Coniferous Host Selection among Primary Mortality-Inducing Bark Beetles in the Western United States

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Abstract

The fitness of phytophagous, foraging bark beetles (Coleoptera: Curculionidae: Scolytinae) is closely related to their ability to use environmental cues in discerning between host and non-host trees in colonization appraisal. Bark beetles, like many insects, have evolved to become specialists at least to the genus level in their host selection and prefer one to multiple arboreal species. To find suitable host material, the beetles utilize an array of physiological remote sensing apparatus; primarily those that give visual and olfactory sensory inputs regarding the external environment. The obtainment and processing of this information regarding a potential host leads to the different behavioral actions of either attacking the potential host or dismissal and continuing to search for another potential host.

Research in the area of bark beetle host selection has traditionally had a narrow focus on the olfactory role that chemical receptors, located in the beetle’s antennae, take in determining suitable host material. Blends of monoterpenes and other volatile host chemicals have been shown to be important information as bark beetles detect and respond to these kairomones. Pheromones emitted by pioneer beetles also play a crucial role in the host selection of non-pioneer bark beetles and can lead to the aggregation of other beetles to a convergent host.

Recent publications have alluded to the similar importance of visual information (color, texture, form) in determining host selection behavior. This information is especially useful when similar blends of kairomones are volatilized, and/or when distinguishable visual differences exist, from both a host and non-host species. Pheromones plumes can be present near coniferous host species but if other non-host species are in close proximity visual information becomes increasingly important for accurate host selection in foraging beetles.

The integration of information from the separate olfactory and visual sensory tools can be additive, synergistic, or redundant in nature depending on the bark beetle, host species, environmental conditions, and the content of the information. This paper specifically discusses the effects that olfactory and visual stimuli have on host selection behavior of mortality-inducing bark beetles.

Introduction

Primary mortality-causing, coniferophagous bark beetles (Coleoptera: Curculionidae: Scolytinae) complete much of their life cycles inside the protected environment of the phloem layer of a tree but must disperse to find suitable host material
for overwintering and reproduction. This “dispersal flight” leaves the migrating beetles vulnerable to predator species and exposed to harsh environmental conditions that readily cause exhaustion and dehydration (Pureswaran and Borden 2005). Direct fitness consequences have been associated with the dispersing beetle’s ability to adequately locate their specific host specie(s) and promote aggregative, group-attack behavior through pheromone production (Pureswaran et al. 2006, Berryman 1985). The quicker an exposed bark beetle can identify a suitable host and chemically communicate with others of the same species, the greater its chance for reproductive success.

There have been two hypotheses put forward to explain the apparatus used by bark beetles in their host selection. The first is that the beetles randomly land on any tree and test it to see if it is the correct species for colonization (Elkinton and Wood 1980). The second is that dispersing beetles use remote sensory input to aid in gathering information concerning host recognition and susceptibility that is subsequently used for colonization decisions (Moeck et al. 1981). The majority of the literature available and presented in this paper supports the second hypothesis of active host appraisal before landing, although this is not always the case in certain species of bark beetles (Pureswaran and Borden 2005, Faccoli 2005). The research in the area of sensory input and host selection had traditionally focused on the role of the olfactory information system but recent studies are showing that visual stimuli can be utilized as well.

**Olfactory Stimuli in Host Selection**

In many forests throughout the Western United States, there are mixed compositions of gymnosperm and angiosperm tree species. In these environments, bark beetles could potentially distinguish between semiochemicals emitted by the different
types of potential hosts with an array of chemoreceptors located mainly on their antennae (Huber et al. 2000). Huber et al. (2000), tested whether the different volatile compounds produced by non-host trees would elicit different responses in the antennae of the mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*), pine engraver (*Ips pini*), and three other coniferphagous bark beetles. They found that a wide array of angiosperm semiochemicals were able to produce antennal responses in the tested bark beetles. These beetles do have the ability to sense many of the angiosperm semiochemicals and they may react to such stimuli by avoiding the potential host outright (Huber et al. 2000). The angiosperm trees also produce favorable semiochemicals, such as certain monoterpene compounds (Huber et al. 2000). Since they produce the negative attractant chemicals as well, the bark beetles might utilize the volatile chemical information in a manner that compares the ratio of positive to negative attractive cues (Dethier 1982). Interestingly, the physiology involved in the broad range of recognition to non-host, angiosperm chemicals might be attributed to an ancestral host (the angiosperm trees) that these coniferphagous bark beetles previously utilize as hosts rather than solely an adaptive mechanism for non-host discrimination (Huber et al. 2000).

