Forest Ecology and Management 256 (2008) 1825–1839

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Protection of spruce from colonization by the bark beetle, *Ips perturbatus*, in Alaska

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ARTICLE INFO

Article history:
Received 17 November 2007
Received in revised form 1 July 2008
Accepted 9 July 2008

Keywords:
Alaska
Antiaggregation pheromones
Bark beetles
Coleoptera
Conifer
Conophthorin
(*E*)-7-Methyl-1,6-dioxaspiro[4.5]decane
Interruption
Ips concinnus
Ips perturbatus
Lutz spruce
Methyl jasmonate
3-Oxo-2-(2-pentenyl)-cyclopentaneacetic acid, methyl ester
Non-host volatiles (NHV)
Pheromones
Picea × *lutzii*
Scolytidae
Semiochemicals
Verbenone
4,6,6-Trimethylbicyclo[3.1.1]hept-3-en-2-one

ABSTRACT

Field bioassays were conducted in south-central Alaska in a stand of Lutz spruce, *Picea* × *lutzii*, to determine whether a semiochemical interruptant (verbenone and *trans*-conophthorin) and/or a defense-inducing plant hormone (methyl jasmonate, MJ) could be used to protect individual standing trees from bark beetle attack. During two experiments (initiated in May 2004 and 2005, respectively), attacks by *Ips perturbatus* on standing trees were induced by using a three-component aggregation pheromone (ipsenol, *cis*-verbenol, and ipsdienol) and prevented by using the interruptant. In 2005, treatments from 2004 were repeated and additional treatments were evaluated by using MJ spray or injection with and without the interruptant. Aggregation began before 3 or 7 June, and attack density was monitored through 3 or 16 August. During both years, tree mortality caused by *I. perturbatus* was recorded twice (in August, and in May of the following year). In both experiments, attack density was greatest on trees baited with the three-component attractive pheromone, but was significantly reduced by addition of the semiochemical interruptant to trees baited with the attractant. There were no significant differences in attack density between attractant + interruptant-treated trees and unbaited trees. In 2004, mortality was highest among attractant-baited trees, whereas addition of the interruptant significantly reduced the level of initial (10 week post-treatment) and final (54 week post-treatment) mortality. In 2005, no significant reduction in attack density occurred on trees baited with the attractant when MJ was sprayed or injected. The highest initial (10.6 week post-treatment) and final (49.4 week post-treatment) mortality was observed among trees that had been injected with MJ and baited with the attractant. Mortality at the final assessment was significantly lower in all other treatment groups. As in 2004, addition of the interruptant to attractant-baited trees significantly reduced the level of final mortality compared to attractant-baited trees. MJ was not attractive or interruptive to *I. perturbatus* or associated bark beetles in a flight trapping study. However, MJ-treated trees (sprayed or injected) exuded copious amounts of resin on the bark surface. Anatomical analyses of felled trees from four treatment groups [Tween (solvent)-sprayed, MJ-sprayed, Tween-injected, and MJ-injected + attractant baited] showed that treatment with MJ increased the number and size of resin ducts produced following treatment. These analyses also revealed a reduction in radial growth in MJ-treated trees. Our results show that during both years, treatment with a simple, two-component interruptant system of verbenone and *trans*-conophthorin significantly reduced *I. perturbatus* attack density and tree mortality on attractant-baited trees and provided a full year of protection from bark beetle attack.

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1. Introduction

Lutz spruce, *Picea* × *lutzii* Little, a natural hybrid of white spruce, *Picea glauca* (Moench) Voss, and Sitka spruce, *Picea sitchensis* (Bong.) Carr., occurs primarily where their distributions overlap on the Kenai Peninsula of Alaska (Viereck and Little, 1972). A major pest of young *P.* × *lutzii* is the northern spruce engraver, *Ips perturbatus* (Eichhoff) (Coleoptera: Scolytidae), which is distrib-

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0378-1127/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.foreco.2008.07.008

