Chemical Ecology of the Southern Pine Beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera:Scolytidae)

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Introduction

The southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), is considered to be the most important cause of damage and mortality to pine trees in the southeastern United States (Drooz 1985). Over the last several decades, entomologists have striven to unlock the secrets that allow this native beetle to rise up in epidemic proportions that lead to such vast tree mortality. It is now well known that bark beetles possess elaborate semiochemical communication systems which they use to orientate to host material to feed, mate, and reproduce. Many detailed reviews have been provided in this area (Birch 1978, 1984; Borden 1974, 1977, 1982, 1984, 1985, 1989; Brand et al. 1979; Byers 1989; Geizler and Gara 1978; Geizler et al. 1980; Renwick and Vité 1970, 1980; Rudinsky and Ryker 1977; Ryker 1984; Smith et al. 1993; Vité and Francke 1976; Wood 1970, 1973, 1982; Wood and Bedard 1977). The chemical ecology of SPB involves a complex host of beetle- and host-produced compounds. Scientists are continually revealing the once hidden nature of these compounds and their role in insect ecology, but far more important, their significance in manipulating insect behavior. The broader aspects of SPB chemical ecology and implications for bark beetle management are addressed.

Semiochemical Communication System

Semiochemicals are natural compounds produced and released by individuals of a species which elicit a behavioral response in members of the same or different species (Nordlund 1981). Semiochemicals which are used in intraspecific communication are referred to as pheromones. Behavioral responses to pheromones include searching for mates by one sex (e.g., sex pheromones), aggregation of both sexes at a host plant (e.g., attractant or aggregation pheromones), and dispersal of both sexes away from a specific area (e.g., inhibitor or antiaggregation pheromones). Semiochemicals used in interspecific communication are referred to as kairomones when the species receiving the chemical message benefits and allomones when the emitter of the chemical message benefits at the expense of the receiver. There is considerable overlap with regards to the functions of a compound, i.e., the same compound may serve both intra- and interspecific functions. For example, frontalin serves as an pheromone to SPB and a kairomone to its natural enemy, *Thanasimus dubius* (Fabricius) (Vité and Williamson 1970).

A series of studies conducted at the Boyce Thompson Institute for Plant Research provided the foundation by which the semiochemical system of SPB was first described (Coster 1970; Coster and Gara 1968; Gara 1967; Gara and Coster 1968; Renwick 1970; Renwick and Vité 1969, 1970; Vité and Crozier 1968; Vité and Renwick 1968) and later revised (Vité and Francke 1976). Recently, Smith et al. (1993) presented an extensive historical review of research on the semiochemical communication system of SPB and other members of the southern pine bark beetle guild. Although several host- and beetle-associated chemicals have been found to be produced and/or utilized by SPB as part of its communication system, behavioral responses of this beetle have only been determined for a few of these compounds.

Chemical Structure, Blends and Concentration in Species Specificity

The activity of a semiochemical is dependent on many factors including its size, shape, functional groups, degree of saturation and chirality (Tumlinson and Teal 1987). Small molecules are used when a fast response is required (e.g., alarm pheromones), while large compounds, which tend to be less volatile, are used when long, extended exposure is required (e.g., sex, aggregation, and antiaggregation pheromones). Although the structure of pheromones differs greatly between insect orders and families, generally compounds are of similar structural types within genera as seen with terpene pheromones of *Ips* and *Dendroctonus* bark beetles. The position, number, and geometry of double bonds and functional groups are also important with regard to the activity of compounds. Payne et al. (1988), evaluating the antennal olfactory and behavioral response of SPB to different frontalin analogs, showed that response to frontalin was significantly greater than to any of the analogs. Chirality, in turn, imparts a greater degree of specificity to a species' pheromone system. Silverstein (1979) described nine possible categories of behavioral response to enantiomers or diastereomers. At least two of these categories have evolved as part of the SPB semiochemical-based system. For example, SPB produce both enantiomers of frontalin, but is significantly more attracted to (?)-frontalin than to the (+)-antipode (Payne et al. 1982). On the other hand, Vité et al. (1985) showed that (+)-endo-brevicomin significantly enhanced attraction of SPB to frontalure, whereas (?)-endo-brevicomin inhibited response. Thus, one enantiomer may be active and the other inactive or each enantiomer may elicit different responses. Seybold (1993) provided an extensive review on the roles of chirality in olfactory-directed behavior.

