# IMPROVEMENT    THROUGH

# SELECTION    OF    WILD    TYPES

Chairman: Henry I. Baldwin

## RACIAL VARIATION AND INDIVIDUAL TREE SELECTION IN THE NORTHEAST

Jonathan W. Wright

Geneticist, Northeastern Forest Experiment Station
Morris Arboretum, Philadelphia 18, Pa.

I should like to start with a brief discussion of the variation encountered in a tree species. If we see minor differences from one part of a species' range to another we split the species into geographic varieties. But sometimes we cannot see the differences at all in the field.  To detect them we have to collect seed from different localities and grow it in one place. In that case we have geographic races.

In turn these geographic races may be split up.  Nearly always there are small genetic differences between one tree and another in the same stand.  If these differences occur pretty much at random, we have individual tree variation. On the other hand we have local races if all the trees in one stand show up as different from the trees in a neighboring stand.

We have a fair amount of factual information about the geographic races. This I intend to summarize for the native species.    But we have little or no factual information about individual tree variation and local races.    Hence the last part of this report must be longer on theory than on facts.

Geographic races .--White ash is broken up into at least three geographic races: northern, intermediate, and southern. The dividing line between North and South runs through Pennsylvania and Maryland, Ohio, and Indiana. Material from the North is considerably hardier than that from the South. The northern trees are all glabrous and diploid, the southern trees are rather variable in hairiness and chromosome number. The leaves of the southern trees are glossy and have a reddish tinge.

The green ash also has at least three geographic races, probably more. But the ranges of these races do not coincide with those of the white ash trees. The southern trees are faster growing and less hardy than the northern race with regard to growth rate. This is probably individual tree variability.

Eastern cottonwood is broken up into at least two races.    Here  the dividing line is in the deep South.    Coastal Plain states produce a far less hardy tree than do the states farther north.    We don't know how many races there are in the trembling aspen but there seem to be a lot.    Trees from New England, Alaska, Wyoming, or Guatemala all look different in the nursery.

We seem to have at least two races in black walnut but they are not so distinct as those in ash.    For this species the dividing line occurs in the

medium South.

There is a shortleaf pine racial test in Pennsylvania. We seem to have a number of races in this species as almost every origin included showed up differently. The local trees far outstrip any from farther south in growth rate.

The Lake States and Northeastern Forest Experiment Stations cooperated on a racial test of red pine and New York State also has a racial test under way. In the Pennsylvania planting trees from central and northeastern Wisconsin and the northern portion of the Lower Peninsula of Michigan grew 10-20 percent faster than trees of other origins, and native Pennsylvania stock showed up very poorly. In the Minnesota plantings the local and near-local stock was the best. In the New York tests a Canadian origin consistently shows up best.

In these species the racial differences are too important to be overlooked by the planter. In the red pine test, trees from all over the range are still living and thriving but there is better than a 2 to 1 ratio in volume production between the best and poorest origins° In the ash and shortleaf pine the poorer races for any one locality just pass out of the picture after a few years. In going from Maine to Minnesota we encounter the same geographic race in both white ash and green ash, but we find different races in red pine. So we cannot generalize for untested species like white pine or sugar maple to say that New England contains one, two, three, or many races.

Individual tree selection.--In the past few years there has been a tremendous amount of interest in individual tree selection--the selection of superior gum trees in the South of blister-rust-resistant white pine, of fast-growing and better-formed Scotch pines and Norway spruces, of "sweet" sugar maples, etc. Hardly any of this work has progressed far enough to show the full possibilities.

Individual tree selection always starts with phenotypic selection, picking the trees as they actually occur in the woods where they are the product of both heredity and environment. But the goal is always genotypic selection, selection for their genetic potentialities. One sure way of evaluating a tree's genetic potentialities is to root a few cuttings of it. Since we cannot do that for every tree in the woods we must narrow the field a little before we start our clonal or progeny tests.