Bark beetles might utilize olfactory stimuli to discern between host and non-hosts in many of the mixed-coniferous forests as well. These mixed-conifer forests often contain one gymnosperm host species and multiple other gymnosperm non-hosts. Pureswaran et al. (2004) tested antennal responses to volatile monoterpene compounds emitted by the different host trees of four species of mortality-inducing bark beetle to determine whether there were notable chemical differences that caused response in each of the beetle species’ host and non-host semiochemicals tested. They found that the bark
beetles, depending on the species tested, showed response to almost all of the monoterpene volatiles tested, even those from the non-host conifers. Pureswaran et al. (2004) theorized that since there were no qualitative differences in the chemicals given off by the host and non-host trees, the bark beetles are most likely responding to different proportions of these chemical compounds.

Pheromones, or specie-specific chemical cues, can also play a crucial role in the host selection process. Pureswaran et al. (2004) tested antennal responsiveness to the pheromones of the four heterospecific bark beetles, found that they were all able to recognize the other species pheromone signals, and concluded these could be utilized as cues to avoiding non-host tree species as well. Poland and Borden (1998) found similar results in baited, multi-funnel trap catches of spruce beetles. They saw significantly decreased trap catches of spruce beetles when the traps were baited with heterospecific aggregation pheromones, even when the traps were also baited with the conspecific, spruce beetle aggregation pheromones.

**Visual Stimuli in Host Selection**

Different insects in the order Coleoptera have the physiological apparatus that enable them to discern different wavelengths of light in the ultraviolet (UV) band and the color band of the light spectrum. Compound eyes have photoreceptors that can sense at least the green and UV light waves. Differences in the perception of light among Coleoptera insects are related to differences in behavior and habitat (Lin and Wu 1992). The Douglas-fir (*Dendroctonus pseudotsugae*) and California five-spined ips (*Ips paraconfusus*) bark beetles have at least the photoreceptors available to respond to both blue and green light wavelengths (Groberman and Borden 1982). Recently, researchers
have begun to question the role that the known and unknown photoreceptors play in providing informational cues leading to host selection behavior.

Strom and Goyer (2001) tested different colored Lindgren multi-funnel traps, baited with aggregation pheromones, to see if there were significant differences in the trap catches of southern pine beetles (*Dendroctonus frontalis*). They found that the yellow and white traps had significantly higher trap catches than the black, blue, brown, gray, and green traps. Through statistical analysis, Strom and Goyer (2001) discerned that it was the reflectance value of the colors tested rather than the actual wavelength of light that influenced proxy-host selection in the southern pine beetle. The western pine beetle (*Dendroctonus brevicomis*) responds similarly to the southern pine beetle when presented with light and dark proxy-host colors (Strom et al. 2001).

Visual stimuli might be useful in environments that have contrasting colors or reflectance values associated with host and non-host tree species (Campbell and Borden 2006b), such as in forests with both angiosperm and gymnosperm tree species. In discriminating between host and non-host coniferous species, it is hypothesized that differences in texture, form, and color are too minute for visual cues to be effective in host selection processes (Campbell and Borden 2005).

**Visual and Olfactory Interactions in Host Selections**

Different species, even ones that are closely related, can have different levels of utilization of visual and olfactory sensory methods in host appraisal and selection. Strom et al. (2001) showed that the western pine beetle shows greater reactions to disruptive olfactory cues (antiaggregation pheromones) than disruptive visual cues (white silhouette). Conversely, the southern pine beetle, whose taxonomy is closely related to
the western pine beetle, shows divergent behavior regarding the stimuli and has a preference for utilization of visual information rather than olfactory (Strom et al. 1999). This difference can potentially be explained by the fact that the southern pine beetle has multiple generations per year and usually emerges to attack neighbor trees (Strom et al. 1999). When beetle population levels and pheromone concentrations are high in a given area, the insects need a method of host appraisal with greater accuracy than the olfactory technique due to the presence of potentially confusing or conflicting volatilized chemical information (Borden 1974, Raffa et al. 1993).