Just after the discovery of the first pheromone, bombykol, from the silkworm moth, *Bombyx mori* (L.)., it was generally thought that each insect species produced and responded to a single pheromone (Karlson and Butenandt 1959). However, *Ips paraconfusus* was later found to produce and respond to a blend of three pheromones (e.g., (S)-(?)-ipsenol, (S)-(+)-ipsdienol, and (S)-(?)-cis-verbenol) (Silverstein et al. 1966). It has since been discovered that most insects produce multicomponent blends of pheromones and that the single component system is the exception rather than the rule. The blend of pheromones is important because some or all components may act as synergists; individually they elicit little or no attractiveness, but together they are highly attractive. The pheromone blend of *I. paraconfusus* is one example. Another example is the SPB attractant blend of frontalin, trans-verbenol, turpentine (containing a-Pinene and other monoterpenes), verbenone, and (+)-endo-brevicomin. Individual components of a blend may also function in concert to maximize steps in a behavioral sequence as has been found in several Lepidoptera species (Baker and Carde 1979, Linn et al. 1984, Teal et al. 1986). Blends and component ratios within blends play important roles in maintaining or increasing reproductive isolation of closely related species or reducing competition in sympatric species. A species may release a component which is inactive to conspecifics, but inhibitory to related species (Tumlinson and Teal 1987). On the other hand, a component, essential to reproductive behavior in the releasing species, may also be inhibitory to members of related species. Finally, two species may produce different component ratios of the same chemicals.

Mechanism of Host Tree Colonization by SPB

A summary of known or speculated biosynthetic pathways and responses to some of the most studied semiochemicals are discussed below in relation to their respective roles within an actively expanding infestation.

Initial Attack

Upon landing on a tree, "pioneer" females bite into the bark. If the host is found to be suitable, the females begin releasing the primary aggregation pheromone, frontalin, and the synergist trans-verbenol (Fig. 1). At the same time, females release small quantities of Verbenone and endo-Brevicomin, both serving as synergists to enhance the attractiveness of frontalin. These compounds, in combination with host volatiles, primarily a-Pinene, stimulate mass aggregation of conspecifics (predominantly males) to the host (Renwick and Vité 1969, Rudinsky 1973) and are described in greater detail below.

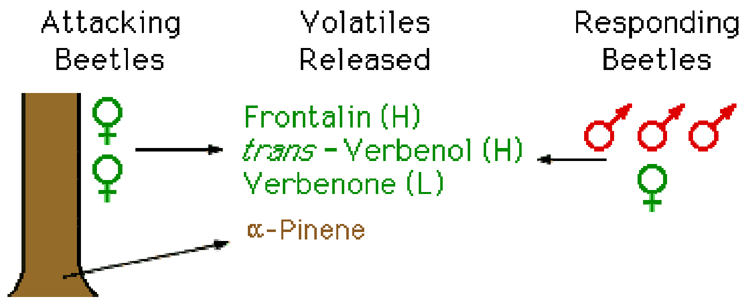

Fig. 1.

a-Pinene - As the pioneer beetles begin to invade the host, conductive phloem tissues are cut and copious amounts of oleoresin exude from these wounds. The monoterpine, a-Pinene, is the major component in the resin of most *Pinus* spp. (Mirov 1961) and serves as one of the more important host-tree odors in the behavioral chemical complex of SPB (Renwick and Vité 1969). Although, a-Pinene alone has not been shown to be attractive to field populations (Payne et al. 1978), it does synergize the attractiveness of frontalin (Kinzer et al. 1969). In combination with frontalin, a-Pinene appears to function as a kairomone arrestant; whereby, the pheromone draws beetles to the tree and the kairomone arrests their flight so they land (Renwick and Vité 1970; Payne 1980). In laboratory studies, a-Pinene also causes arrestment of walking beetles (McCarty et al. 1980, Payne 1979).

Frontalin - Found in the hindguts of newly emerged SPB females (Coster and Vité 1972), frontalin is a primary aggregation pheromone produced by several *Dendroctonus* species including SPB. It is most likely released by flatulation or in frass when females land on a tree and have determined it to be a suitable host. Frontalin likely plays a dual role, as sex pheromone to males (McCarty et al. 1980) and aggregation pheromone to both sexes, functioning in close-range communication, to bring individual beetles together in sufficient numbers to overcome host tree defenses (Johnson and Coster 1978, Payne et al. 1978). The natural enemy, *Thanasimus dubius*, responds to frontalin as a kairomone, thereby allowing the predator to find its prey (Vité and Williamson 1970).

