# GENETIC VARIATION IN DISEASE RESISTANCE OF NATIVE FOREST-TREE SPECIES

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Forest-tree diseases may be classified in many ways but for the purpose of this discussion I should like to separate them into two groups, those that can operate only when tree vigor is reduced and those that can and do operate regardless of tree vigor. In both groups the severity of the disease depends upon the interaction of two factors, the virulence of the pathogen and the resistance of the host to successful attack. In the first group, however, the resistance of the host can be increased by cultural practices that raise the vigor of individual trees and stands, whereas in the second group the only method of increasing individual tree resistance in a stand is to weed out the susceptible trees and replace them with trees that are resistant. This basic distinction should be the deciding factor in determining the type of control program recommended for any disease. For diseases that are dependent upon reduced tree vigor from whatever cause, control should be secured by improving cultural practices or by growing the crop on sites and in geographic locations where the tree species is most vigorous.

Examples of forest-tree diseases that are dependent upon reduced tree vigor are common and include most of our native endemic diseases. Tympanis canker of red pine has never been observed upon naturally reproduced trees or on planted trees within the optimum range of the species, but it has been found in plantations south of the optimum range where the tree may be considered as occupying an unfavorable site or when stagnation has resulted from the lack of cultural practices. Adelopus needle cast of Douglas-fir is harmless and inconspicuous within the natural range of the species in western North America but has caused serious losses in plantations in eastern United States and in Europe. Diplodia twig blight of hard pines is practically unknown in naturally reproduced stands but is one of the important factors in the complete failure of Scotch pine plantations in the United States and of other hard pines planted here and elsewhere. Fomes annosus root rot of conifers occurs rarely and causes slight damage in healthy natural stands but has caused extensive losses in plantations of red and eastern white pines on unfavorable sites. Nectria canker is abundant in stands of northern hardwoods established on cutover and burned coniferous sites and is relatively unimportant in similar stands on good hardwood sites. Cytospora canker of poplar species and hybrids is common in low-vigor trees and rare in fast-growing trees on good sites. These examples are sufficient to illustrate the many forest-tree diseases that may be controlled by growing the right tree on the right site and giving it adequate care throughout its rotation. Why resort to expensive, long-range tree improvement programs for disease control when losses can be eliminated or maintained at a low level by applying good cultural practices?

For the second group of forest-tree diseases, those not associated with reduced tree vigor, control is far more complex and depends for its success not only upon the application of good silvicultural practices but also upon special direct control measures or selection and breeding to improve the genetic resistance of the host to the disease. Special direct control measures include the eradication of ribes to control white pine blister rust, the eradication of infection centers to suppress oak wilt, the elimination of mistletoe-infected trees to stop the spread of the parasite, and sanitation measures and vector control programs to suppress the Dutch elm disease and phloem necrosis of elms; however, these are expensive and comparatively temporary in their effectiveness. As expedients to protect enormous values in forest and shade trees they are essential but they should be supplemented by additional research to select or produce seed or planting stock that is genetically resistant to disease attack so that eventually the direct control measures may be discontinued.

What is the evidence that genetic resistance to disease in forest trees does occur or may be secured? Examples are numerous and well documented. Chestnut blight, caused by the fungus Endothia parasitica, was discovered in this country in 1904; it probably was introduced from the Orient on nursery stock of Asiatic chestnuts. It found a highly susceptible host here in the American chestnut, Castanea dentata. The combination of an extremely virulent pathogen and a host with very little resistance has resulted in the elimination of American chestnut from our forests where it is today represented only by root sprouts from killed trees, by occasional seedlings, and by isolated individuals that have excaped infection. Within the genus Castanea, however, resistance to chestnut blight varies from practically zero in American and European species to high level resistance, approaching immunity, in some Asiatic species. The program to select and breed for blight resistance in chestnut will be treated at some length later; therefore I shall only indicate in passing that genetic resistance to this disease does exist.

White pine blister rust, caused by the fungus Cronartium ribicola, was introduced into North America about 1900 from northern Asia by way of Europe. It attacks only the white or five-needle pines, of which there are a dozen or more species known, with five species in North America. Within these white pine species, resistance varies from high in the Asiatic pines to very low in those from North America. Furthermore, within the North American species that as a whole are highly susceptible, individual trees have remained rust-free for many years even though abundantly exposed to infection. Many of these trees when artificially inoculated have continued to be free of the disease; therefore it is evident that they are genuinely resistant. Selection and breeding of white pines to secure resistant trees for the future are part of current research projects, and it is far from a vain hope that eventually there will be blister rust resistant pines available for forest planting.

The Dutch elm disease was discovered in this country in 1930 and since that time has spread widely over eastern United States and Canada and has been found in Colorado. It is caused by the fungus Ceratostomella ulmi and is spread from tree to tree by two species of elm bark beetles. Within the genus Ulmas, susceptibility to the disease varies from low among Asiatic species to moderate in some European species and high in American species. Selections from some of the susceptible American and European species have exhibited limited resistance but all have eventually failed when inoculated with virulent strains of the fungus. About 100,000 American elm seedlings collected

throughout the natural range of the species have been grown in nurseries and inoculated with the causal organism. Only two seedlings withstood these tests for three seasons and are now being tested with additional isolates of the fungus. From about 20,000 controlled crosses between American elm and the resistant Siberian elm, U. pumila, less than 100 seeds were obtained and only a few germinated. Of the few hybrid seedlings so secured, only one resisted repeated inoculations but has recently been killed by the disease. These data indicate that resistance to the Dutch elm disease does occur in elms and that it may be increased through hybridization but it is a genetically recessive and rare quality.

