

SELECTION FOR INSECT RESISTANCE IN FOREST TREES

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An interdisciplinary approach to resistance breeding is discussed with emphasis placed on documenting genetic variation and developing an understanding of the causal mechanisms responsible for variation in host susceptibility. The specific features and effectiveness of phenotypic and genetic selection are contrasted and examples of documented genetic variation in susceptibility of trees to insects are provided.

Introduction

Despite progress in controlling insects through chemical application and biological manipulation, economic losses from insect damage to forest and ornamental trees remain enormous. Although genetic methods have proved successful in development of insect-resistant crop plants (Maxwell and Jennings 1980), progress in breeding insect resistant trees has lagged behind. As pointed out by Hanover (1980), that lag can be attributed, at least in part, to relatively long generation intervals in trees and a dearth of knowledge about host physiology and insect biology. In addition, the development of resistance in a long rotation host such as trees requires an interdisciplinary research effort which has only rarely been put forth. The objective of this paper is to discuss the major components and implications of resistance breeding strategies for trees rather than to provide a review of resistance concepts or physiological mechanisms involved in resistance. The latter information with respect to trees is addressed in reviews by Stark (1965), Gerhold *et al.* (1966), Hanover (1975 and 1980). Hopefully this paper will contribute to the stimulation of interdisciplinary discussions and perhaps cooperative research endeavors among geneticists, physiologists, and entomologists from the northeast.

Components of Resistance Breeding

In the simplest sense, one can identify two major components of the resistance breeding strategy for trees. The existence and accurate demonstration of host variation in resistance (or susceptibility) to insect attack is prerequisite to selection or breeding for insect resistance. Secondly, a thorough understanding of the nature and underlying mechanism(s) responsible for the observed variation in resistance is important to determine the feasibility and directions of future breeding efforts. A third component, the actual breeding of resistant strains, is dependent upon the success of the first two components. In my estimation slow progress toward developing

resistant strains of trees (or, at least, strains with reduced susceptibility) can be attributed to the lack of a concerted interdisciplinary effort in the documentation and understanding of insect resistance and its mechanisms. For instance, genetic improvement programs have been established for balsam fir in the Lake States and New England, but none of the many provenance and progeny test plantations have been placed within major spruce budworm regions. As a result, the most productive method for revealing variation in insect susceptibility has not been utilized and no progress has been made in the development of balsam fir resistant to the budworm. With respect to the second component, numerous examples exist of physiologists and biochemists who have thoroughly studied the morphology, anatomy, and/or chemistry of tree populations with purported but not documented resistance to an insect pest. In contrast, enough information on the actual breeding of resistant strains has been generated from crop research (Painter 1966) to provide an adequate foundation of breeding information once the first two components are successfully investigated for a particular host-insect system.

Variation in Host Susceptibility

The development of host resistance to insect attack must be preceded by at least some level of heritable variation in susceptibility to an insect pest. Such genetic variation may occur naturally within species and may be represented by variation among races, provenances, families or individual trees growing side by side in the same stand. In the absence of natural intraspecific variation in susceptibility, interspecific variation may exist and species selection may be a reasonable means of circumventing economic losses resulting from insect attack (Wright and Gabriel 1959; Wilkinson 1961). If species selection is not appropriate, then species hybridization may be an expedient way to generate sufficient heritable variation to allow selection to be productive.

When considering the distribution and biology of the host, the potential for variation in susceptibility of trees to insect attack is expected to be quite high. For instance, tree species have large natural ranges and are, therefore, subjected to a diversity of climatic, edaphic, and biological pressures which tend to promote genetic variation, at least at the population or regional level. Rangelwide provenance tests of many species have revealed considerable genetic variation in morphological, anatomical, biochemical, and physiological characteristics, and would suggest that the potential for variation in insect susceptibility might also be high. In addition, despite the increase in tree cultivation during recent years, the vast majority of the forest resource exists in extensive, relatively wild stands. As a result, there probably has not been much gene depletion or a drastic narrowing of the genetic base for most species. Furthermore, tree species are largely outcrossing organisms and are considered to be highly heterozygous with respect to most traits. High heterozygosity can be expected to lead to considerable genetic diversity among

individual trees as well as at population and racial levels. Finally, a substantial level of interspecific compatibility seems to exist within many genera of forest trees and numerous hybrids among species have been produced and documented. Therefore, even in cases where natural variation within a tree species is quite low, the possibility of creating new variation through species hybridization is possible and plausible.