trans-Verbenol - The production of this compound results from the oxidation of a-Pinene upon consumption of phloem material or exposure to vapors while in the host (Hughes 1973, 1975; Renwick et al. 1973), and is found in the hindgut of newly emerged female SPB (Renwick 1967). trans-Verbenol is also produced outside the beetle by the autoxidation of a-Pinene upon exposure to air (Hughes 1975, Hunt et al. 1989, Moore et al. 1956). This may explain why trans-verbenol can substitute for a-Pinene as a synergist for the pheromone frontalin (Kinzer et al. 1969; Payne et al. 1978; Renwick and Vité 1969, 1970).

trans-Verbenol is also reported to be metabolized from a-Pinene internally by bacteria in the beetle's gut (Brand et al. 1975) and externally by other microbial activity (Prema and Bhattacharyya 1962). As with a-Pinene, trans-verbenol alone is unattractive to walking and flying beetles (Vité and Crozier 1968).

Verbenone - During initial attack, verbenone is released by females in small quantities and acts as a synergist to enhance the attractiveness of frontalin. A multifunctional pheromone, verbenone is produced predominantly by male SPB (Renwick 1967) and other scolytid species (Borden 1985). The SPB derives verbenone from a-Pinene upon the oxidation of trans-verbenol (Hughes, 1973, 1975). This compound is also produced outside the beetle in two ways. One is by the autoxidation of trans-verbenol in the presence of air (Hunt et al. 1989, Moore et al. 1956). A second external source of verbenone is the symbiotic fungi introduced into the host tree by SPB (Brand et al. 1976). Verbenone is understood to be a multi-functional population regulator (Renwick and Vité 1980, Rudinsky 1973).

Mass Attack

During mass attack, arriving males land on the host, locate the entrance hole of single females and begin to release frontalin, endo-brevicomin, and verbenone in low concentrations (Fig. 2). The resulting aggregation, along with the introduction of symbiotic fungi, enables SPB to successfully attack a host tree and produce brood which emerge to attack other trees.

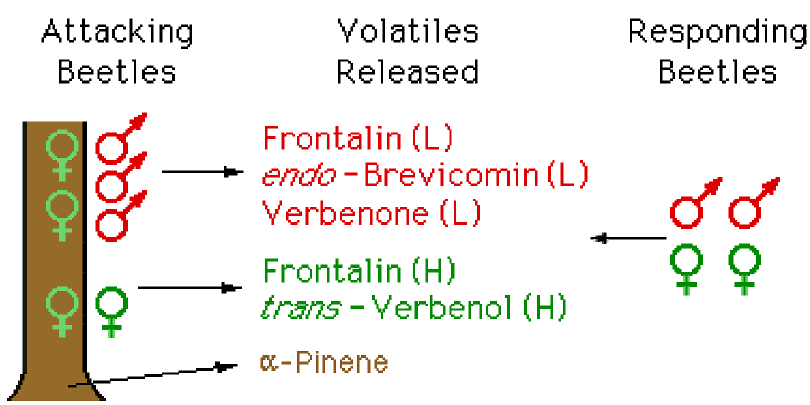

Fig. 2.

Frontalin - Females continue to produce large amounts of frontalin. Males have also been found to produce frontalin (Rudinsky et al. 1974), where it is used in short range communication, frontalin acts to reduce rivalry fighting and competition with other males.

endo-Brevicomin - Synthesized by male SPB in very small quantities (+)-endo-brevicomin is released by males during mass attack in low concentrations which functions to enhance the attractiveness of frontalin and host volatiles.

Verbenone - During mass attack verbenone is released primarily by males in low concentrations where it acts to balance the sex ratio of beetles attracted to the host by enhancing the attractiveness of aggregation pheromones to females (Billings 1985, Rudinsky et al. 1974).

trans-Verbenol - As mentioned previously, females produce large amounts of trans-Verbenol during initial attack. After 48 hours of feeding, the level of trans-verbenol declines significantly (Coster and Vité 1972).

a-Pinene - As attacks increase over the bole of the tree the primary host attractant a-Pinene is still being produced in large quantities.

Switching of Attack

As the population of attacking beetles increases, the concentration of verbenone and (?) endo-brevicomin released by males also increases. At some unknown threshold, these compounds begin to inhibit beetle response to the aggregation pheromones and cause arriving beetles to switch their attack to neighboring trees (Payne et al. 1978, Rudinsky 1973, Rudinsky et al. 1974, Vité and Renwick 1971) (Fig. 3). It has been suggested that the switching of mass attack from one host tree to a neighboring tree may be the result of both the cessation of release of attractive compounds (frontalin and a-Pinene) and the increased concentration of inhibitor pheromones (verbenone and endo-brevicomin) released from the tree as was found for *Ips typographus* (L.) (Schlyter et al. 1987, 1989).