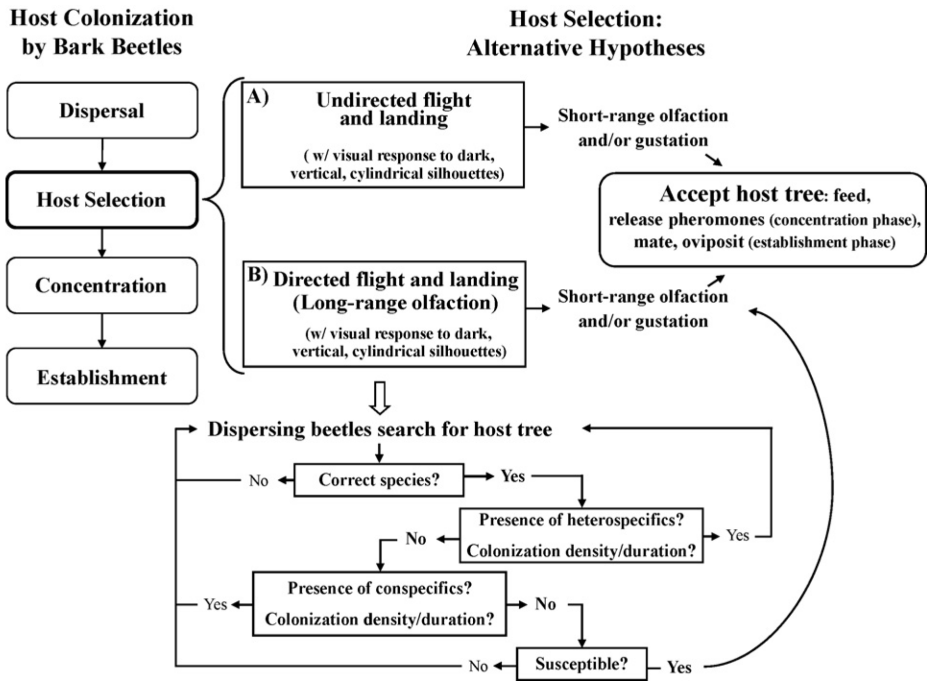

Fig. 1. Host colonization by bark beetles can subdivided into four phases (dispersal, host selection, concentration, and establishment) according to D.L. Wood (1982a). Two major hypotheses to describe host selection are based on (A) undirected flight or (B) directed flight in response to long-range olfactory signals (Wood, 1982a; Borden, 1997). Prior to (long-range) or after landing, a bark beetle may undergo a series of binary decisions to evaluate the species status, followed by the level of occupancy, suitability, and susceptibility of a host (Borden, 1997). Figure adapted from Graves (2008).

uted transcontinentally in the boreal region of North America (Gobeil, 1936; Bright, 1976; Wood, 1982b; Robertson, 2000). Normally, endemic populations infest individual standing spruce trees under environmental stress, but during warm, dry summers following mild winters, engraver beetle populations can increase significantly and kill groups of standing spruce trees (Holsten and Werner, 1987; Holsten, 1996, 1997, 1998). Økland et al. (2005) considered two species of *Ips* [the spruce bark beetle, *I. typographus* (L.) in Eurasia and *I. perturbatus* in North America] "tree-killing bark beetles." Damage caused by *I. perturbatus* and other *Ips* spp. in northern regions may assume greater economic importance as more habitat is provided through climate change and human activities (Robertson, 2000). For example, in 1996 more than 47% of the residual spruce trees in a thinned area near Granite Creek on the Kenai Peninsula became infested with *I. perturbatus* and *I. tridens* (Mannerheim). Spring drought conditions as well as the recent overall warming of the Kenai Peninsula apparently led to this rapid increase in *Ips* activity in 1996 (Holsten, 1996, 1997, 1998; Anon., 1999).

In the spring, male *I. perturbatus* disperse from overwintering sites in the forest litter or downed trees to seek out new host material. After finding a host (see below), males bore through the outer bark and begin excavating a nuptial chamber in the phloem. They release aggregation pheromones and are joined by one to four females, which oviposit in the phloem following mating. Larvae feed on the phloem and develop throughout the summer. Following pupation and eclosion in the late summer and fall, the adults either remain in or leave their brood host to overwinter in the forest litter. *I. perturbatus* has one generation per year in Alberta, Canada (Robertson, 2000), and this is likely the case in Alaska as well.

When selecting a coniferous host to colonize (Wood, 1982a), bark beetles like *I. perturbatus* encounter a series of alternatives. Under the hypothesis of directed flight and landing guided by long-range olfaction, a searching beetle must determine if a tree is (1) the correct species; (2) not occupied at a high colonization density or for a long duration by other bark beetle species or woodborers; (3) not occupied at a high colonization density or for a long duration by bark beetles of the same species; and (4) susceptible to attack (Fig. 1, Borden, 1997). If these criteria are met, a beetle may be able to accept and successfully colonize its host. If not, the beetle may reject the host and continue searching. Each of these decision nodes, save perhaps the final one, is marked by an olfactory behavioral chemical that is either attractive or interruptive to the flying or walking insect. Because of the reliance by the beetle on this chemical communication-based decision process, there is potential to exploit this process to reduce the impact of bark beetles on forest trees (Borden, 1997).

Increased tree mortality in Alaska caused by *Ips* spp. has stimulated research on new management tactics based on semiochemicals from these decision nodes. Field tests of various bark beetle semiochemicals (Fig. 2) showed that racemic ipsenol (2-methyl-6-methylene-7-octen-4-ol) (**1A, B**), 83%-(−)-*cis*-verbenol (*cis*-4,6,6-trimethyl-bicyclo[3.1.1]hept-3-en-2-ol) (**2A, B**), and racemic ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (**3A, B**) were highly attractive to *I. perturbatus* (Holsten et al., 2000). Addition of a high release rate (~7 mg/day) of 84%-(−)-verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) (**4A, B**) to the three-component attractant significantly reduced trap catches (Holsten et al., 2001). Verbenone is known to be produced by bark beetles, symbiotic fungi, and by auto-oxidation of α-pinene (reviewed in Seybold et al., 2000). Verbenone has also been found among volatiles trapped above both sexes of *I. perturbatus* feeding in cut logs of *P.* × *lutzii* (Graves, 2008). *trans*-Conophthorin [(*E*)-7-methyl-1,6-dioxaspiro[4.5]decane] (**5A, B**), another bark beetle semiochemical, is found in the bark of at least seven angiosperm trees (*Populus tremuloides* Michx., *P. trichocarpa* Torr. and A. Gray, *Acer macrophyllum* Pursh., and *Betula papyrifera* Marsh. in North America), and (*B. papyrifera*, *B. pubescens* Ehrh., *P. tremula* L., and *Quercus suber* L. in Europe) (Huber et al., 1999, 2000; Zhang et al.,