

Chemical Ecology and Management of Bark Beetles in Western Coniferous Forests

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Bark beetles (Coleoptera: Curculionidae, Scolytinae) are a large and diverse group of insects that include several species capable of causing extensive amounts of tree mortality in coniferous forests of western North America. These mortality events are part of the natural ecology of western forests, but the negative impacts of severe outbreaks can be substantial. For about a century, researchers in western North America have studied the biology, ecology, and management of the principle species of tree-killing bark beetles, including Douglas-fir beetle, *Dendroctonus pseudotsugae*, fir engraver, *Scolytus ventralis*, mountain pine beetle, *Dendroctonus ponderosae*, pine engravers, *Ips* spp., spruce beetle, *Dendroctonus rufipennis*, and western pine beetle, *Dendroctonus brevicornis*. Substantial basic and applied research has been executed with the goal of developing effective tools and tactics that mitigate undesirable levels of tree mortality.

In the early 20th century, an emphasis was placed on direct control in hopes of reducing beetle populations and thereby assumedly reducing levels of bark beetle-caused tree mortality. Several methods were developed and employed, principally the felling of infested trees and killing of developing brood through solarization (i.e., placement of infested material in the direct sun, which is often sufficient to kill brood beneath the bark); applications of insecticides; and/or burning of infested hosts. After it became apparent that large-scale implementation of direct control methods was rather ineffective, researchers began to focus on development of silvicultural tactics (indirect control) to reduce the susceptibility of forests to bark beetle infestations.

In the 1960s, the first bark beetle pheromone was identified by Silverstein et al. [1], creating a new era of research that lasts today. After their discovery several bark beetles were among the first insects investigated for pheromones [2], however it was not until decades later that semiochemical-based tools were used in forests in an operational context. The development of these tools has centered on the use of aggregation pheromones to attract the subject species for purposes of retention and later destruction, or antiaggregation pheromones to reduce host finding and colonization success. In regard to the latter, methylcyclohexenone (MCH) (3-methylcyclohex-2-en-1-one) is the most effective antiaggregation pheromone used for tree protection in western North America, and is highly effective for protecting Douglas-fir, *Pseudotsuga menziesii*, from Douglas-fir beetle in the Pacific Northwest, U.S. [3].

Verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) is the most extensively-studied antiaggregation pheromone used in tree protection in western North America, and was first identified in male western pine beetle by Renwick [4]. Verbenone is now recognized as the primary antiaggregation pheromone of mountain pine beetle, western pine beetle and southern pine beetle, *Dendroctonus frontalis*, and is produced by auto-oxidation of the host monoterpene α -pinene via the intermediary compounds *cis*- and *trans*-verbenol, by the beetles themselves, and/or through degradation of host material typically by microorganisms associated with bark beetles. Many researchers believe verbenone reduces intra- and interspecific competition by altering adult behavior to minimize overcrowding of developing brood within the host, which increases fitness and survivorship.

Because of its behavioral activity, as demonstrated in numerous trapping bioassays, verbenone has been evaluated for protecting individual trees and small-scale (e.g., <10 ha) forest stands from mortality attributed to mountain pine beetle and western pine beetle in numerous studies. Results have been mixed. Negative results have been linked to a variety of factors including photoisomerization of verbenone to behaviorally inactive chrysanthenone; inconsistent or inadequate release; rapid dispersal of verbenone; and/or limitations in the range of inhibition of verbenone, particularly when bark beetle populations are high [5]. In my own research, verbenone was found ineffective for protecting ponderosa pine from mortality attributed to western pine beetle during a three-year study [5]. In general, verbenone is considered much more effective for protecting pines from mortality attributed to mountain pine beetle compared to western pine beetle, but in some cases efficacy is still quite limited. Verbenone was registered by the U.S. Environmental Protection Agency in December 1999 for management of southern pine beetle in the southern U.S. Since then, the label has been expanded to include mountain pine beetle and western pine beetle in forests, recreational and municipal settings, and in rights of way and other easements.

Recently, efforts to more fully explore volatiles produced by host and nonhosts in forests have led to the use of systems-level concepts in the development of semiochemical-based tools and tactics for tree protection [6]. When searching for new hosts, bark beetles encounter a variety of tree species and associated host volatiles suggesting that bark beetles should be able to discriminate among olfactory cues in order to locate suitable hosts and associated habitats [6]. Based on the semiochemical-diversity hypothesis [7], this seems critical for bark beetle species (e.g., western pine beetle) that have narrow host ranges and often search for hosts in forests containing numerous tree species. In the context of pest management, a diverse array of chemical cues from con and hetero-specifics and nonhosts likely disrupt bark beetle searching more than high doses of a single semiochemical (e.g., verbenone) or even mixtures of semiochemicals intended to mimic one type of signal (e.g., antiaggregation pheromones), as they represent heterogeneous stand conditions to foraging insects [6,7]. This is because the odds of finding a suitable and susceptible host are lower in a heterogeneous forest than in a more homogeneous forest of similar overall tree density. A foraging bark beetle encountering a variety of inhibitory semiochemicals may be induced to leave the

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area instead of landing on and testing candidate trees by taste or close range olfaction. Such concepts have shaped my research on the development of semiochemical-based tools for tree protection in recent years, and are fruitful ground for additional research in other systems. For example, related research has led to the development of the only effective semiochemical-based tool for protecting ponderosa pine from western pine beetle [8], and expansion of that product (i.e., “Verbenone Plus”, a mixture of nonhost volatiles and verbenone) into other systems where the efficacy of verbenone has been limited [9].

In recent years, significant advances have been made regarding the molecular biology and biochemistry of pheromone production in bark beetles; regarding the synthesis of semiochemicals in the laboratory; regarding the deployment of semiochemicals in the field; and regarding the fate of semiochemicals once released into the active airspace of forests. The future looks bright for the development and use of semiochemical-based tools in forests, particularly in remote and sensitive areas where other management techniques (e.g., the use of insecticides) may not be appropriate.

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