Mechanisms Responsible for Variation in Susceptibility

Upon identifying variation in host susceptibility, it is important to confirm a genetic component to that variation and to understand the underlying causal mechanism(s) responsible for the observed variation. It is important, for instance, to understand whether variation in susceptibility is due to some genetically-controlled avoidance factor (eg. phenological asynchrony) or whether the host is actually capable of resisting the insect. Although resistance can theoretically be identified, and perhaps even captured through breeding, without an understanding of causal mechanisms, the efficiency of breeding and stability of resistance will increase considerably with knowledge of the chemical, physical and/or physiological basis for resistance. This is especially true for long rotation crops such as trees. Instead of "blindly" breeding for resistance, one can select directly for the character(s) which confer that resistance. Or, as emphasized by Hanover (1980), study of causal mechanisms could facilitate indirect selection for traits with a strong genetic correlation with resistance but not causally related to it. Furthermore, physiological investigations of resistance mechanisms may reveal host chemicals which can be used as insecticides or as vehicles of insect behavior modification (Hanover 1980).

Studies addressing mechanisms of tree resistance often examine specific biological properties of the host (and perhaps the insect) and attempt to relate variation in such characteristics to variation in susceptibility to an insect pest. Hanover (1976) has discussed tree resistance to insects in terms of variation in the following broad categories of host characteristics: morphology and anatomy of the host, chemical repellants produced by the host, chemical attractants produced by the host, and the nutritional status of the host. In my opinion, research into mechanisms of insect resistance is necessary for the development of an effective resistance breeding program, but is complicated by environmental influences, tree responses to injury, and developmental, seasonal, and within-tree variation.

Selection for resistance

Before physiological or chemical mechanisms of resistance can be described and natural variation in insect resistance can be exploited toward the development of resistant strains, it is essential that individual trees or tree populations with inherently low susceptibility to insect

attack be accurately identified. This involves some form of selection. Since "selected" trees will be the source of investigations of resistance mechanisms and may form the basis of a resistance breeding program, it is mandatory that resistance of these trees is documented rather than assumed or inferred. Although often taken for granted, the chore of selection for resistance is difficult because of the quantitative and complex nature of the host-insect relationship, environmental influences on this relationship, and interactions between host and insect genotypes and the environment. The major approaches to selection are phenotypic selection of resistant trees in natural or planted stands and genetic selection of families or provenances from replicated progeny tests.

Phenotypic selection

If no previous information on genetic variation in resistance is available for a given host-insect situation, phenotypic selection of unattacked or completely recovered individuals in heavily infested stands is a logical initial step in an artificial regeneration program designed to improve insect resistance. Obviously, in such situations, one hopes that the apparent resistance or recovery ability of the parent tree is inherited and can be transmitted through seed or vegetative propagules to the offspring. For phenotypic selection to be effective, a high selection differential should be maintained (i.e., many trees should be observed but only the one or two best should be selected in each stand) and factors that could lead to escape or an apparent resistant condition must be considered in the assessment of candidate trees (McDonald 1981). However, since the genetic component of phenotypic variation is not readily ascertained without replicated progeny tests, there can be no assurance that progeny will exhibit increased resistance. In fact, there can be no assurance that the selected parent tree has exhibited true resistance. Although phenotypic selection is a reasonable improvement approach when no other information or alternatives are available, it is not the most efficient approach toward initiating a research program involving physiological investigations into resistance mechanisms and actual resistance breeding. Clearly, the rigorous demonstration and documentation of genetic resistance to insect attack should be prerequisite to physiological investigations and advanced breeding efforts. Such documentation can not be attained with phenotypic selection in the absence of progeny tests. Unfortunately, the vast majority of research addressing the physiology and genetics of insect resistance in trees has been conducted in the absence of documented genetic resistance of the host.

Specific features of phenotypic selection which limit its utility in screening for and understanding the nature of insect resistance are as follows:

1. Selection procedures. The effectiveness of phenotypic selection is influenced largely by the selection differential employed and the specific methods utilized in selecting can-

didate trees as well as the heritability of the trait in question. Although it may be possible to standardize selection methods, the selection differential may vary with the size, age, and degree of infestation in the stands.