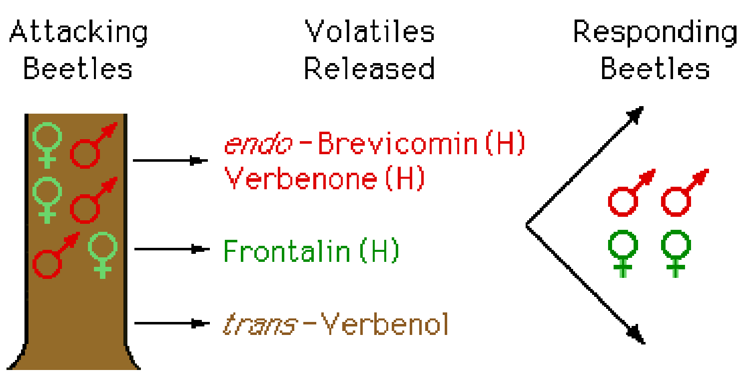

Fig. 3.

Verbenone - At the height of mass attack (3 to 5 days after initial attack) large numbers of males release high concentrations of verbenone which inhibit the response of both sexes to frontalin and causes a significant drop in the number of arriving beetles (McCarty et al. 1980, Payne et al. 1978, Renwick and Vité 1969). Ryker and Yandell (1983) determined for *D. ponderosae* that verbenone must exceed the level of trans-verbenol (the primary aggregation pheromone of this species) by approximately 15 percent before it would exert its antiaggregative properties. It is unknown if such a verbenone threshold level is required to inhibit SPB response to frontalin.

(?)-endo-Brevicomin - Vité et al. (1985) demonstrated that (?)-endo-brevicomin significantly reduced beetle response and was more inhibitory than racemic (equal proportions of + and -) endo-brevicomin. Racemic endo-brevicomin was previously demonstrated to inhibit the aggregation of both male and female SPB to attractive trees and thus switch the mass attack to new host trees (Payne et al. 1978, Vité and Renwick 1971).

Behavioral Chemicals and the Management of Bark Beetles

The history of methods used to manipulate or control SPB are varied and imaginative (Billings 1980). Some of the earliest tactics included rapid conversion of infested material into lumber (e.g., salvage) and burning the slabs (Hopkins 1909, 1911); immersing unbarked logs in water; and exposing unsalvageable infested trees to solar heating (e.g. cut-and-leave) (St. George and Beal 1929). Some of these methods, i.e. salvage and cut-and-leave, are still used today. Other treatments, more recently evaluated, include the use of pesticides, the application of mechanical and silvicultural controls, and the use of behavioral chemicals. The use of behavioral chemicals is summarized below.

There is extensive literature regarding the use of semiochemicals in the management of insect pests (Beroza 1970, 1976; Birch 1974; Borden 1989, 1993; Mitchell 1981; Wood 1982,). Borden (1989) described five principal means by which semiochemicals can influence the population dynamics of bark beetles: mediation of aggregation and mass attack on new hosts; cessation of aggregation and shifting of attack to an unexploited region of the host or to new hosts; induction of aggregation by species that compete for the same host resource; inhibition of aggregation and attack by species that compete for the same resource; and mediation of host finding by commensal and entomophagous insects. The author listed six fundamental strategies for potential pest management of scolytids, including:

1. **Prevention of Aggregation Pheromone Production** - For the SPB, examples of Strategy 1 have involved removing sources of attraction (e.g. cut-and-leave or salvage) to disrupt aggregation (Swain and Remion

1981), or cause the tree to become toxic to the beetle (e.g., pesticides) (Berisford et al. 1981).

2. **Disruption of Olfactory Perception** - Although, Strategy 2 has not been tested in the field, electrophysiological evidence (Payne and Dickens 1976) and behavioral data (Borden 1967) indicate that sensory adaptation or habituation occurs in pheromone-saturated environments.

3. **Exploitation of Semiochemical-based Secondary Attraction (Monitoring)** - Examples of Strategy 3 tested to monitor or control SPB include: use of frontalin and turpentine-baited traps to determine predator : prey (*Thanasimus dubius* : SPB) ratios for predicting regional SPB population trends (Billings 1988); the trap tree method (Vité 1970); and deployment of elution devices containing frontalure (1:2 mixture of frontalin and a-Pinene) on all non-host and host brood trees within an SPB infestation in order to draw beetles away from the active head (Richerson et al. 1980).

