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TREE RACES AND FOREST TREE IMPROVEMENT

by

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The general aim of forest tree improvement work is to discover and develop better forest trees. Basic to such work is a knowledge of the hereditary or genotypic variation within forest tree species.

Doubtless the first forester noted variation among trees of the same species. For a long time, however, it was assumed that such differences reflected chiefly tree age and environment. Probably the first published inference that individual tree variation might be hereditary was by Richard Brandley in England in 1717 (3). He recommended that seed be obtained from trees which combined high yield and other desirable characters. An anonymous Swedish author in 1769 correctly interpreted the deformities of some planted trees as resulting from unsuitable seed (1). The first actual demonstration of racial variation was initiated in France in 1820 by de Vilmorin (10). He planted Scotch pine (Pinus sylvestris L.) of 10 different seed origins over a period of years and some 20 to 40 years later described three types or races among these plantings.

1/ Maintained by the U. S. Department of Agriculture, Forest Service, in cooperation with the University of Minnesota, St. Paul 1, Minnesota.

WHAT WE KNOW ABOUT RACIAL VARIATION

Despite de Vilmorin's pioneer study, foresters paid little attention to seed origin until the early 1900's when the bad effects of the wholesale planting of Scotch pines grown from cheap seed (usually of poor sources) became evident in Europe. Since then a number of studies have been made, and experimental evidence of racial variation has been accumulated for about 25 North American tree species and some 20 foreign species (8). There is good observational evidence of such variation in about 20 more forest tree species. Altogether these include Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), ponderosa pine (Pinus ponderosa Laws.), the southern pines, eastern white pine (P. strobus L.), red pine (P. resinosa Ait.), jack pine (P. banksiana Lamb.), and most of the commercially important forest trees of North America and Europe.

The forest tree species, like any biological species, is merely a group of individuals with a certain number of characters in common and reproductively isolated from other related groups. If the species grows over a geographic or altitudinal range containing a wide variety of conditions there probably will be great variation within it. If distribution is continuous over the range there probably will be gradual, or clinal, differentiation in characters. In such instances, races may represent merely samples of a continuously varying genetical population. On the other hand, where natural barriers break up the species into more or less isolated segments, variation may be sharp within relatively small distances. The southern pines probably represent well the first type of continuous, or clinal, variation. Ponderosa pine and quaking aspen (Populus tremuloides Michx.), on the other hand, represent both types of variation.

Most of the seed source studies made so far have been somewhat exploratory in nature. As Wakeley has said, "They have not been attempts to improve trees, but merely to preserve the status quo in terms of hardiness, growth rate, and the like" (11). How many races 3/ there are and their approximate delimitations have been worked out partially and somewhat tentatively for only about five American species--Douglas-fir, loblolly pine (Pinus taeda L.) ponderosa pine, red pine, and white ash (Fraxinus americana L.).

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3/ The term "race" is used here in a broad sense, essentially equivalent to ecotype. Many modifying adjectives have been used with the term race (geographic, altitudinal, climatic, local), but they are not very precisely defined.
However, some more comprehensive studies have been made. For example, the Lake States Forest Experiment Station in 1933 field-planted red pines of 154 seed sources. About 10 years later Wright, in the Northeast, studied the 2-year-old progeny of 155 parental sources of white ash (12). More recently a number of new studies have been initiated. The most comprehensive ones yet undertaken are the Southern pines seed source studies sponsored by the Southern Forest Tree Improvement Committee. We need much more research of that scope to help clarify the pattern of variation among our important forest tree species.

RACES AS A BASIS FOR TREE IMPROVEMENT

The primary object of forest tree improvement usually is to develop trees which combine large size, relatively rapid growth, desirable form and branching habit, and good quality wood. Unless such trees are hardy in the locality in which they are to be grown, however, possession of these valuable characters will be of little importance.

This is where racial variation enters the picture. Local races, which have developed over centuries in place, are well adapted to the climatic extremes and the biotic enemies native to the locality. It might be assumed, therefore, that the best procedure would be to base improvement practices on the best trees of the native race. In many instances this may be the best practice, but we still have to know the distribution of the native race. Where variation is discontinuous, delineation of the native race may be easy, but where variation is continuous, arbitrary, but soundly based, racial boundaries will have to be drawn.

However, the solution is not so simple as this. Certain races of some tree species have proved better than local races in some localities. For example: (1) The East Baltic race of Scotch pine produces a better tree than local races in a number of German localities, (2) Norway spruce (Picea abies (L.) Karst.) from certain German sources develops better trees in southern Sweden than do local races, (3) the Burmese race of teak (Tectona grandis L.) produces better trees than do local races in some parts of India, (4) Douglas-fir from the Palmer area in northern Oregon out-performs local Douglas-fir at Wind River, Washington, and (5) ponderosa pine from the Lolo Mountains in Montana yields more wood than do local sources in northern Idaho. The same may well be true of many other trees, so there should be a thorough search for superior races among all our important forest tree species. Furthermore, insects and other biotic enemies sometimes are introduced into new areas and may find the local races highly susceptible hosts. In such instances, other races may be more resistant to damage. The obvious conclusion is that comprehensive research into racial variation is of great importance.
Such eminent researchers as Baldwin, Duffield, Pauley, Perry, Righter, Wakeley, and Zobel have stressed the importance of seed source tests as a basis for tree improvement work (2, 5, 6, 7, 11, 14). Perhaps this point can best be illustrated by a few examples.

