	EFFECT	REFER [2]
M	none	2									
M	trace	1									
M	appears	1, 3	M	none	4, 5	M	trace	1	M	much	1
M	present	2									
M	present	2									
M	present	2									
M	appears	3									
M	appears	3									
M	present	2									

Appendix 6. Range in size (um) and suggested function of six sensilla types on antennae of five species of Scolytidae [a].

Sensilla Type	**chaetica [b]**	**trichodea [c]**	**trichodea [d]**	**trichodea [e]**	**trichodea [f]**	**basiconica [g]**
		I	II	III	long	short
Suggested Function [h]	MR	PR	OL	CCR	OL	OL
SPECIES						
Dendroctonus frontalis	7-115	8-12	6-32	14-30	6-33	4-8
Dendroctonus terebrans [i]	17-155	16 [j]	11-44	4-28	6-15	3-8
Ips calligraphus	15-225	8-26	8-40	20-65	4-25	5-8
Ips avulsus	10-145	10-33	14-21	15-25	8-16	6-10
Ips grandicollis	14-275	6-21	9-30	15-47	7-25	4-9

[a] reconstructed from Payne et al. 1973.

[b] long, stiff hairs attached at the base to a socket by an articulating membrane; found on all parts of the antennae, butt most abundant on the scape.

[c] short, thin hairs articulating in a socket; found only on the very base of the scape and first funicular segment.

[d] long, thin-walled hairs, sharply pointed and gently curved; found only on the club, along the margins, and sporadically within the sensory fields.

[e] thick-walled, blund-tipped hairs with a pronounced curvature; found only on the club and primarily along the sensory field margins.

[f] thin-walled hairs, cylindrical for most of their length and tapering sharply to a point; make up the bulk of sensilla in the sensory fields.

[g] short, flask-shaped pegs that occur in very small numbers; scattered over the distal area of the club, along the margins, and within the sensory fields.

[h] MR = mechanoreption; PR = proprioception; OL = olfaction; CCR = contact chemoreception.

[i] sex undetermined

[j] only one measurement possible.

Appendix 7. Sensilla on *Dendroctonus frontalis* antennal club as discerned from SEM's [a].

Sensilla	Number	Location on Club	Function
basiconica [b]	700	Primarily in sensory bands	Olfaction
trichodea II [c]	80	Just distal and between sensory bands	Olfaction
trichodea III [d]	60	Between sensory bands and generally distal to trichodea II.	mechanoreception
fluted [e]	female = 20 male = 10	Within sensory bands.	undetermined

[a] reconstructed from Dickens and Payne 1978a.

[b] numerous pores; circular pore kettle and associated pore tubules contact dendritic branches within amorphous sensillum liquor; 1 or 2 bipolar neurons innervate each basiconicum

[c] porous; pore tubules and dendritic branches within sensillum liquor.

[d] non-porous and ridged; no dendritic branches within homogeneous sensillum liquor.

[e] non-porous; no electrophysiological recordings were made.

Appendix 8. Electrophysiological analysis of olfaction in *Dendroctonus frontalis*.

Compound	Electroantennogram [1]		Single Cell Recordings		
	Sex [2]	Ref [3]	Sex [2]	Sensilla type	Ref [3]
frontalin	M > F	1	---	s. basiconica long	5
	M = F	2, 3	---	s. basiconica long	6
	M = F	4	F	s. basiconica	7
	---	5	F	s. trichodeum II	7
	M > F	6	---	s. basiconica	8
	M, F	8	---	---[7]	9
	M = F	9			
	M [5]	9			
(+)-frontalin	M > F	9	---	---	9
(-)-frontalin	M = F	9	---	---	9
15% (+) : 85% (-)-frontalin	M = F	9			
trans-verbenol	---	5	F	s. basiconica	7
	M > F	6	---	s. basiconica	8
	M, F	8			
brevicomin	M < F	1			
endo-brevicomin	---	5	F	s. trichodeum II	7
	M < F	6	F	s. basiconica	7
exo-brevicomin	M = F	3, 4	F	s. basiconica	7
	---	5			
	M < F	6			
(+)-*exo*-brevicomin		---	---	s. basiconica long	6
(-)-*exo*-brevicomin		---	---	s. basiconica long	6
verbenone	---	5	F	s. basiconica	7
	M < F	6	---	s. basiconica	8
	M, F	8			
alpha-pinene	M, F	1, 3	---	s. basiconica long	5
	M = F	4	---	s. basiconica long	6
	---	5	F	s. trichodeum II	7
	M > F	6	F	s. basiconica	7
3-carene	M < F	1	F	s. basiconica	7
	M = F	3, 4			
	---	5			
	M = F	6			
ethanol	M, F	1			
5-methyl-6, 8-dioxabicyclo [3.2.1] octane [5]	---	3			
5,7-dimethyl-6,8-dioxabicyclo [3.2.1] octane [5]	---	3			
2-propyl-2,5-dimethyl-1,3-dioxalane [5]	---	3			
2-ethyl-2,5-dimethyl-1,3-dioxalane [5]	---	3			
2-butyl-1,3-dioxalane [5]	---	3			
2-isopropyl-5,5-dimethyl-1,3-dioxalane [5]	---	3			
2-isobutyl-2-methyl-1,3-dioxalane [5]	---	3			
2-amyl-2-methyl-1,3-dioxalane [5]	---	3			
endo-5,7-dimethyl-(frontalin) [6]	M [4]	10			
exo-5,7-dimethyl-(frontalin) [6]	M [4]	10			
endo-7-methyl-(frontalin) [6]	M [4]	10			
exo-7-methyl-(frontalin) [6]	M [4]	10			

Compound	Electroantennogram [1]		Single Cell Recordings		
	Sex [2]	Ref [3]	Sex [2]	Sensilla type	Ref [3]
1-methyl-(frontalin) [6]	M [4]	10			
5-methyl-(frontalin) [6]	M [4]	10			
6,8-dioxabicyclo [3.2.1] octane [6]	M [4]	10			

[1] The relative magnitude of the EAG response in male and female beetles is apparently correlative with acceptor population size.

[2] M = male; F = female; --- = sex not indicated.

[3] [1] Payne 1970; [2] Payne 1971; [3] Payne 1974; [4] Payne 1975; [5] Payne and Dickens 1976; [6] Dickens and Payne 1977; [7] Dickens and Payne 1978a; [8] Dickens and Payne 1978b; [9] Payne et al. 1982; [10] Payne et al. 1988.

[4] Only males tested.

[5] Parapheromones of frontalin (1,5-dimethyl-6,8-dioxabicyclo [3.2.1] octane).

[6] Analog of frontalin (1,5-dimethyl-6,8-dioxabicyclo [3.2.1] octane).

[7] --- = sensilla type not indicated.

Appendix 9. Electroantennographic analysis of olfaction in *Dendroctonus terebrans*.

Compound	**Sex** [1]	**Reference** [2]
frontalin	M = F	1,2
trans-verbenol	M = F	1,2
endo-brevicomin	M = F	1,2
turpentine	M > F	1,2
verbenone	M = F	2
alpha-pinene	M = F	2
beta-pinene	M = F	2
ipsenol	M = F	2
ipsdienol	M = F	2

[1] M = male; F = female.

[2] [1] Payne et al. 1987; [2] Delorme and Payne 1990.

Appendix 10. Electroantennographic Analysis of Olfaction in *Ips calligraphus*, *Ips avulsus*, and *Ips grandicollis*.

Compound	*Ips calligraphus* Sex [1]	*Ips avulsus* Sex [1]	*Ips grandicollis* Sex [1]	Reference [2]
frontalin				
(+, -)	M = F	M = F	M = F	1
(+)	M = F	M = F	M = F	1
(-)	M = F	M = F	M = F	1
verbenone				
(+, -)	M = F	M = F	M = F	1
(+)	M = F	M = F	M = F	1
(-)	M = F	M = F	M = F	1
endo-brevicomin	M < F	M = F	M = F	1
cis-verbenol	M = F	M = F	M = F	1
trans-verbenol	M = F	M = F	M = F	1
alpha-pinene	M = F	M = F	M = F	1
ipsdienol	M = F	M = F	M = F	1
ipsenol	M = F	M = F	M = F	1

[1] M = male; F = female.

[2] [1] Smith et al. 1988.

Appendix 11. Behavioral response of *Dendroctonus frontalis* to beetle-produced frass and body parts under controlled laboratory conditions.