Campbell and Borden (2006a) show that mountain pine beetles show preferential behavior to baited, multi-funnel traps that exhibit darker painted colors to simulate host trees than those with lighter colors painted to mimic non-hosts. They also showed, through the baiting of host, non-host, and mixed cluster-simulating multi-funnel traps, that at different times the mountain pine beetle is responding to visual, olfactory, or both sensory input categories. Campbell and Borden (2006a) found that the mountain pine beetle primarily uses olfactory stimuli in distant appraisal of suitable host trees but can use both olfactory and visual information when in close proximity to the suitable host and choosing whether to land or not. This interaction can be additive, redundant, or synergistic in nature depending on whether the stimuli is positive or negative, in terms of attraction, and the sex of the mountain pine beetle involved (Campbell and Borden 2006a). The ability to utilize different sources of information can be potentially very useful especially in mixed gymnosperm/angiosperm forests and where there is an abundance of volatile compounds present (Campbell and Borden 2006a).
Other species have been tested and shown to rely less on visual sensory input and more on olfactory information when compared to the mountain pine beetle. These bark beetles include: the western balsam bark beetle (*Dryocetes confuses*) and the Douglas-fir beetle (Campbell and Borden 2006b).

**Other Factors Important to Host Selection**

Besides visual and olfactory, there has been research identifying many different realms that divulge potentially useful information to foraging bark beetles that may aid in their host selection appraisal and associated behaviors. The magnitude of factors and interactions involved in host appraisal is alluded to by the broad range of informational categories presented subsequently.

The impact of the forced feeding of non-host material was analyzed by Faccoli et al. (2005) with the European spruce bark beetle (*Ips typographus*) to analyze short-range, on the bark host selection behavior. They found that the bark beetles responded with progressively decreased diet acceptance as the concentrations of angiosperm, non-host compounds increased. This implies that close range consumption of potential host material can lead to discerning host trees from non-host trees (Faccoli et al. 2005).

The residual affects of past experience can affect the host selection behavior of a bark beetle as well. Wallin and Raffa (2002) showed that pine engraver beetles can vary their host selection behavior based on previous host-encounter experiences. They found that the beetles preferred host material with low monoterpene concentrations, but after being presented with continuous host material with only high monoterpene concentrations, they lowered their “acceptance threshold” and proceeded with colonization behavior. It was hypothesized that this mechanism enables the pine
engraver to mechanistically choose stressed trees with high susceptibility to bark beetle invasion (Wallin and Raffa 2002).

Surface bark temperature has also been identified as a potential factor involved with mountain pine beetle host selection. Schmid and Mata (1991) the mountain pine beetle, in regards to their ponderosa pine (Pinus ponderosa) tree host, shows a negative thermotactic response and might be avoiding bark surfaces with warmer temperatures.

The interaction between pine engraver beetles choosing a host and the densities of beetles on the surface and in the medium of a potential host were both assessed by Wallin and Raffa (2002) in a laboratory study. In this experiment, they found that the probability and the temporal rate of beetle entry into the host medium was positively correlated with the density at both respective locations. These density-mediated responses could be telling the beetles that there are sufficient beetles to overcome the tree’s defenses and the rapid speed of beetle entry might be due to a “scramble competition” where the invading beetles are competing for limited phloem resources (Wallin and Raffa 2002).

Stand microclimate has been hypothesized to be a factor in bark beetle host selection colonization by Bartos and Amman (1989). In their paper, the authors mention that thinning forests immediately reduce stand susceptibility to bark beetle-induced mortality while individual tree vigor, and thus tree health, actually takes multiple years to increase. Bartos and Amman (1989) hypothesize that microclimate characteristics such as wind speed, bark temperature, and/or canopy-caused inversion layer reduction might have an effect on bark beetle host selection.
Summary

It is clear that there are many factors, multi-level interactions, and informational stimuli available for bark beetles to utilize when making their host selection decisions. Olfactory inputs have traditionally been thought of as the primary mechanism involved in host selection behavior. While this might be the case in many bark beetle species, other sensory inputs and sensing apparatus are frequently utilized, especially when other information is contradictory or confusing (Borden 1974, Raffa et al. 1993). Recent research has focused on the impact of visual stimuli on host selection and has found in many cases that the bark beetles tested can potentially use visual host characteristics in host appraisal and potential selection (Strom et al. 1999, Campbell and Borden 2006a, Campbell and Borden 2006b). Other factors, discussed previously in this paper, that have been shown to contribute to bark beetle host selection include: bark temperature, conspecific population density, host material composition (as a food source), stand microclimate, and past individual beetle experience. There is a vast potential for other factors or interactions being involved and future research endeavors will bring light to many of the unknown mechanisms influencing bark beetle host colonization behavior.
Work cited:


