

Current Status and Critical Research Needs in Scolytid Genetics¹

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During the past two decades, our knowledge of bark beetle behavior and ecology has greatly expanded. In particular, studies of pheromone communication, host plant relations, and population dynamics have increased our basic knowledge of bark beetle biology, improved our ability to manage pest species, and provided strong models for research on other insect groups. However, bark beetles remain our most damaging forest pests nationwide. In addition, the various components of scolytid biology are usually studied in isolation, and some key gaps in our knowledge preclude effective synthesis. In my opinion, a major reason for these difficulties is that insufficient attention has been given to bark beetle genetics. Increased knowledge in this area could serve as a powerful unifying theme among the various subdisciplines, and improve our management capabilities.

The lack of attention to scolytid genetics is well evidenced by the major books and review articles on this family. Most texts and chapters make no, or relatively brief, mention of genetics or the role genetics could play in population behavior. Some areas of scolytid genetics have received well-focused attention, in particular isozyme variation within and between species (Langor and Spence 1991, Stock and Guenther 1979, Stock and others 1984). These studies established polymorphism, heterozygosity, and population structuring across geographic regions and sometimes host species. Some basic work has been done on cytology (e.g., Lanier 1981), before the development of modern methods. However, a number of critical areas, ranging from the molecular to population levels, remain unexplored.

A number of new tools are now available for studying insect genetics. However, I feel the most critical need is to generate testable hypotheses regarding how heritable aspects of scolytid biology relate to their behavior and population dynamics. Milton and Schneider (1987) summarized two basic approaches to the role of genetics in insect outbreaks: (1) start with a heritable marker, and conduct a broad search for correlations between gene frequencies and population fluctuation, and (2) identify life history traits whose variation would greatly influence population behavior, and determine heritable variation. Both approaches are valid, and **both** must be pursued to make relevant gains. As a population ecologist, I will approach the issue from the latter perspective. Hopefully, this perspective will complement equivalent suggestions arising from the marker-up, and more molecular approaches. From an ecological/population management view, I think that three critical genetic issues must be addressed.

Host Selection and the Genetics of Outbreak Behavior

Genetic traits associated with host selection may be useful in predicting the onset of bark beetle outbreaks. Low density populations are typically concentrated within severely stressed trees. Yet during outbreaks, almost all trees are attacked and killed, regardless of their vigor. The mechanisms by which high beetle numbers kill trees is fairly well understood: aggregation pheromones coordinate rapid mass attacks on entered trees, and the tree's resistance capabilities are exhausted. More beetles are required to kill vigorous trees than stressed trees. However, this tells us nothing about how beetles' decisions to enter trees could be influenced by their population densities. Each beetle undergoes a strict behavioral repertoire, which culminates in either host entry or resumed flight (Raffa 1988). This suggests that different selective pressures may operate on individual beetles at different beetle densities. At low populations, the likelihood of an entered beetle being joined by enough recruits to successfully colonize healthy trees is low, and so relatively discriminating behavior may be favored. Conversely, at high densities, beetles that enter healthy trees are more likely to be joined by sufficient recruits to kill the host, and so less discriminating behavior is adaptive (also, discriminating types may never find acceptable hosts, as the weakest trees are colonized by generations leading to the outbreak). Therefore, changes in gene frequencies associated with host acceptance could both result from, and partially cause, bark beetle population increases (Raffa and Berryman 1983, Raffa 1988). The relatively high levels of within-tree, compared to spatial and temporal, genetic (electrophoretic) variation in *Dendroctonus frontalis* (Florence and Kulhavy 1981), and the high levels of genetic diversity that can be maintained in dispersed populations (Florence and others 1982) could lead to such directional selections. Observed behavioral differences between outbreak and nonoutbreak *Ips typographus japonicus* (Futura 1989) are consistent with such a pattern.

There are alternative explanations of how host selection could change through time, such as individuals becoming less discriminating as their stores deplete, or pheromones eliciting host entry in addition to attraction [although Hynum (1978) observed the proportion of beetles resuming flight after landing does not decrease during mass attack]. However, the genetics of host selection should be considered a high-priority area. This can be approached by: (1) quantifying for heritable variation in beetle selectivity, (2) quantifying genetic diversity throughout the endemic and epidemic phases within an area, and between endemic and epidemic populations at one time, using polymorphic DNA markers such as RFLP's or RAPD's, and (3) testing alternative hypotheses.

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Role of Natural Enemies

Biological control of bark beetles has received only scant attention, largely because the major pests are native species. However, geographic and local variation in predator behavior may provide some avenues for better exploiting natural enemies. These include introducing predators from distant populations, and biasing against natural enemy removal during semiochemically based population control measures.

The major insect predators locate prey by responding to bark beetle aggregation pheromones. Prey mortality is often extremely high. Thus, selective pressures exerted by predators may favor alterations in prey semiochemistry that reduce their attractiveness to predators, yet retain intraspecific functionality. Several lines of evidence support this view: (1) predacious beetles, although attracted to scolytid pheromones, may show greater affinity for stereoisomers that are relatively less attractive to (and produced by) the prey (Herms and others 1991, Payne and others 1984, Raffa and Klepzig 1989); (2) minor pheromone components can have markedly different effects on predator and prey species (Seybold and others 1992c, Miller and others personal communication); (3) local predator guilds may be more attracted to distant than local populations of the same prey species (Lanier and others 1972, Raffa and Dahlsten personal communication).

The underlying genetics of predator-prey interactions are completely unknown. No studies on the heritability of predator responses to bark beetle pheromones have been conducted, and only recently has individual variation in bark beetle semiochemistry been explored (see #3 below). Studies should be aimed at: (1) conducting classical hybridization studies of divergent perception phenotypes within predator species, (2) identifying DNA markers associated with pheromone perception among both predators and prey, and (3) quantifying selective pressures imposed by predators on beetle reproductive success (at both the colonizing cohort and individual beetle levels) and on predators to locate a particular prey guild.

Pheromone Synthesis and Attraction

Pioneering work by Lanier (1970c) demonstrated Mendelian control over *Ips* pheromone production and response. Such inheritance patterns can contribute to demic structuring (Cane and others 1990c). Recent studies of scolytid pheromone communication have shown strong inter- and intrapopulation differences within species (Berisford and others 1990, Birgersson and others 1988, Miller and others 1989, Seybold and others 1992c). These results could have strong implications for bark beetle biology and management, particularly in guiding semiochemically based management strategies and biological control (see above).

Several factors have been proposed as possible contributors to heritable genetic variation in scolytid semiochemical synthesis and response. For example, it has been proposed that some beetles do not actively engage in host searching, but only react to pheromone plumes indicative of others' success. The frequency of such types may change with beetle density (Birgersson and others 1988), in a fashion similar to the host selection model proposed in #1. If so, accompanying genetic or phenotypic markers may be useful in predicting outbreak behavior. Genetically based variation in pheromone chemistry may also be important in maintaining the structure of scolytid mating populations (Teale personal communication). Studies should (1) conduct classical hybridization tests among beetles, putatively divergent types (based on arrival time in aggregation sequence and relative responsiveness to host cues in laboratory assays), (2) identify DNA markers associated with putatively different behavioral types, and (3) determine the level of gene flow and demic integrity among putatively different types.