ATTRACTIVE			REPELLENT		
Treatment[1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]
F.D.F. frass	M > F	1	F.D.F. frass	F [4]	1
M.D.F. frass	M < F	1	M.D.F. frass	M [4] > F [4]	1
Inner bark	M , F	1			
ethanol [5]	M , F	1	benzene [6]	M , F	1
water [5]	M , F	1	acetone [6]	M , F	1
F.D.F. frass extract	M > F	1			
F.D.F. ABP	M , F	1			
F.D.F. PBP	M > F	1	F.D.F. PBP	F [4]	1
M.D.F. PBP	M , F	1	M.D.F. ABP	F [4]	1
M.D.F. PBP	M , F	1	M.D.F. PBP	M , F	1
F.D.F. ABP extract	M [4]	1	F.D.F. ABP extract	F [4]	1
F.D.F. PBP extract	M	1	F.D.F. PBP extract	F	1
M.D.F. ABP extract	M [4]	1	A.D.F. ABP extract	M [4], F [4]	1
M.D.F. PBP extract	M [4]	1	M.D.F. PBP extract	M , F	1

[1] ABP = anterior body part included the crushed head and a prothorax.
D.F. = *Dendroctonus frontalis*.
F. = female.
Frass = boring dust and fecal material.
M. = male.
PBP = posterior body part includes the crushed mesothorax, metathorax, and abdomen.

[2] M = male; F = female.

[3] [1] Tsao and Yu 1967.

[4] A small percentage of the beetles responded in this manner.

[5] Slightly attractive.

[6] Strongly repellent.

[1] a = *alpha*-pinene.
DF. IB = female *D. frontalis* infested bolt.
ENB = *endo*-brevicomin.
EXB = *exo*-brevicomin.
F = frontalin.
(+)-F = (+)-frontalin.
(-)-F = (-)-frontalin.
M = myrtenol.
T = turpentine.
TV = *trans*-verbenol.
V = verbenone.

FA1 = frontalin analog 1 = *endo*-5,7-dimethyl-(frontalin).
FA2 = frontalin analog 2 = *exo*-5,7-dimethyl-(frontalin).
FA3 = frontalin analog 3 = *endo*-7-methyl-(frontalin).
FA4 = frontalin analog 4 = *exo*-7-methyl-(frontalin).
FA5 = frontalin analog 5 = 1-methyl-(frontalin).
FA6 = frontalin analog 6 = 5-methyl-(frontalin).
FA7 = frontalin analog 7 = 6,8-dioxabicyclo[3.2.1] octane.

[2] M = male; F = female;

[3] [1] Rudinsky 1973; [2] McCarty et al. 1980; [3] Rudinsky et al. 1974; [4] Payne et al. 1988; [5] Payne et al. 1982; [6] Payne et al. 1976; [7] Roberts et al. 1982; [8] Andryszak et al. 1982.

[4] only male *D. frontalis* tested.

[5] a 1:1:1 mixture of frontalin, *trans*-verbenol, and *alpha*-pinene.

[6] 0.01% concentration.

[7] no elution rate provided.

[8] 0.0001% - 0.001% concentrations.

[9] 0.01% - 1.0% concentrations.

[10] 0.0001% - 1.0% concentrations.

[11] 0.001% - 0.1% concentrations.

[12] 2.0% concentration.

[13] 1.0% concentration.

[14] 0.1% concentration.

[15] 0.01% concentration.

[16] 0.5% concentration.

[17] elution rate of 10^{-4} - 10^{-1} ug/ul/min.

[18] a 1:2 mixture of frontalin and *alpha*-pinene eluted at 10^{-5} - 10^{1} ug/ul/min.

[19] elution rate of 10^{-1} - 10^{2} ug/ul/min.

[20] elution rate of 10^{-3} - 1.0 ug/ul/min.

[21] elution rate of 10 ug/min.

[22] elution rate of 40 ug/min.

[23] a 15:85 mixture of (+)-frontalin and (-)-frontalin.

[24] mixed results.

[25] a 1:1:12 mixture of frontalin, *trans*-verbenol and turpentine.

[26] elution rate of 10^{-3} ug/ul/min.

[27] elution rate of 10^{-1} ug/ul/min.

[28] elution rate of 10^{0} ug/ul/min.

[29] elution rate of 10^{-2} - 10^{1} ug/ul/min.

[30] elution rate of 10^{-5} - 10^{2} ug/ul/min.

[31] elution rate of 14 ug/min.

[32] elution rate of 60 ug/min.

[33] elution rate of 1 ug/ul/min.

[34] analogs of frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1] octane).

Appendix 12. Behavioral response of *Dendroctonus frontalis* to pheromones under controlled laboratory conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]
Ethanol[6]	M	1[4]	F+TV+a[5,6]	M	1[4]	V[8]	M	1[4]	V[9]	M	1[4]
Ethanol[6]	---	2	F+TV+a[5,6]	M	3[4]	V[8]	M	3[4]	V[9]	M	3[4]
M[13]	M	3[4]							ENB[10]	M	3[4]
M[13]+a[13]	M	3[4]	(F+TV+a)[5]+M[13] DF. IB F[17] F[33] a[19] F[21]+a[22] (+)-F[21]+a[22] (-)-F[21]+a[22] (+)-F[21]+(-)-F[21]+a[22]	M M M>F M=F M=F M,F M,F M,F M,F	3[4] 1[3] 2 4 2 5 5 5 5	M[11] a[18]	M M>F	3[4] 2	M[12] V[13] ENB[14] V[15]+ENB[15] V[16]	M M M M M	3[4] 3[4] 3[4] 3[4] 1[4]
V[19,23]	M,F	2	V[21,24] F+TV+T[25,27] F+TV+T[25,26] F+TV+T[25,30] F+TV+T[25,31] F+TV+T[25,32] FA1[33,34] FA2[33,34] FA3[33,34] FA4[33,34] FA5[33,34] FA6[33,34] FA7[33,34]	M F M M>F M,F --- M,F M,F M,F M,F M,F M,F M,F	2 2 2 6 7 8 4 4 4 4 4 4 4	V[26]	F	2	V[28] V[29]	F M	2 2

Appendix 13. Behavioral response of *Dendrocronus frontalis* to beetle-infested pine under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]
			DF.IB. --- DF.AT.M=F	1,2[4],3 4							
M.DF.IB.	---	6	F.DF.IB.--- F.DF.IB.M,F F.DF.IB.M=F F.DF.IB.M>F M.+F.DF.IB. M.+F.DF.IB. M.+F.DF.IB. M.+F.DF.IB.	1,5 6 7,8[6] 9[7] --- M,F M=F M>F	1 6 8[6] 9[7]				M.IG.IB. M.IG.IB.	--- M=F	5 7[5]
M.IC.IB.	---	1,5,7,8[6]									
F.IC.IB.	---	1									
M.+F.IC.IB.	---	8[6]									
M.IA.IB.	---	5,7,8[6]									
M.+F.IA.IB.	---	1,8[6]									
M.IG.IB.	---	1,5,7,8[6],9[7]									
M.+F.IG.IB.	---	8[6]									
M.IC.+M.IA.IB.	---	7	F.DF.+M.IC.IB.	M=F	7						
M.IC.+M.IG.IB.	---	7	F.DF.+M.IA.IB.	M=F	7						
M.IA.+M.IG.IB.	---	7	F.DF.+M.IG.IB. F.DF.+M.IC. +M.IA.+M.IG.	M=F M=F	7[5] 7						
UB.	---	6,7,8,9	UB. ---	1[8]							

[1] A.T. = Attacked tree
D.F. = *Dendroctonus frontalis*
F. = female
I.A. = *Ips avulsus*
I.B. = infested bolt
I.C. = *Ips calligraphus*
I.G. = *Ips grandicollis*
M. = male
U.B. = uninfested bolt

[2] M = male; F = female; --- sex not indicated.

[3] [1] Vité et al. 1964; [2] Gara et al. 1965; [3] Coster and Gara 1968; [4] Renwick and Vité 1970; [5] Svihra et al. 1980; [6] Coster et al. 1977b;[7] Birch et al. 1980; [8] Svihra 1982; [9] Birch and Svihra 1979.

[4] *D. frontalis* was more attracted to infested bolts wired to vertical trees than to those wired to horizontal trees.

[5] Mixed results

[6] 25 beetles.

[7] 30 beetles.

