

An (Ecologically Biased) View of the Current Status of Bark Beetle Genetics and Future Research Needs¹

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Bark beetles are commonly considered the most destructive insect pests in pine forests in North America. Despite the relatively intense interest in this group because of their pest status and uniquely complex ecological and evolutionary relationships, many aspects of their biology, including genetics, are poorly understood. Most genetic research on bark beetles has concerned inferences about the evolution of species, especially the phylogeny of important genera (e.g., Cane and others 1990b, Lanier 1967, 1981, Lewis and Cane 1990b, Mitton and Sturgeon 1982). Relatively little emphasis has been placed on population genetics, particularly on genetic variation within and among populations over time and space (reviewed in Milton and Sturgeon 1982, and ref. below).

The natural history of this group is probably the single most significant deterrent to studies of population genetics, because sampling and laboratory rearing is either difficult or impossible. Improved sampling of adults has paralleled advances in semiochemical research, which in turn have prompted and permitted recent investigations into variation in the production and response to semiochemicals at the population level (e.g., Birgersson and others 1984, Herms and others 1991, Miller and others 1989, Teale and Lanier 1991). However, most of the life cycle is spent under bark, limiting observations and necessitating destructive sampling of brood in order to obtain requisite estimates of fitness (e.g., fecundity, age to first reproduction). Most species are relatively intractable in the laboratory, thus precluding classical genetic studies, estimations of heritability, and development of molecular genetics techniques based on phenotypic studies. It is not surprising that recent advances in our understanding of both molecular and phenotypic variation are concentrated in the more easily reared species such as *Ips* spp. (e.g., Cane and others 1990b, Gast 1987, Lanier and others 1972, 1980, Miller and others 1989, Piston and Lanier 1974, Stauffer and others 1992a; but see Langor and Spence 1991, Teale 1990, Teale and Lanier 1991). The newest molecular techniques (e.g., Restriction Fragment Length Polymorphism and Randomly Amplified Polymorphic DNA) may mitigate sampling deficits, are likely to lead to gene mapping, and vastly accelerate the molecular exploration of genetic variation. Even with these advanced techniques, however, dramatic advances depend on novel application and well-

designed experimentation. Ultimately, these results must be tied to ecologically relevant characteristics (phenotypic expression).

Emphasizing an ecological genetics approach, our (other team members include Alosi, Greene, and Preisler, see contributions this proceedings) investigations have involved estimates of both genotypic and phenotypic variation within and among bark beetle populations and communities, as well as across ecologically similar species (mountain, western, and southern pine beetles). Our research includes aspects of the technology such as starch gel electrophoresis that were used in the earlier studies of differences between populations (e.g., Roberds and others 1987, Stock and others 1979, 1984). Besides genetic inferences made by electrophoresis, we are examining differences in the levels of the key enzymes that help to adapt beetles to the presence of toxic secondary chemicals in their host trees (see Alosi this proceedings). In contrast with previous gross examinations of terpene levels in host trees (Coyne and Lott 1976, Smith 1975)—their primary defense—we are examining differences in terpene composition by means of more sensitive analyses to detect and monitor changes consistent with changes in population structure.

To date, information acquired from five years (1985-90, see Greene this proceedings) of monitoring mountain pine beetle populations in Central Oregon suggests that patterns of esterase enzymes detected by electrophoresis have shifted concomitantly with a shift in population status from endemic to epidemic and back to endemic. In addition, quantities of esterases measured biochemically have changed, even for mountain pine beetles in the same host species. Glutathion *S*-transferase levels also seem to be involved in the transition. We have initiated (1991-present) comparable studies with western and southern pine beetles and begun investigations of phenotypic variation between and within populations including analyses of behavioral (pheromone response), physiological (lipid content) and morphological (fluctuating asymmetry) variation. These studies represent modifications to previous efforts to quantify and relate phenotypic variations to genotypic variation among beetle populations (e.g., Langor and Spence 1991, Sturgeon and Mitton 1986). For example, morphological variability within individuals may provide a valuable early guide to changes in beetle quality. Fluctuating asymmetry (nondirectional deviations from bilateral symmetry) has been shown to be an effective and inexpensive tool for detecting stress in natural populations (Leary and Allendorf 1989) and in cultures (Clarke and McKenzie 1992), because it provides a reasonably direct measure of developmental stability (Palmer and Strobeck 1986). Environmental and genetic perturbations could affect fluctuat-

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ing asymmetry analogously, i.e., as the level of stress of any kind increases, fluctuating asymmetry and its variability should increase provided that the stress is sufficiently intense to produce an effect (Parsons 1990a, b).

In addition, in most genetic studies done to date, standard statistical methods involving chi-square comparisons of observed gene frequencies versus those predicted by Hardy-Weinberg equilibrium have been used for data analyses. Our investigations emphasize the use of exploratory statistics to examine actual numbers rather than frequencies (see Preisler this proceedings). Uses of these new procedures will permit us to model patterns in biotic communities of which bark beetles are a part, to estimate realistic models of species overlap, and to formulate causal hypotheses about changes in bark beetle populations in transition from endemic to epidemic states.

Priority Research Needs

1. Long-term (multi-generation, multi-season) qualitative and quantitative genetics studies are needed to detect genetic changes that result in changes on the population structure.

2. Likewise, changes in the component(s) that comprise the gene-environment interaction (e.g., host-insect interactions)

must be assessed to understand the sources of pest population variation.

3. Continuous rearing technology (e.g., artificial bark beetle diet) must be developed for *Dendroctonus* spp.

Needs in Quantitative Studies

1. Estimate heritabilities of key traits over space and time
2. Identify genetic markers and develop DNA/RNA probes, estimate frequencies, and study changes in population structure over space and time
3. Having identified one or more markers that differ constantly with space, time (or both), quantitative investigations are needed to establish sources of variation (selection pressures), including
 - a. Biochemical traits: levels of key enzymes such as esterases, mixed function oxidases, or any other enzyme that can be directly linked to survival (fitness)
 - b. Phenotypic or quantitative traits: the expression of life history traits (e.g., fecundity, longevity, age to first reproduction, phenology), or behavioral, physiological or morphological traits.