Phloem necrosis of elms is a virus disease first observed in this country in 1918. It is now known in 15 Central and North Central States and has caused enormous mortality to American elm and the winged elm, U. alata. Seedlings and clones from survivor elms in the Ohio River Valley are highly resistant, perhaps immune, to the disease. The ultimate goal is an American elm selection resistant to both phloem necrosis and the Dutch elm disease, a difficult but not an impossible task. The Christine Buisman elm, a selection from U. carpinifolia, is resistant to both diseases and offers a valuable tool for further research. The American elm selections resistant to Dutch elm disease are susceptible to phloem necrosis.

Mimosa wilt, caused by a species of Fusarium, is a serious disease problem in several Southeastern States. Seed were collected from survivor trees over the entire area and more than 500 seedlings were tested for resistance. Thirty-one resistant seedlings were secured and 20 of them, together with hundreds of rooted cuttings, have remained wilt-free for over 10 years in severely infested soil. Over 50 percent of the seedlings grown from the seed of these trees are highly resistant to wilt; this indicates that selection of resistant individuals offers a ready method of controlling this disease. Two clones of the resistant mimosas have been released to the nursery trade.

Poplar breeding to produce fast-growing hybrids for reforestation has been done extensively both in the United States and in Europe. Among the many hybrids produced there is tremendous variation in susceptibility to the several serious diseases affecting poplars. Field tests of resistance to natural infections and nursery and greenhouse tests of resistance to inoculations indicate that it is feasible to produce desirable poplar hybrids that are resistant to the important diseases affecting poplars. This evidence of genetic variation in disease susceptibility in poplar hybrids is based upon inoculations of 202 clones representing 50 combinations of parentage, including cottonwoods and black and balsam poplars, with the canker fungus, Septoria musiva, and inoculations of 92 clones selected from the above population with the canker fungus, Dothichiza populea.

To the above examples of the existence of genetic variation in disease resistance in trees may be added many more that have received less study and less publicity. It is probable that in all our timber trees there is genetic variation in susceptibility to decay of the heartwood, both in the living tree and in service. Laboratory and field tests of the decay susceptibility of the heartwood from individual trees of Douglas-fir, black locust, and several species of oak show great variation in the rate of decay in all species tested. It may ultimately be possible to select for future crop trees only those with high decay resistance, and to eliminate in preliminary weedings and thinnings those with lesser resistance; thus through mass selection, it may be

possible eventually to raise the level of decay resistance in forest stands and possibly in the progeny produced by them.

In Douglas-fir stands susceptibility to Rhabdocline needle cast varies from complete immunity to high susceptibility in adjacent trees. In Colorado blue spruce plantations in Eastern States, susceptibility to Rhizosphaera needle cast varies from high in the green form to low in the blue form. There are indications of a similar variation in susceptibility of white fir to Rehmiellopsis needle cast. Oak wilt is highly infectious on all oak species tested and kills red and black oaks within a few weeks, yet in Missouri one black oak tree is known to have recovered from wilt and to resist subsequent inoculations. Willow blight, caused by the joint attack of scab and black canker, has taken an enormous toll in native willows in northeastern United States and eastern Canada, yet individual trees of susceptible species have survived. Perhaps they are natural hybrids or perhaps they are simply resistant individuals. In these and other instances the cause of the observed resistance to disease has not been investigated but the indications are that in all cases it probably stems from some genetic variation.

So far as is known, all of our native tree species are heterozygous and exhibit tremendous variation in many respects. So far as variation in genetic resistance to disease is concerned, in only one instance, chestnut blight, has continued search and selection not yielded individuals of practical value resistant to disease. Such a record indicates the overall possibilities for success in selecting and breeding for resistance to the diseases attacking our native tree species.

In the limited time at my disposal I considered it most profitable to cite the evidence for genetic variation in disease resistance and consequently have little time left in which to elaborate upon the methodology of selecting and breeding for disease resistance. Search for resistance should first be made within the species attacked, as any resistant individuals found will already be ecologically adapted to their habitat. If selection within the species is fruitless, then the search should extend to related native species and finally to exotics. When resistance is found, the adaptability of resistant selections may be studied at the same time that hybridization of the attacked species and the resistant relatives is attempted. Finally, all resistant hybrids must be tested exhaustively for their adaptability. In all studies of resistance, true genetic resistance must be distinguished from apparent resistance that may be due to escape from infection, to variations in susceptibility at different times in the life cycle of the tree, or to certain environmental influences that may be unfavorable to the pathogen. Natural infections must not be depended upon to reveal the true resistance of any selection. It should be subjected to the most severe inoculation tests known for the transmission of the disease in question. Furthermore, many isolates of the pathogen from all parts of its range should be included in the tests so that the plants to be tested are subjected to the most virulent forms, races, or strains of the pathogen.

In the actual breeding work all recognized techniques may be utilized, including the production of first-generation hybrids, backcross hybrids, and inbreds. There is a wide field in which the breeder may exercise his ingenuity, the only curb being the inherent capacities of the plants with which he is working to form new combinations of genes. There is no guarantee of eventual success in finding or producing adaptable resistant individuals but the possi-

bilities are boundless and past successes are an abundant incentive to future work along these lines.

In closing I should like to stress one point above all others--that no tree improvement program should be initiated without due consideration of the problem of resistance to pests of all kinds. In this country today crop improvement programs are recognized as indispensable to the continued welfare of our gardening, our farming, and our orcharding industries. It is inconceivable that selection and breeding research in these fields should not include disease resistance as a primary goal. Pathologists and entomologists work hand in hand with the breeder. Can you imagine resistance to rust being neglected by the wheat breeder or resistance to smut by the corn breeder? In our search for fast-growing trees of good form with wood having desirable mechanical properties, let us never lose sight of the fact that from seedling to mature tree, our forest crop is subject to the attacks of innumerable pests, any one of which may be the limiting factor in the production of usable timber.