[8] Very low attractancy.

Appendix 14. Behavioral response of *Dendroctonus frontalis* to crushed bodies of *Dendroctonus* species.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION		
Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]
			250M+250F. DF. 250M+250F. DF. 250M+250F. DF.[4] 250M+F. DF. plus oleoresin	--- M<F --- M<F	3,4 2 3 1			
600 F.DF.[6]	---	3	600F. DF.[5]	---	3			
			250M.+250F. DB.	---	4			
			250M.+250F. DB.	M<F	2			
			250M. DB.	---	4	TV	---	4
			250M. DB.	M<F	2	TV	M>F	2
300M. DP.	---	4	300F. DP.	---	4			

[1] DB. = *Dendroctonus brevicomis*; DF. = *Dendroctonus frontalis*; DP. = *Dendroctonus pseudotsugae*.

[2] M = male; F = female; --- = sex not indicated.

[3] ^{1} Kinzer et al. 1969; ^{2} Pitman et al. 1969; ^{3} Vité and Renwick 1968; ^{4} Renwick and Vité 1968.

[4] Live beetles.

[5] Hindgut plus malpighian tubules only.

[6] Entire body minus the hindgut.

Appendix 15. Behavioral response of *Dedroctonus frontalis* to pheromones under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
F[32]	---	1	F[5]	---	2[4]	a[5]	---	4			
						a[5]	M>>F	2	V[5]	M=F	2
						TV[5]	---	2,4			
			F[5]	M>F[4]	3	a[5]	M>F	3			
			F[7]	M>F	4	TV[7]	M=F	4			
						T[13]	M=F	4			
						TV[7]+T[13]	M=F	4			
			F[4][23][33]	---	4						
			F[5]+A[5]	M>F	3, 5				V[4][5]	M>F	6
									V[14]	M=F	3
									ENB[4][5]	M>>F	6
									EXB[4][5]	M>>>F	6
			F[7]+A[10]	M>F	3				V[12]	M=F	4
									V[14]	M<F	4[42]
									ENB[7]	M>F	4
			F[7]+A[13]	M>F	3						
			(F+a)[6][8][15]	---	6						
			(±)F[7]+a[10]	M=F	7						
			(+)F[7]+a[10]	M=F	7						

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
			(-)F[7]+a[10]	M=F	8						
TV[5]	---	9	F[5]+TV[5]	M>F[4]	3	a[5]	M>F	3			
TV[7]	M>F	4									
			F[5]+a[5]+TV[5]	M>F	3				V[7]	M>F	3
			F[7]+a[10]+TV[7]	M>F	4						
			F[7]+a[13]+TV[7]	M>F	4						
			F[5]+B[5][41]+TV[5]	M>F	3						
			F[5]+CAM[5][41]+TV[5]	M>F	3						
			F[5]+CAR[5][41]+TV[5]	M>F	3						
			F[5]+F[5][41]+TV[5]	M>F	3						
			F[5]+L[5][41]+TV[5]	M>F	3						
			F[5]+M[5][41]+TV[5]	M>F	3						
			F[5]+MC[5][41]+TV[5]	M>F	3						
			F[5]+TER[5][41]+TV[5]	M>F	3						
T[28]	---	5	F[7]+T[13]	M>F	4				V[12]	M<F	4
T[16]	---	11							V[14]	M=F	4
T[13]	M>F	4							ENB[7]	M>F	4
ENB[7]	M>F	4							ENB[7]+EXB[7]	M>F	4
EXB[7]	M=F	4	F[7]+T[13]+EXB[7]	M=F	4						
			F[19]+T[26]	M<F	10						
			FA1[18]+T[26]	M=F	10						

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
			FA2[22]+T[26]	M,F	10						
			FA3[18]+[26]	M,F	10						
			FA4[20]+T[26]	M,F	10						
			FA5[20]+T[26]	M,F	10						
			FA6[20]+T[26]	M,F	10						
			FA7[17]+T[26]	M,F	10						
			F[7]+TV[7]+T[13]	M=F	4				ENB[7]	M=F	4
									ENB[7]+EXB[7]	M>F	4
			F[7]+TV[7]+T[13]+EXB[7]	M=F	4				ENB[7]+EXB[7]	M>F	4
			F[7]+TV[7]+T[13]+EXB[7]	M=F	4						
V[5]	---	9	F[5]+V[7]	M<F[4]	3	TV[4]	M=F	3			
V[5]	M=F	4									
			F[7]+a[10]+V[7]	M>F	4						
			F[7]+a[10]+V[11]	M=F	4						
			F[7]+a[10]+V[14]	M>F	4[42]				ENB[7]	M>F	4
			F[7]+T[13]+V[7]	M>F	4						
			F[7]+T[13]+V[11]	M<F	4						
O[5]	---	1,12[38]	F[31]+O[5]	M>>F	1						
O[5]+TV[5]	---	1	F[32]+O[5]+TV[5]	M>>F							
			FL[24][33][35]	M>F[4]	5	T[27]	M>F	5			
						T[28]	M>>F	5			

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
						(ENB:V)[36][21]	M=F	5			
			FL[22][35]	---	13						
			FL[9][35]+T[16]	M>>>F	11				(-)ENB[5]	M>F	11
						(±)ENB[5]	M>>F	11			
						(+)ENB[5]	M>>F	11			
F:T[23][34]	---	4	F:T[23][34]+T[28]	M>F	5						
IPSPH[25][37]	---	5									
IPSPH[25][37]+T[28]	---	5									
			HT	---	14				(ENB:EXB)[39][30]	---	14
									(ENB:EXB)[39][31]	---	14
									(ENB:EXB)[40][31]	---	14
									(ENB:EXB)[39][30]+V[29]	---	14
			HT+V[29]	---	14						
I.C.A.	---	12	D.B.A.	---	12						
			F[43]+A[44]	M,F	15				V[45]	M	15
			F[43]+A[44]+V[46]	M,F	15						
			F[43]+A[44]+V[47]	F	15						
			F[48]+T[28]	M,F	15	V[53]	F	15	V[49]	M	15
									V[50]	F	15
									ENB[54]	M	15
			F[48]+T[28]+V[51]	M	15						

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
			F[48]+T[28]+V[52]	F	15						
			F[48]+T[28]+ENB[55]	F	156				V[56]	M	15
									V[57]	F	15

[1] A = *alpha*-pinene.
B = *beta*-pinene.
cam = camphene.
car = 3-carene.
D.B.A. = *Dendroctonus brevicomis* attractant.
ENB = *endo*-brevicomin.
(±)-ENB = racemic *endo*-brevicomin.
(+)-ENB = (+)-*endo*-brevicomin.
(-)-ENB = 9-0-*endo*-brevicomin.
EXB = *exo*-brevicomin.
F = frontalin.
(±)F = racemic frontalin.
(+)-F = (+)-frontalin.
(-)-F = (-)-frontalin.
FL = frontalure.
Fr = fresh resin.
Ht = host tree.
I.C.A. = *Ips confusus* attractant.
IPSPH = *Ips* pheromone.
L = limonene.
M = myrcene.
MC = methyl chavicol.
O = oleoresin.
T = turpentine.
TER = terpinolene.
TV = *trans*-verbenol.
V = verbenone.
FA1 = frontalin analog 1 = *endo* - 5,7 - dimethyl - (frontalin).
FA2 = frontalin analog 2 = *exo* - 5,7 - dimethyl - (frontalin).
FA3 = frontalin analog 3 = *endo* - 7 - methyl - (frontalin).
FA4 = frontalin analog 4 = *exo* - 7 - methyl - (frontalin).
FA5 = frontalin analog 5 = 1 methyl - (frontalin).
FA6 = frontalin analog 6 = 5 - methyl - (frontalin).
FA7 = frontalin analog 7 = 6,8 - dioxabicyclo [3.2.1] octane.

[2] M = male; F = female; --- = sex not indicated.

[3] 1 Kinzer et al. 1969; 2 Renwick & Vité 1970; 3 Renwick & Vité 1969; 4 Payne et al. 1978; 5 Billings 1985; 6 Vité and Renwick 1971a; 7 Vité 1971; 8 Payne et al. 1982; 9 Vité & Crozier 1968; 10 Payne et al. 1988; 11 Vité et al. 1985; 12 Vité et al. 1964; 13 Richerson et al. 1980; 14 Richerson and Payne 1979, 15 Salom et al. 1992.