2. Escape rather than resistance. Unless a reliable repeatability estimate can be included in the selection criterion, the possibility exists a candidate has escaped rather than resisted attack. Although the probability of escape is inversely proportional to the degree of infestation in the stand, it can theoretically never be zero.
3. Microsite effects on host and insect phenotype. Localized climatic, soil, or biological factors can influence the morphology, chemistry, and phenology of the host, insect, and/or insect predators and perhaps create a temporarily induced resistance (pseudoresistance). Such confounding environmental factors also muddle interpretation of physiological parameters measured on phenotypically-selected trees.
4. Developmental and age variation of host. Individual trees may not be attacked because of developmental factors associated with age rather than genetically controlled physiological factors.
5. Narrow genetic base. Since phenotypic selection is often concentrated in a relatively small portion of a species range, only a small portion of the species genome is assessed. This narrow genetic base limits the potential for developing resistant strains and could lead to some level of inbreeding depression in advanced generation populations.
6. Nature of genetic control. Even if escape, microsite factors and age can be eliminated as confounding variables and genetic resistance is strongly suspected, the transmissibility of resistance through seed is dependant on the nature of genetic control. If resistance of an individual is the result of a specific combination of non-additive genes, one can not expect a consistently high level of resistance in offspring of that parent.
7. Stability of resistance. Since for an individual tree there is no way to test the repeatability of resistance over space, it is not known whether the apparent resistance is stable over different environments or is the result of a specific genotype x environment interaction.
8. Cost and logistics. The cost of maintaining a high selection differential and broad genetic base in a phenotypic selection program can be prohibitive. Furthermore, the logistics of field measurements of physiological traits and of actual breeding are made complicated by tree size, and travel distances as well as confounding environmental factors.

Phenotypic variation in insect susceptibility has been observed for many forest tree species, but only rarely has there been documentation of genetic variation or a physiological explanation for the apparent resistance. For instance, based on phenotypic observations, Hall (1937) reported that "Shipmast" and "Higbee" cultivars of black locust were resistant to the locust borer, but the apparent resistance "broke down" following additional testing. In balsam fir, phenotypic variation in susceptibility to black-headed budworm and spruce budworm has been reported but genetic resistance has never been substantiated (Bakuzis and Hansen 1966). Numerous attempts have been made at phenotypically selecting eastern white pines that are resistant to the white-pine weevil. For instance, Wright and Gabriel (1959) used sophisticated probability estimates and adjustments for microenvironmental factors in assessing weevil resistance but were unable to reliably select resistant trees. In fact, despite phenotypic variation in susceptibility, recent research has indicated that there is no natural resistance of eastern white pine to the white-pine weevil (Wilkinson, personal communication). Finally, in a review paper, Hanover (1980) noted that the American bark beetles and their tree hosts have received more research emphasis than any tree-insect system in the world. Although apparent resistance has been observed in natural populations and considerable research has been done on possible resistance mechanisms, there has been no documentation of genetic resistance to bark beetles among their primary hosts, the pines, spruces, and Douglas-fir (Hanover 1980). Although phenotypic selection has been the foundation of most plant breeding programs, its limitations and expenses with respect to selection of insect resistant trees must be recognized. Wright and Gabriel (1959) provide a realistic account of the effort involved in selecting and testing apparently resistant phenotypes and McDonald (1981) has provided an excellent illustration of the potential complexity of a host-insect system and the numerous factors which could lead to phenotypic variation in response of a host to insect attack.

Genetic Selection

The most productive means for determining the magnitude and nature of intraspecific variation in insect resistance has been carefully designed progeny tests which are replicated within plantations and by several plantations at different locations. Such experiments include rangewide or localized provenance tests, half-sib and full-sib progeny tests and interspecific hybridization studies. These tests may examine progeny of phenotypically selected or unselected parents. In many cases, genetic plantations have been established with tree improvement objectives other than insect resistance in mind. However, if properly designed, such studies can be conveniently and accurately used to assess genetic variation in incidence of attack, degree of injury, feeding and oviposition preferences as well as physiological or biochemical characteristics which may be directly or indirectly related to host susceptibility. Some examples of documented genetic varia-

tion in susceptibility of tree species to insects are included in Table 1.

Some features of progeny tests which contribute to their value in assessing genetic variation in insect susceptibility are as follows:

1. Partitioning of variation. Variation in insect susceptibility and other traits of interest can be quantitatively partitioned into genetic, environmental, and genetic x environment components. As a result, the heritability of specific traits, stability of resistance, and expected gain from selection and breeding can be assessed. Also, genetic variation can be confirmed before expensive and time-consuming studies of resistance mechanisms are initiated.
2. Distribution of genetic variation. The distribution of genetic variation among races, regions, populations, families, and individual trees can be accurately estimated. Such information can help elucidate the nature of variation, such as adaptive strategies, as well as influence subsequent selection and breeding strategies.
3. Broad genetic base. Because trees grown from seed collected throughout a species range can be incorporated into a single study, a relatively broad portion of the species genome can be assessed. As a result, the probability of discovering genetic resistance is increased and the potential for maintaining a broad breeding population is enhanced.
4. Related traits can be accurately measured. Genetic variation in morphological, anatomical, physiological, and biochemical characteristics that may be related to insect susceptibility can be accurately assessed because the measurement of several trees per population or family provides a repeatability estimate.
5. Indirect selection. Genetic correlations among traits can be calculated so the effectiveness of indirect selection for resistance can be tested.
6. Developmental variation. Repeated assessments of variation in insect susceptibility provide an assessment of developmental and age x genetic variation. Juvenile-mature correlations can be estimated and used in judging the reliability of selections.

Table 1. Examples of documented natural genetic variation in susceptibility of tree species to insects.

Host	Insect	Reference
Scotch Pine	Pine Root Collar Weevil	Wright and Wilson, 1972
	European Pine Sawfly	Wright <i>et al.</i> , 1967
	Eastern Pineshoot Borer	Steiner, 1974
	Zimmerman Pine Moth	Wright <i>et al.</i> , 1976
	White-Pine Weevil	Wright <i>et al.</i> , 1976
Eastern White Pine	White-Pine Weevil	Wright and Gabriel, 1959; Garrett, 1972
Austrian Pine	Zimmerman Pine Moth	Wheeler <i>et al.</i> , 1976
Jack Pine	Eastern Pineshoot Borer	Jeffers, 1978
	White-Pine Weevil	Arend <i>et al.</i> , 1961
	Red-Headed Pine Sawfly	Arend <i>et al.</i> , 1961
	Northern Pitch Twig Moth	Hodson <i>et al.</i> , 1982
Douglas-Fir	Sitka Spruce Gall Aphid	Teucher, 1955
	Douglas-fir Woolly Aphid	Meinartowicz and Szmidt, 1978
	Western Spruce Budworm	McDonald, 1979
White Spruce	Eastern Spruce Gall Aphid	Canavera and DiGennaro, 1979
Japanese Larch	Larch Sawfly	Harman and Genys, 1970
European Larch	Larch Sawfly	Genys and Harman, 1976
Norway Spruce	White-Pine Weevil	Holst, 1955
	Black-Marked Tussock Moth	Schonbörn, 1966
Balsam Fir	Balsam Twig Aphid	DeHayes, 1981

7. Convenience for breeding work. Since all trees are gathered in one place and are all of the same age, breeding can be done with limited travel and usually on trees of relatively small size.
8. Immediate production of low susceptible populations. If a genetic component to variation in insect susceptibility is confirmed, open-pollinated seed can be collected from races, populations, or individual trees with low susceptibility and some level of resistance can be expected from the trees produced.
9. Phenotypic selection still possible. If genetic variation among populations or progenies is not evident, then phenotypic selection of individual trees can still be practiced in the even-aged test plantations in hopes of exploiting within-family genetic variation.

Although progeny tests are an excellent source of information concerning genetic resistance, they are only effective when located in insect prone areas and when they are of an age (or size) in which the trees are susceptible. For instance, progeny tests may not be an immediate source of information on genetic variation in susceptibility to most bark beetles, since these insects generally attack mature trees. Certainly, forest geneticists and entomologists can and should work cooperatively to insure that forest genetics test plantations are established in areas where insect populations are high so that differential susceptibility can be assessed some time in the future. Perhaps the most serious limitation to genetic selection for insect resistance through progeny tests, is that variation in susceptibility is assessed in unnatural plantations containing a diverse mixture of genotypes. It is possible that insects will select for or against certain seedlots when they are included in a mixed planting, but will attack indiscriminantly in commercial plantings containing trees from one or a few selected seedlots. Despite this potential difficulty, progeny tests still appear to be the only reliable means of documenting a genetic component to variation in susceptibility.

Much of the information documenting genetic variation in susceptibility of tree species to insect pests has been generated from observations of differential damage or feeding in rangewide provenance tests. Other tests, including species and hybrid trials as well as single-parent progeny tests, should also be monitored for such variation whenever possible. Many such tests already exist in the northeast and represent an as yet untapped source of potentially valuable information. Although documentation of genetic variation in susceptibility is an important initial step, studies defining the nature of the variation (eg. resistance vs. avoidance) and elucidating physiological causes for such variation need to be pursued. Cooperative research among geneticists, physiologists and entomologists will likely be the most expedient approach toward the development of forest trees that are resistant to insects.

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