4. **Exploitation of Repellent Allomones** - A promising example of Strategy 4 involves the recent discovery that 4-allylanisole, a host-produced compound, repelled several bark beetle species from the allomone source in laboratory bioassays and significantly reduced capture of both sexes of SPB in attractant-baited traps in the field (Hayes et al. 1994). In addition, SPB may be repelled by a unknown compound released by *I. grandicollis* (Birch et al. 1980, Svihra et al. 1980), however this phenomena is in need of further study.

5. **Exploitation of the Kairomonal Response by Entomophagous Insects** – In the case of Strategy 5, several natural enemies of SPB have demonstrated response to kairomones emitted from the beetles or associated fungi, including: the clerid, *Thanasimus dubius*, to the aggregating beetle pheromone, frontalin (Vité and Williamson 1970); the predatory fly, *Medetera bistriata*, to the semiochemicals released from of the associated bark beetle (e.g., SPB and *I. grandicollis*) infested logs (Williamson 1971); the parasitoid, *Dinotiscus dendroctoni* to a blend of compounds collected from beetle-infested trees (Salom et al. 1991); and numerous species whose arrival coincide with various stages of beetle attack and brood development (Camors and Payne 1973, Dixon and Payne 1980).

6. **Exploitation of Antiaggregation Pheromones** - Recently, Strategy 6, i.e., exploitation of inhibitor or antiaggregation pheromones, has demonstrated the greatest potential for use in the control of the SPB. Both endo-brevicomin and verbenone each have been shown to significantly reduce capture of SPB in attractant-baited traps; however, combining the two compounds did not significantly reduce SPB capture

over the reduction obtained with either inhibitor alone (Payne et al. 1978, Salom et al. 1992). Field tests of a 1:1 mixture of brevicomin isomers and verbenone caused reductions of 84% in beetle landing and 92% in galleries on treated trees (Payne and Richerson 1979, Richerson and Payne 1979). However, the treatment did not prevent the trees from succumbing to beetle attack even though mass attack by SPB did not occur. *Ips avulsus*, a sympatric species, was found to be capable of competitively replacing SPB (Payne and Richerson 1985). Ultimately, the treatment was considered successful, because the less aggressive *Ips* species could not sustain the growth of an infestation in the absence of SPB stressed trees. The apparent equality of response of SPB to verbenone and endo-brevicomin alone or combined and the cost of pheromones led to the sole evaluation of verbenone in the suppression of SPB infestation growth (T.L. Payne, personal communication). The treatment of freshly attacked trees and uninfested trees at the active head of SPB infestations with verbenone-only has shown considerable success in slowing or halting the growth of small to moderate-sized infestations (Billings et al. 1995; Payne and Billings 1988, 1989; Payne et al. 1992,). In large infestations, the verbenone-only treatment was less successful, but better success has been obtained when the verbenone treatment (treating a buffer strip only) is combined with the cut-and-leave tactic (felling freshly attacked trees only or felling all infested trees) (Billings et al. 1995).

Significance

Bark beetles of the genera *Dendroctonus*, *Ips*, and *Scolytus* are the most destructive pests of forests in the Northern Hemisphere. Damage from these insects causes losses of billions of cubic feet of timber valued at millions of dollars each year (Drooz 1985; Furniss and Carolin 1977). Tactics currently used to control bark beetles, such as salvage, cut-and-leave, or chemical control are not always successful and/or are of environmental concern.

The use of semiochemicals as management tools show considerable promise in reducing damage and mortality by bark beetles. Some of these compounds have already been successfully used to monitor population trends or as a mass trapping and/or disruption tactic (Borden 1993). The exploitation of semiochemicals as management tools requires a thorough understanding of the mechanisms involved in the production and release of and response to these chemicals by the target species. In addition, it is important to have an understanding of the effects of semiochemicals applied on the target species and associated organisms. Lanier et al. (1972) was one of the first to suggest that the indiscriminate use of semiochemicals could theoretically lead to resistance. Such a phenomenon has been studied with regards to use of pheromones in mating disruption of the pink bollworm moth, *Pectinophora gossypilla* (Saunders) (Haynes et al. 1984, Haynes and Baker 1988). Just as there is the potential for the development of semiochemical resistance in the target insect, there is also the potential for the development of response "resistance" in natural enemies as many of these insects use host pheromones as kairomones.

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