[4] Very few beetles caught.

[5] No elution rate provided.

[6] Elution rate of 0.3 mg/h

[7] Elution rate of 0.5 mg/h

[8] Elution rate of 0.9 - 3.0 mg/h

[9] Elution rate of 1.0 mg/h

[10] Elution rate of 2.0 mg/h

[11] Elution rate of 2.5 mg/h

[12] Elution rate of 5.0 mg/h

[13] Elution rate of 6.0 mg/h

[14] Elution rate of 10.0 mg/h

[15] Elution rate of 10.0 - 100.0 mg/h

[16] Elution rate of 150 mg/h

[17] Elution rate of 3 mg/24h

[18] Elution rate of 4 mg/24h

[19] Elution rate of 5 mg/24h

[20] Elution rate of 7 mg/24h

[21] Elution rate of 10 mg/24h

[22] Elution rate of 18 mg/24h

[23] Elution rate of 20 mg/24h

[24] Elution rate of 50 mg/24h

[25] Elution rate of 100 mg/24h

[26] Elution rate of 1440 mg/24h

[27] Elution rate of 1800 mg/24h

[28] Elution rate of 3600 mg/24h

[29] Elution rate of 80 mg/24h/tree (16 caps/tree at 5 mg/24h/cap).

[30] Elution rate of 160 mg/24h/tree (16 caps/tree at 10 mg/24h/cap).

[31] Elution rate of 320 mg/24h/tree (32caps/tree at 10 mg/24h/cap).

[32] 1 mg dispensed.

[33] No control trap (blank) tested for comparison.

[34] A 1:2 mixture of frontalin and turpentine.

[35] A 1:2 mixture of frontalin and -pinene.

[36] A 1:2 mixture of *endo*-brevicomin and verbenone.

[37] Ips pheromone (IPSPH) is a mixtureof 2% *cis*-verbenol, 2% ipsenol and 2% ipsdienol in a vaseline-based paste.

[38] Dissolved in gasoline.

[39] A 50:50 mixture of *endo*-brevicomin (ENB) and*exo*-brevicomin (EXB).

[40] An 85:15 mixture of *endo*-brevicomin (ENB) and *exo*-brevicomin (EXB).

[41] No appropriate comparison was provided to determine if the host terpene enhanced or reduced attractiveness of frontalin or frontalin plus *trans*-verbenol.

[42] Mixed or conflicting results.

[43] 50% (+): 50% (-) enantiomeric ratio eluted at 0.5 mg/h.

[44] 50% (+): 50% (-) enantiomeric ratio eluted at 2.0 mg/h.

[45] 50% (+): 50% (-) and 69% (+): 31% (-) enantiomeric ratios eluted at 1.0 mg/h.

[46] 17% (+): 83% (-) enantiomeric ratio eluted at 1.0 mg/h.

[47] 17% (+): 83% (-), 50% (+): 50% (-), and 69% (+): 31% (-) enantiomeric ratios eluted at 1.0 mg/h.

[48] 50% (+): 50% (-) enantiomeric ratio eluted at 0.4 mg/hr.

[49] 17% (+): 83% (-), 34% (+): 66% (-), and 50% (+): 50% (-) enantiomeric ratios eluted at 2.9 mg/h. in June and October, plus 69% (+): 31% (-) enantiomeric ratio eluted at 2.9 mg/h in October, plus the 34% (+): 66% (-) enantiomeric ratio eluted at 5.8 mg/h, 12.5 mg/h, and 18.8 mg/h.

[50] 34% (+): 66% (-), and 50% (+): 50% (-) enantiomeric ratios eluted at 2.9 mg/h in June.

[51] 69% (+): 31% (-) enantiomeric ratio eluted at 2.9 mg/h in June, plus the 34% (+): 66% (-) enantiomeric ratio eluted at 4.2 mg/h.

[52] 17% (+): 83% (-) and 69% (+): 31% (-) enantiomeric ratio eluted at 2.9 mg/h in June and October, plus 34% (+): 66% (-) and 50% (+): 50% (-) enantiomeric ratios eluted at 2.9 mg/h in October, plus the 34% (+): 66% (-) enantiomeric ratio eluted at 4.2 mg/h, 5.8 mg/h, 12.5 mg/h and 18.8 mg/h.

[53] 69% (+): 31% (-) enantiomeric ratio eluted at 2.9 mg/h in October.

[54] 50% (+): 50% (-) enantiomeric ratio eluted at 0.5 mg/h in August and October.

[55] 50% (+): 50% (-) enantiomeric ratio eluted at 0.5 mg/h in August and October.

[56] 17% (+): 83% (-) and 34% (+): 66% (-) enantiomeric ratios eluted at 18.8 mg/h in August and October.

[57] 17% (+): 83% (-) in August and 34% (+): 66% (-) enantiomeric ratios eluted at 18.8 mg/h in August and October.

Appendix 16. Behavioral response of *Dendroctonus terebrans* to pheromones under controlled laboratory conditions.

ATTRACTIVE		
Compound(s) [1,2]	Sex [3]	References [4]
F	M > F	1
ENB	M < F	1
TV	M	1
T	M	1

[1] ENB = *endo*-brevicomin.
F = frontalin.
T = turpentine.
TV = *trans*-verbenol.

[2] Elution rate of 1 ug/min.

[3] M = male; F = female.

[4] ^{1} Payne et al. 1987.

Appendix 17. Behavioral response of *Dendroctonus terebrans* to beetle-infested pine under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE		
Treatment [1]	**Sex [2]**	**Ref [3]**	**Treatment [1]**	**Sex [2]**	**Ref [3]**
F.D.T.I.B	F	2[4]	F.D.T.I.B.MIT	M	2[4]
			F.D.T.I.B.	M=F	2
			F.D.T.I.B.	M>F	3[5]
M.D.T.I.B.	M=F	2[4]	M.D.T.I.B.	M>F	3[5]
M.+F.D.T.I.B.	F	2[4]	M.+F.D.T.I.B.	M	2[4]
			M.+F.D.T.I.B.	M>F	3[5]
			F.D.T.I.T.	---	4
			M+F.D.F.I.B.	---	5[6]
M.+F.I.A.I.B.	---	5			
M.I.C.I.B.	---	5			
F.I.C.I.B.	---	5			
M.I.G.I.B.	---	5			
W.T.	---	1	M.I.T.	M=F	2
			P.I.T.	M=F	1,2
			U.T.	M<F	3
U.B.	M,F	2	U.B.	M>F	3

[1] D.F. = *Dendroctonus frontalis*.
D.T. = *Dendroctonus terebrans*.
F. = female.
I.A. = *Ips avulsus*.
I.B. = infested bolt.
I.C. = *Ips calligraphus*.
I.G. = *Ips grandicollis*.
I.T. = infested tree.
M. = male.
MIT = mechanically injured trees via axe blazes into the sapwood from the ground line to breast height, and where the number of blazes were equal to the number of visible *D. terebrans* attacks on the corresponding attacked trees.
PIT = paraquat-treated trees; a 4% aqueous solution applied to the outer xylem exposed by a bark wound equal to one third the bole circumference of the tree and made at approximately 60 cm above ground level.
UB = unattacked bolt
UT = unattacked tree
WT = wounded tree; the outer xylem was exposed by a bark wound 2.5 cm wide and extending one-third the circumference at 60 cm above ground level.

[2] M = male; F = female; --- sex not indicated.

[3] ^{1} Siegfried et al. 1986; ^{2} Phillips et al. 1989; ^{3} Godbee and Franklin 1976; ^{4} Smith 1963; ^{5} Vité et al. 1964.

[4] 13 beetles.

[5] 12 beetles.

[6] Low attractancy.