1. The study of loblolly pine established at Bogalusa, Louisiana, in 1925, showed that moving seed in from a lower temperature zone only 350 to 400 miles northwest or northeast reduced pulpwood production over the next 22 years by about 60 percent. Differences in disease resistance between sources were notable.

2. A study of red pine seed sources in the Lake States showed that at age 18 (years from seed) trees from the home locality (northeastern Minnesota) on the average had produced more total cubic-foot volume than those from any other locality, nearly three times as much as that from the poorest region. However, seven sources from the home locality varied more widely in volume per acre than did the regional averages. The best of the local sources had produced about seven times as much wood as the poorest one. Some sources from other seed collection regions had produced more wood than some local sources. These findings point out the need not only for delimiting geographic races, but also for discovering local races.

3. In a study of black walnut (Juglans nigra L.), Wright found evidence of three broad geographic races but with considerable variation in juvenile growth rate within them. He concluded: "Further work will be needed to show whether the races are moderately distinct or merely portions of clines; and whether there are local races within the broad geographic races or the local variation is merely random" (13).

4. Recently Duffield made this statement: "Some results of the pine crossings made at the Institute of Forest Genetics, as well as birch and aspen crossings by the Cabot Foundation, show that the performance of species hybrids is greatly influenced by the racial origin of the parents. Western white pine of western Washington origin produces much faster growing hybrids when crossed with eastern white pine than does western white pine of Sierra Nevada origin. The species hybridizer cannot escape the provenance problem" (9). Had more races been available for both parent species, it is possible that even a greater variety of results might have been obtained. Similarly Righter, in speaking of exploratory hybridization of pines said: "The next step is to develop improved forms of the hybrids through genotypic selection of the parental stocks within the proper proveniences" (7).

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5. Photoperiodic growth response must also be recognized as one of the genetically controlled reactions important in racial diversity (6, 9). Pauley and Perry, in discussing the significance of results of their comprehensive study of the photoperiodic response in *Populus* said this: "Theoretically, by the initial use of parental ecotypes which give reactions approaching the extremes in day-length response, an $F_2$ will result which may be expected to contain gene combinations adaptable to almost any growing season length at any latitude" (6).

A Suggested Procedure

Accepting the fact that a knowledge of racial variation is a necessary basis for tree improvement work, it is evident that a great many more seed source or provenience studies are needed. Not only must such studies be made for all the important forest tree species, but also they must be localized so as to cover the range of growing conditions (site as well as climatic conditions) in which the species is to be used. Except for the southern pine studies none of those yet established appear to approach this intensity.

Much of the possible improvement of forest trees, however, depends upon the recognition and utilization of individual tree variations. Logically such selection could be the second step--after tree races have been delimited. To avoid the prospective long delay, however, both racial and individual tree studies can be carried on concomitantly. A number of individual tree collections can be used to represent various localities. Wright has suggested such a procedure based on his considerable experience with seed source tests (13). To avoid great expansion of the size of test plantations, only a small number of trees per source would be used in each planting. This would provide a basis somewhat poor for determining survival but adequate for assessing growth and development of individual parent progenies. Of course, there ought still to be a network of plantations containing enough trees of each source in blocks to indicate their development under stand conditions.

The forest tree breeder does not have available to him the highly improved lines that the agricultural plant breeder has. Yet he too should use the best material available to reduce the work of eliminating undesirable genes. His best chance for obtaining desirable germ plasm probably is from locally adapted races. Stands on average sites probably will provide a greater diversity of germ plasm than those on either good or poor sites.
Some other aspects of tree breeding also are dependent on a knowledge of tree races. For example, Wakeley has suggested the possibility that hybrids between geographic races within a species may be adapted to a wider range of environments than either parent race (11). I might add the possibility that they may be adapted to environments different from those of either parent race. There is also the possibility that inter-racial hybrids may be more vigorous than either parent. Such a situation was demonstrated for Scotch pine by Dengler in Germany in the 1950's (4). The breeder too, can make some progress prior to the delimitation of geographic or local races by utilizing the most desirable trees in stands growing within homogeneous climatic zones. He recognizes, of course, that the pattern of racial development probably will differ from species to species, even among those having similar distribution. Nevertheless, useful progress can be made at the risk of some mistakes without decades of delay.

CONCLUSION

I think there is no more fitting conclusion to this paper than to quote once more from Phil Wakeley. Recently he said this: "The inescapable conclusion is that selections and hybrids must be made separately, region by region, within the framework of existing geographic races. To the extent that this is true, provenance studies designed to identify such races and define their territorial boundaries are fundamental to other phases of tree improvement" (11). I would modify this statement to this extent only: I would not limit it to geographic races, and I would point out that the studies of racial variation, selection, and breeding, although interdependent, can be carried out more or less simultaneously.
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