Appendix 18. Behavioral response of *Dendroctonus terebrans* to pheromones under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
			pine resin	M,F	1						
			fresh gum	---	3						
T[11,12]	M,F	8	T[4]	---	2,3	E[4]	---	2			
			T[4]	M,F	6	TV[24]	F[12]	6			
						E[4]	M,F	6			
						E[4] + TV[24,25]	M,F	6			
			TP[29]	M,F	12	(-)-F[26]	M>F	12			
						(+)-F[26]	M	12			
						(±)-F[26]	M	12			
						(-)-EXB[27]	F	12			
						(+)-EXB[27]	F	12			
						(±)EXB[27]	F	12			
						(+)-ENB[28]	M<F	12			
						(±)-ENB[28]	F	12			
						(±)-F[26] + (-)-EXB[27]	M	12			
			TP[29] + (+)-F[26]	F	12						
			TP[29] + (±)-F[26]	F	12	(+)-EXB[27]	F	12			
						(±)-EXB[27]	F	12			
			TP[29] + (-)-EXB[27]	M	12						
			TP[29] + (+)-EXB[27]	M	12						

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
			TP[29] + (±)-EXB[27]	M	12						
			TP[29] + (-)-ENB[28]	M<F	12						
			TP[29] + (±)-ENB[28]	M	12						
			TP[29] + (±)-F[26] + (-) -EXB[27]	F	12						
F[10]	M,F	7	T[5]	---	4,5	E[6]	---	4,5			
F[13]	M,F	8	T[7]	M>F	7						
T:F[14]	M,F	7	T[8]	M>F	7	ENB[9]	F	7			
T[11] + F[13]	F	8	T[11,12]	M	8	FL[10]	M	7	ENB[9]	M	7
			T[7] + F[10]	M>F	7				ENB[15]	M	8
			T[11] + F[13]	M>F	8				EXB[16]	M	8
									ENB[15] + EXB[16]	M	8
									V[17]	M	8
ENB[9]	M,F	7									
ENB[15]	M,F	8	T[8] + ENB[9]	M<F	7						
T[11] + ENB[15]	M,F	8									
T[11] + F[13] + ENB[15]	M,F	8									
EXB[16]	M,F	8									
T[11] + EXB[16]	M,F	8									
T[11] + F[13] + EXB[16]	M,F	8									
T[11] + F[13] + ENB[15] + EXB[16]	M,F	8									

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
MT[19]	M,F	8									
T[11]+MT[19]	M,F	8									
T[11]+F[13]+MT[19]	F	8	T[11]+F[13]+MT[19]	M	8						
V[17]	M,F	8									
T[11]+V[17]	M,F	8									
T[11]+F[13]+V[17]	M,F	8									
TV[4]	M,F	9									
TV[18]	M,F	8									
TV[24,25]	M,F	6									
T[11]+TV[18]	M,F	8	T[4]+TV[4]	---	9						
			T[4]+TV[24,25]	M	6						
			T[4]+TV[24,25]	F[12]	6						
T[11]+F[13]+TV[18]	F	8	T[11]+F[13]+TV[18]	M	8	MT[19]	M	8			
T[11]+F[13]+TV[18] +MT[19]	F	8									
FL[10]	M,F	7	T[8]+FL[10]	M>F	7						
FL[10]+ENB[9]	M,F	7	T[8]+FL[10]+ENB[9]	M>F	7						
E[4]	---	10,11	E[4,20]	---	4,5						
E[4]	M,F	6	WGT	---	10						
A[20]	---	10	WGT[21]	---	10						
B[20]	---	10	DWGT	M>F	11						
C[20]	---	10	E+DWGT[22]	M,F	11						

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
MC[20]	---	10	E+DWGT[23]	M,F	11						
BP[20]	---	10	MM[21]	---	10						
L[20]	---	10									

[1] A=*alpha*-pinene.
B=*beta*-pinene.
BP=*beta*-phellandrene.
C=camphene.
DWGT=distilled whoe gum turpentine = 66.4% *alpha*-pinene; 29.41% *beta*-pinene; 1.67% camphene; 1.67% limonene; 0.09% *beta*-phellandrene; and 0.01% myrcene.
D.T.IB=female *D. terebrans* infested bolt.
E=ethanol (95%).
ENB=*endo*-brevicomin.
(+)-ENB=(+)-*endo*-brevicomin (99%)
(-)-ENB=(-)-*endo*-brevicomin (98%)
(±)-ENB=(±)-*endo*-brevicomin
EXB=*exo*-brevicomin.
(+)-EXB=(+)-*exo*-brevicomin (98%)
(-)-EXB=(-)-*exo*-brevicomin (97%)
(±)-EXB=(±)-*exo*-brevicomin
F=frontalin.
(+)-F=(+)-frontalin (97%)
(-)-F=(-)-frontalin (98%)
(±)-F=(±)-frontalin (>99%)
FL=frontalure = a 1:2 mixture of frontalin and *alpha*-pinene.
L=limonene.
MC=myrcene.
MM=monoterpene mixture = *alpha*-pinene+*beta*-pinene+camphene+myrcene+*beta*-phellandrene+limonene.
MT=myrtenol.
P=paraquat.
T=turpentine.
TV=*trans*-verbenol.
TP=turpentine composed of: *alpha*-pinene (58.8%), *beta*-pinene (22.4%), *beta*-phellandrene (4.5%), limonene (1.9%), camphene (0.8%), myrcene (0.8%) and *alpha*-phellandrene (0.7%).
WGT=whole gum turpentine.
WHT=wounded host tree.

[2] M=male; F=female; --- = sex not indicated.

[3] ^{1} Hughes 1975; ^{2} Fatzinger 1975; ^{3} Clements and Williams 1981; ^{4} Fatzinger 1984; ^{5} Fatzinger 1985; ^{6} Fatzinger et al. 1987; ^{7} Payne et al. 1987; ^{8} Phillips et al. 1989; ^{9} Siegfried 1984;
^{10} Siegfried et al. 1986; ^{11} Phillips et al. 1988; ^{12} Phillips et al. 1990.

[4] No elution rate provided.

[5] Elution rates ranged from 0.4 - 711.4 mg/h

[6] A 1:1 (vol:vol) mixture of turpentine plus ethanol eluted at 57 ± 0.7 mg/h

[7] Elution rate of 3,600 mg/24 h

[8] Elution rate of 1,400 mg/24 h

[9] Elution rate of 10 mg/24 h

[10] Elution rate of 20 mg/24 h

[11] Elution rate of 10.14 g/24 h

[12] Mixed results.

[13] Elution rate of 5.77 mg/24 h

[14] A 1:12 mixture of frontalin and turpentine, eluted at 20 mg/24 h

[15] Elution rate of 3.93 mg/24 h

[16] Elution rate of 5.05 mg/24 h

[17] Elution rate of 4.17 mg/24 h

[18] Elution rate of 4.4 mg/24 h

[19] Elution rate of 1.82 mg/24 h

[20] Very few beetles trapped.

[21] 10% solution in 95% ethanol.

[22] Ethanol and distilled whole gum turpentine in separate, but side by side, dispensers.

[23] Ethanol and distilled whole gum turpentine in a 1:1 solution.

[24] Elution rate of 50 ul/24 h

[25] Elution rate of 50 ul/3-4 da.

[26] elution rate of 900 ug/24 h

[27] elution rate of 450 ug/24 h

[28] elution rate of 300 ug/24 h

[29] elution rate of 180 mg/24 h

Appendix 19. Behavioral response of *Ips calligraphus* to beetle-infested pine under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]
F.I.C.I.B.	---	1	M.I.C.I.B.	---	1,2				M.I.A.I.B.	---	2
			M.I.C.I.B.	M<F	3[4],4,5[5]	M.I.G.I.B.[7,9]	M=F	4	F.I.C.I.B.[6]	M<F	5[5]
									M.I.G.I.B.	M<F	4
									M.I.A.I.B.	M=F	4
M.I.A.I.B.	---	4[9],T[5]	M.I.A.I.B.	M=F	4[9,10]						
M.+F.I.A.I.B.	---	1,5[5]									
M.I.G.I.B.	---	1,4[7,9],5[5]	M.I.G.I.B.	M=F	4[8,9]						
M.+F.I.G.I.B.	---	5[5]									
M.I.A.+M.I.G.I.B.	---	4									
M.I.G.+F.D.F.I.B.	---	4	I.P.I.B.	---	1						
F.D.F.I.B.	---	4,5[5]	F.D.F.I.B.	---	6						
M.+F.D.F.I.B.	---	1,5[5]									
U.B.	---	4,5	M.I.C.+F.D.I.B.	M=F	4						
			M.I.C.+M.I.A.+M.I.C.+F.D.F.	M=F	4						

[1] D.F. = *Dendroctonus frontalis*.
F. = female.
I.A. = *Ips avulsus*.
I.B. = infested bolt.
I.C. = *Ips calligraphus*.
I.G. = *Ips grandicollis*.
I.P. = *Ips paraconfusus*.
M. = male.
U.B. = uninfested bolt.

[2] M = male; F = female; --- = sex not indicated.

[3] ^{1} Vité et al. 1964; ^{2} Svihra et al. 1980; ^{3} Renwick and Vité 1972; ^{4} Birch et al. 1980; ^{5} Svira 1982; ^{6} Dixon and Payne 1980.

[4] 40 beetles.

[5] 25 beetles.

[6] Although attraction was reduced, attraction was still significantly greater than that of uninfested bolts.

[7] Low *I. calligraphus* population levels.

[8] High *I. calligraphus* population levels.

[9] Mixed results.

[10] Attraction was low, but significantly greater than uninfested bolts.

Appendix 20. Behavioral response of *Ips calligraphus* to pheromones under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
IPSD [4]	---	1	IPSD[4]+CV[4]	M<<F	1	UB	M<<<F				
CV[4]	---	1	IPSD[4]+TV[4]	M<F	1						
IPSD+(*R*)CV[6]	---	2	IPSD[5]+(*S*)CV[6]	M<F	1				(*R*)CV[7]	M<F	2
			IPSD[5]+(*S*)CV[6]+(*R*)CV[6]	M<F	2						
(+)-IPSD[8]+(*S*)CV[8]	---	3	(-)-IPSD[8]+(*S*)CV[8]	M<F	3				(+)-IPSD[8]	M<F	3
			IPSD[9]+(*S*)CV[8]	M<F	3						
F[10]	---	4									
TV[10]	---	4									
T[11]	---	4									
ENB[10]	---	4									
EXB[10]	---	4									
V[12]	---	4									
F[10]+TV[10]	---	4									
F[10]+T[11	---	4									
F[10]+TV[10]+T[11]	---	4									
F[10]+T[11]+ENB[10]	---	4									
F[10]+T[11]+EXB[10]	---	4									
F[10]+T[11]+ENB[10]+EXB[10]	---	4									
F[10]+ENB[10]+EXB[10]	---	4									
TV[10]+ENB[10]+EXB[10]	---	4									

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
T[11]+ENB[10]+EXB[10]	---	4									
			IPSB[13]	---	5						
T[11]	---	6	IPSPH[15]	M<F	6						
FL[16]+T[11]	---	6	IPSPH[15]+T[14]	M<F	6						

[1] CV=*cis*-verbenol
ENB=*endo*-brevicomin
EXB=*exo*-brevicomin
F=frontalin
FL=frontalure is a 1:2 mixture of frontalin and turpentine.
IPSB=*Ips* bait is a mixture of 2% frontalin, 19% *alpha*-pinene, 2% (s)-*cis*-verbenol, 1% racemic ipsdienol, 1% racemic ipsenol, and 75% inert petroleum carrier by volume.
IPSD=ipsdienol
(+)-IPSD=(*S*)-(+)-ipsdienol
(-)-IPSD=(*R*)-(-)-ipsdienol
IPSPH=*Ips* pheromone is a mixture of 2% *cis*-verbenol, 2% ipsenol, and 2% ipsdienol in a vaseline-based paste.
(*R*)CV=(*R*)-*cis*-verbenol
(*S*)CV=(*S*)-*cis*-verbenol
T=turpentine
TV=*trans*-verbenol
UB=uninfested bolt
V=verbenone

[2] M=male; F=female; --- = sex not indicated.

[3] ^{1} Renwick & Vité 1972; ^{2} Vité et al. 1976b; ^{3} Vité et al. 1978; ^{4} Dixon & Payne 1980; ^{5} Rose et al. 1981; ^{6} Billings 1985.

[4] Eluted at 1 mg/h

[5] Eluted at 0.4 mg/h

[6] Eluted at 0.1 mg/h

[7] Eluted at 1-2 mg/h

[8] Eluted at 2 mg/h

[9] Eluted at 4 mg/h

[10] Eluted at 0.5 mg/h

[11] Eluted at 6.0 mg/h

[12] Eluted at 0.5-10.0 mg/h

[13] Eluted at 100 mg/24 h. for 15 days.

[14] Eluted at 3600 mg/24 h.

[15] Eluted at 100 mg/24 h.

[16] Eluted at 20 mg/24 h.

Appendix 21. Behavioral response of *Ips avulsus* to beetle-infested pine under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]
			M.I.A.I.B.	---	1	M.I.G.I.B.	---	1			
			M.I.A.I.B.	M=F	2[4]						
			M.I.A.I.B.	M<F	3	M.I.G.I.B.	M=F	3[5]			
			M.+F.I.A.I.B.	M=F	2[4]						
M.I.C.I.B.	---	3[5]	M.I.C.I.B.	---	1,4						
F.I.C.I.B.	---	4	M.I.C.I.B.	M=F	3[5]	M.I.G.I.B.	M=F	3[5]	F.D.F.I.B.	M=F	3
			M.I.C.I.B.	M<F	2[4]				F.I.C.I.B.	M>F	2[4,8]
			M.+F.I.C.I.B.	---	3						
M.I.G.I.B.	---	2[4],3[5],4	M.I.G.I.B.	M=F	3[5,6]						
M.+F.I.G.I.B.	---	2[4]									
			D.F.I.B.	---	4						
F.D.F.I.B.	---	2[4],3	F.D.F.I.B.	---	1						
M.+F.D.F.I.B.	---	2[4]	M.+F.D.F.I.B.	---	4[7]						
M.I.G.+M.I.C.I.B.	---	3[5]	M.I.A.+M.I.C.I.B.	M=F	3						
M.I.G.+F.D.F.I.B.	---	3	M.I.A.+M.I.G.I.B.	M=F	3[5]						
			M.I.A.+F.D.F.I.B.	M<F	3						
			M.I.A.M.I.C.+M.I.G.+F.D.F.I.B.	M<<F	3						
U.B.	---	2,3,4									

[1] D.F. = *Dendroctonus frontalis*.
F. = female.
I.A. = *Ips avulsus*.
I.B. = infested bolt.
I.C. = *Ips caligraphus*.
I.G. = *Ips grandicollis*.
M. = male.
U.B. = uninfested bolt.

[2] M = male; **F** = female; --- = sex not indicated.

[3] [1] Svihra et al. 1980; [2] Svihra 1982; [3] Birch et al. 1980; [4] Vité et al. 1964.

[4] 25 beetles.

[5] Mixed results.

[6] Attraction was low, but significantly greater than uninfested bolts.

[7] Very low attraction.

[8] Although attraction was reduced, attraction was still significantly greater than that of uninfested bolts.

Appendix 22. Behavioral response of *Ips avulsus* to pheromones under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
			IPSD [2]	M>F	1	IPSE[4]	M>F	1			
			(-)-IPSE [4]	M>F	1	(-)-IPSE[4,16]	M>F	1			
			IPSD[4]+(-)-IPSE[4,16]	M>F	1						
			IPSD[4]+(+)-IPSE[4]	M>F	1						
			IPSD[6]+IPSE[6]	M>F	2						
			(+)-IPSD[5]+IPSE[6]	M>F	2						
			(-)-IPSD[5]+IPSE[6]	M>>F	2						
D.B.A.	---	6	HT+D.F.	---	4	ENB:EXB[7,9]	---	3			
						ENB:EXB[7,10]	---	3			
						ENB:EXB[8,10]	---	3			
			HT+D.F.+V[11]	---	3						
			IPSB[12]	---	4						
T[13]		5	IPSPH[14]	M>>F	5				T[13]	M>F	5
FL[15]:T[13]		5									
RO		6									

[1] D.B.A. = *Dendroctonus brevicomis* attractant.
D.F. = *Dendroctonus frontalis* (sex and density not provided).
ENB:EXB = a mixture of *endo*-brevicomin and *exo*-brevicomin.
FL = frontalure is a 1:2 mixture of frontalin and turpentine.
HT = host tree (*Pinus* spp.).
IPSB = *Ips* bait is a mixture of 2% frontalin, 19% *alpha*-pinene, 2% (s)-*cis*-verbenol, 1% racemic ipsdienol, 1% racemic ipsenol, and 7% inert petroleum carrier by volume.
IPSD = Ipsdienol.
(+)-IPSD = (S)-(+)-ipsdienol.
(-)-IPSD = (R)-(-)-ipsdienol.
IPSE = ipsenol.
(+)-IPSE = (R)-(+)-ipsenol.
(-)-IPSE = (S)-(-)-ipsenol.
IPSPH = *Ips* pheromone is a mixture of 2% *cis*-verbenol, 2% ipsenol, and 2% ipsdienol in a vaseline-based paste.
RO = raw oleoresin.
T = turpentine.
V = verbenone.

[2] M = male; F = female; --- = sex not indicated.

[3] [1] Hedden et al. 1976; [2] Vité et al. 1978; [3] Richerson & Payne 1979; [4] Rose et al. 1981; [5] Billings 1985; [6] Vité et al. 1964.

[4] Elution rate not provided.

[5] Elution rate of 2 mg/24 h.

[6] Elution rate of 4 mg/24 h.

[7] A 50:50 mixture of *endo*-brevicomin and *exo*-brevicomin.

[8] An 85:15 mixture of *endo*-brevicomin and *exo*-brevicomin.

[9] Elution rate of 160 mg/24 h/tree.

[10] Elution rate of 320 mg/24 h/tree.

[11] Elution rate of 80 mg/24 h/tree.

[12] Elution rate of 100 mg/24 h over 15 days.

[13] Elution rate of 3600 mg/24 h.

[14] Elution rate of 100 mg/24 h.

[15] Elution rate of 20 mg/24 h.

[16] Mixed results.

Appendix 23. Behavioral response of *Ips grandicollis* to behavior chemicals under controlled laboratory conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
G+F	M	1	G	M[5]	2						
G+TV	M,F	1	G	M>F	1	F+TV	M>F	1	F	M	1
			G+FE	M>F	1						
			M	M<F[6]	2				F	M>F	1
M+TV	M,F	1	M	M=F	1				FE	F	1
MC+F	F	1	MC	M>F[5]	1,2				F	M	1
MC+TV	M,F	1							FE	M	1
									F+TV	F	1
C+TV	M,F	1	C	M[6]<F[5]	1,2				F	M<F	1
									FE	M	1
			C+FE	F	1						
DL+F	M,F	1	DL	M>F[5]	1,2				F+TV	M=F	1
DL+TV	M,F	1	DL+FE	M>F	1						
LL+F	M,F	1	LL	M>F[5]	1,2				F+TV	M	1
LL+TV	M,F	1									
LL+F+TV	F	1									
a+F	M,F	1	a	M>F[6]	1,2				FE	M>F	1
a+TV	M,F	1									
a+F+TV	M,F	1									

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
B+F	M,F	1	B	M>F[5]	1,2						
B+TV	M,F	1									
B+F+TV	M,F	1									
F	F	1	F	M	1	M	M	1			
TV	F	1	TV	M	1						
F+TV	F	1	F+TV	M	1	G	M	1			
						M	M	1			
						MC	M	1			
						C	M	1			
			F+TV+G	M>F	1						
			F+TV+M	M=F	1						
			F+TV+MC	M>F	1						
			F+TV+C	M<F	1						
			F+TV+DL	M=F	1						
FFE			FE	M=F	2,3	G	M	1			
FE+B	M,F	1				M	M	1	C	M	1
FE+LL	M,F	1				C	F	1	DL	F	1
FE+a	F	1				DL	M	1	a	M	1
			FE+M	F	1						
FE+MC	F	1	FE+MC	M	1						

[1] A = D-*alpha*-pinene.
B = L-*beta*-pinene.
C = D,L-camphene.
DL = D-limonene.
F = frontalin.
FE = frass extract of male *I. grandicollis*.
FFE = frass extract of female *I. grandicollis*.
G = geraniol.
LL = L-limonene.
M = myrcene.
MC = methyl chavicol.
TV = *trans*-verbenol.

[2] M = male; F = female; --- = sex not indicated.

[3] [1] Werner 1972c; [2] Werner 1972a; [3] Werner 1972b.

[4] Compound(s) tested at 0.1% and 1.0% concentrations on filter paper.

[5] 1.0% concentration more attractive than 0.1% concentration.

[6] 0.1% concentration more attractive than 1.0% concentration.

Appendix 24. Behavioral response of *Ips grandicollis* to beetle-infested pine under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]	Treatment [1]	Sex [2]	Ref [3]
			I.G.I.B.	---	1						
			M.I.G.I.B.	---	1,2,8,9				M.I.C.I.B.	---	2
									F.D.F.I.B.	---	2
			M.I.G.I.B.	M=F	3				M.I.C.I.B.	M=F	3
									F.D.F.I.B.	M=F	3
									M.I.C.+M.I.G.+F.D.F.	M=F	3
			M.I.G.I.B.	M<F	3,4[4],5[5]				F.I.G.I.B.	M<F	5[5,6]
			M.I.G.I.B.	M<<F	6[7,8]				F.D.F.I.B.	M<F	6[7]
M.I.C.I.B.	---	1,3[9]	M.I.C.I.B.	M=F	3,5[5]				F.D.F.I.B.	M=F	3
			F.I.C.I.B.	---	1						
			M.+F.I.C.I.B.	M=F	5[5]						
M.I.A.I.B.	---	1,3[9],5[5]	M.I.A.I.B.	M=F	3						
M.+F.I.A.I.B.		1,5[5]									
			D.F.I.B.	---	1						
F.D.F.I.B.	---	3[9],5[5]	F.D.F.I.B.	---	2,7						
M.+F.D.F.I.B.	---	1,5[5]	F.D.F.I.B.	M=F	3	M.I.G.I.B.	M=F	3			
			F.D.F.I.B.	M>F	6[7,8]						
			M.I.G.+M.I.A.I.B.	M<F	3						
			M.I.C.+M.I.A.I.B.	M=F	3						
			F.D.F.+M.I.A.I.B.	M=F	3						
U.B.	---	1,3,5,6	D.L.	---	1						

[1] D.F. = *Dendroctonus frontalis*.
D.L. = debarked log.
F. = female.
I.A. = *Ips avulsus*.
I.B. = infested bolt.
I.C. = *Ips calligraphus*.
I.G. = *Ips grandicollis*.
M. = male.
U.B. = uninfested bolt.

[2] M = male; F = female; --- = sex not indicated.

[3] [1] Vité et al. 1964; [2] Svihra et al. 1980; [3] Birch et al. 1980; [4] Vité and Renwick 1971b; [5] Svihra 1982; [6] Birch and Svihra 1979; [7] Dixon and Payne 1980; [8] Hain and Anderson 1976a; [9] Hain and Anderson 1976b.

[4] 100 beetles.

[5] 25 beetles.

[6] Although attraction was reduced, attraction was still significantly greater than that of uninfested bolts.

[7] 30 beetles.

[8] *I. grandicollis* significantly more attracted to bolts infested with *I. grandicollis* than with *D. frontalis*.

[9] Low *I. grandicollis* population levels.

Appendix 25. Behavioral response of *Ips grandicollis* to pheromones under natural field conditions.

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
			G[4]	M	2						
			G[5]	M>F	1	FE	M>F	1			
M[5]	F	1	M	M	3[3,4]						
			MC[5]	M>F	1						
			C[4] C[5]	F M,F	2 1	FE	M<F	1			
DL[5]	F	1	DL	M	3[3,4]	FE	M	1			
a[5]	M,F	1	FE	M,F	1	G[5]	M	1			
FE+a[5]	M,F	1	A[5]	---	9	M[5]	M>F	1			
B[5]	M,F	1	B[5]	---	9	MC[5]	M	1			
FE+B[5]	M,F	1				C[5]	M<F	1			
LL[5]	M,F	1	LL[5]	---	9	DL[5]	M	1	DL[5]	F	1
FE+LL[5]	M,F	1	FE+G[5]	F[5]	1						
			FE+MC[5]	F	1						
IPSE[5,6]	M<F	4	IPSE[5]	M<<F	5	TV[5]	M<F	5			
			IPSE[5,6]	M<F	4						
(+)-IPSE[5]	M,F	4	(-)-IPSE[5]	M<F	4				(+)-IPSE[5]	---	4
IPSD[5]	M>F	4	IPSE[5]+IPSD[5]	M<F	4						
(+)-IPSE[5]+IPSD[5]	M<F	4	(-)-IPSE[5]+IPSD[5]	M<F	4						
F[7]	---	6	F[7]+TV[7]	---	6						

NOT ATTRACTIVE			ATTRACTIVE			ENHANCES ATTRACTION			REDUCES ATTRACTION		
Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]	Compound(s) [1]	Sex [2]	Ref [3]
T[8]	---	6	F[7]+TV[7]+T[8]	---	6						
F[7]+TV[7]	---	6	F[7]+T[8]+EXB[7]	---	6						
TV[7]	---	6	TV[5,6]	M<F	5	a[5]	M=F	5			
TV[5,6]	M<F	5	A	(M<<F)[5]	5	TV[5]	M=F	5			
ENB[7]	---	6	A+CV	(M<F)[5]	5						
EXB[7]	---	6	IPSB	---	7						
V[9]	---	6									
F[7]+ENB[7]+EXB[7]	---	6									
F[7]+T[8]+ENB[7]	---	6									
F[7]+T[8]+ENB[7]+EXB[7]	---	6									
TV[7]+ENB[6]+EXB[6]	---	6									
T[8]+ENB[7]+EXB[6]	---	6									
T[10]	---	8	IPSPH[11]	M<F	8	T[6,10]	M<<F	8			
FL[11]:T[10]	---	8	IPSPH[11]+T[6,10]	M<<F	8						
			RO[5]	---	9						
			I.C.A.	---	9						
			I.C.F.	---	9						

[1] A=D-*alpha*-pinene.
B=L-*beta*-pinene.
C=D,L-camphene.
CV=*cis*-verbenol.
DL=D-limonene.
ENB=*endo*-brevicomin.
EXB=*exo*-brevicomin.
F=frontalin.
FE=frass extract of male *I. grandicollis*.
FL=frontalure is a 1:2 mixture of frontalin and turpentine.
G=geraniol.
IPSB=*Ips* bait is a mixture of 2% frontalin, 19% *alpha*-pinene, 2% (s)-*cis*-verbenol, 1% racemic ipsdienol, 1% racemic ipsenol, and 75% inert petroleum carrier by volume.
IPSD=ipsdienol.
IPSE=ipsenol.
(+)-ipsenol=(R)-(+)-ipsenol.
(-)-ipsenol=(S)-(-)-ipsenol.
IPSPH=*Ips* pheromone is a mixture of 2% *cis*-verbenol, 2% ipsenol, and 2% ipsdienol in a vaseline-based paste.
LL=L-limonene.
M=myrcene.
MC=methyl chavicol.
T=turpentine.
TV=*trans*-verbenol.

[2] M=male; F=female; --- = sex not indicated.

[3] ^{1} Werner 1972c; ^{2} Werner 1972a; ^{3} Vité et al. 1976a; ^{4} Vité & Renwick 1971b; ^{5} Dixon & Payne 1980; ^{6} Rose et al. 1981; ^{7} Billings 1985; ^{8} Vité et al. 1964.

[4] 1% concentration (5ml) on filter paper.

[5] no elution rate provided.

[6] mixed results.

[7] elution rate of 0.5 mg/h.

[8] elution rate of 6.0 mg/h.

[9] elution rate of 0.5-10.0 mg/h.

[10] elution rate of 3600 mg/24 h.

[11] elution rate of 100 mg/24 h.

[12] elution rate of 20 mg/24 h.

Appendix 26. Summary of interspecific olfactory interactions among *Dendroctonus frontalis*, *Dendroctonus terebrans*, *Ips calligraphus*, *Ips avulsus* and *Ips grandicollis* in infested bolts (modified and expanded from Birch et al. 1980).

	RESPONDING SPECIES									
	D. frontalis		*D. terebrans*		*I. calligraphus*		*I. avulsus*		*I. grandicollis*	
TREATMENT SPP.	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]
D. frontalis	XX	XX	GIA	ND	NS/GIA	NE	Mixed/GIA	NE	GIA	R
D. terebrans	ND	ND	XX	XX	ND	ND	ND	ND	ND	ND
I. calligraphus	NS	NE	NS	ND	XX	XX	High	NE	GIA	R
I. avulsus	NS	NE	NS	ND	LN	R	XX	XX	Mixed	NE
I. grandicollis	NS	R	NS	ND	Mixed	E/R	LN	E	XX	XX

[1] A = Behavioral response of responding species to bolts infested with individual treatment species. Conspecific response is designated as XX. Other responses are indicated subjectively as:
GIA = general interspecific attraction;
High = high level of interspecific attraction;
LN = little or no significant interspecific attraction;
Mixed = high and low interspecific attraction in two tests;
ND = no data;
NS = no significant interspecific response.

[2] B = Behavioral effect of the simultaneous presence of treatment species infested-bolts on intraspecific attraction of the responding species to conspecific-infested bolts. Conspecific response is designated as XX. Other responses are indicated subjectively as:

E = enhances intraspecific attraction of the responding species to conspecific infested bolts.
NE = no effect on intraspecific attraction of the responding species to conspecific infested bolts.
ND = no data;
R = reduces intraspecific attraction of the responding species to conspecific infested bolts.

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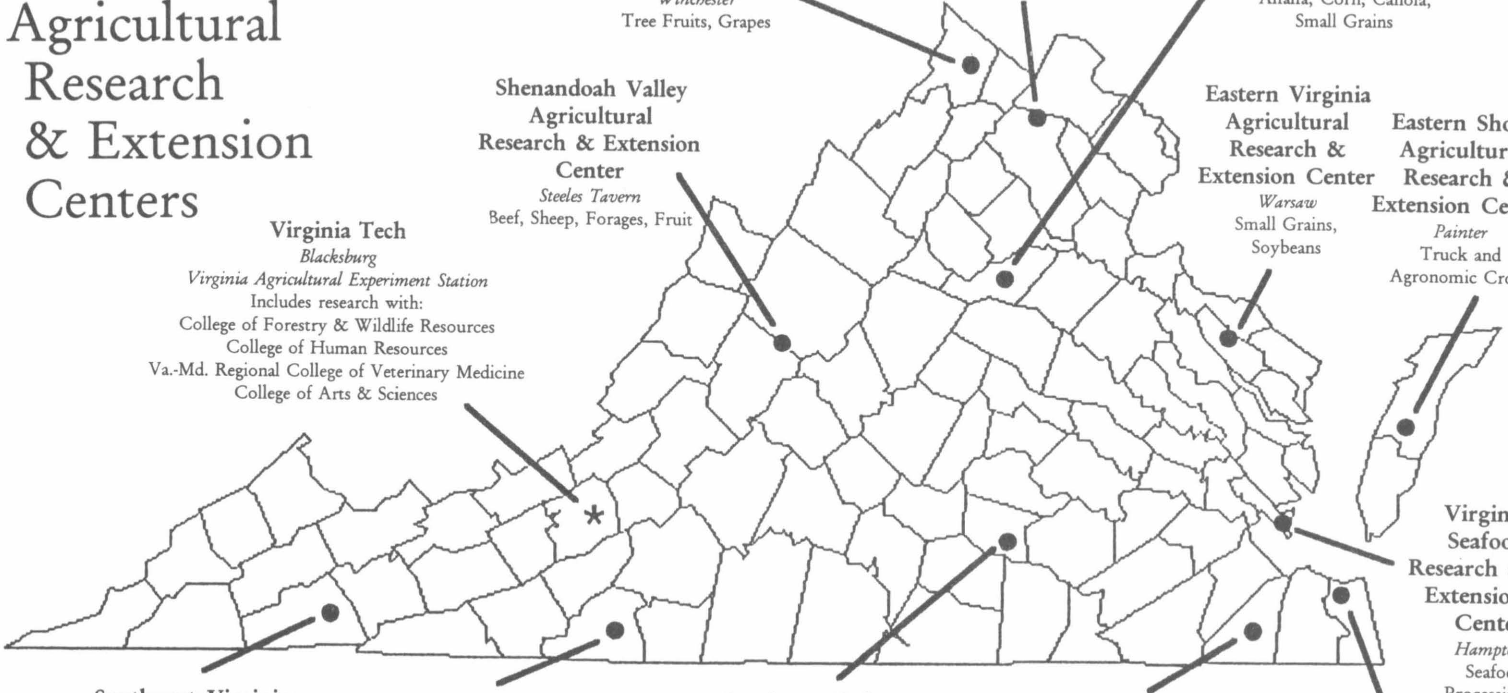

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Critz
Forestry, Wildlife
Va. Agric. Exp. Sta. and
College of Forestry & Wildlife Resources

Southern Piedmont Agricultural Research & Extension Center
Blackstone
Tobacco, Small Fruits, Forages, Small Grains, Turfgrass

Tidewater Agricultural Research & Extension Center
Suffolk
Peanuts, Soybeans, Swine, Small Grains, Corn

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