Intensive silviculture is one form of phenotypic selection, but there is this difference.   In silviculture we are interested primarily in the current rotation and remove poor trees whether or not they contain poor genes.  In phenotypic selection headed toward genetic improvement of the species we are concerned with future rotations. Therefore in such selection work we must make the phenotypic selection reflect the actual genic content of the trees.

How far we can get in the genetic improvement of our trees by the selection and cross-breeding of better individual trees depends on three factors: (1) Amount of genetic variability in the species; (2) heritability of the character selected for; and (3) rigorousness with which selection is practiced.

How much genetic variability is there in our species? Here I refer to individual tree variability within a stand or a small area, for we have ample proof that most widespread species contain a considerable amount of geographic variability. Work in Wisconsin that has been going on for nearly 20 years shows that there are individual trees of white pine that are resistant enough to blister rust to make a resistant strain possible. In one of our own experiments a single white ash in Ontario gave seedlings that were much narrower

leaved than the seedlings of other white ash in the stand. In the same experiment, some green ash parents from Michigan gave faster-growing seedlings than did other green ash parents from the same locality. In silver maple there are quite obvious differences in the branchiness of seedlings from different trees in the same stand. These and a few other experiments show that in some cases at least there is sufficient genetic variability to warrant selection.

Assuming that we have this variability, how are we going to recognize it and make our selections? This is where the heritability of a character enters the picture. But first perhaps we had better define heritability.

$$\text{Heritability} = \frac{\text{Variability due to heredity}}{\text{Variability due to heredity} + \text{Variability due to environment}}$$

If we are studying branch size in a stand and find that 25 percent of the total variability is due to heredity, we say that the branch size in that <u>stand</u> has a heritability of 25 percent. As we can see, from the formula, the heritability depends not only on the character but also on the environment, and can be changed by the way we sample our stand. If we are studying white pine and include some old-pasture pines as well as some intermediates from a crowded stand, we are going to find that branch size has a very low heritability, as most of the variation in branch size will be due to spacing. But if we choose a plantation where every tree was planted at 6 x 6 'spacing and study only the co-dominant trees, we are going to get a much higher value for heritability. In general we should think in terms of a maximum value of heritability for each character, this maximum being the value we get for uniform classes of trees in uniform stands.

The rigorousness of selection refers to how many trees we look at compared with how many we choose. Our selections will not be very good if *we* take the best of the first two trees we see rather than the best of the first 600 trees. For this paper I shall refer to three levels of selection: the best of 6 trees, the best of 40 trees, and the best of 600 trees, because these particular numbers have a definite mathematical significance.

Table 1 shows the amount of improvement possible <u>in a single generation</u> of individual tree selection with varying heritabilities and rigorousness of selection <u>for a single character controlled by a number of genes that show no</u> <u>dominance.</u> Data from crop plants and animals shows that this is probably the best of many possible assumptions for quantitative characters such as growth rate, branchiness, wood density, and the like.

In this table data columns 1, 2, and 3 refer to the average improvement for the stand as a whole; columns 4, 5, and 6 to the percentage of the selected trees which will be in the upper 10 percent of the original stand; columns 7, 8, and 9 to the amount of work we need to do to prove our point.

Looking first at columns 1, 2, and 3 we find that we accomplish little if the heritability is less than 25 percent. Likewise, we accomplish little if we do too little legwork and accept as a superior tree one which is merely the best of 6. But if we choose a character which has a high heritability and every tree we select is the best out of 40 or the best out of 600 we will come out with a worthwhile result. Columns 4, 5, and 6 show about the same thing. Columns 7, 8, and 9 show that we shall have to do a really prodigious amount

of testing to prove our point if the heritabilities are low. Conversely, some of the experiments that are purported to show that selection will not produce results were performed on too small a scale.

The point of this is clear. If we want results, we should do our experiments on a fairly large scale and be very careful in making our selections.

Table 1 refers to a single character. It can be made to apply to two characters if instead of taking the best of 6, 40, or 600 trees we take the best of 36, 1,600, or 360,000 trees. This multiplies the work so much that it is probably best to work on a single character at a time.

What heritabilities are we likely to encounter in our trees? The follow -ing estimates (based on indirect evidence) are indicatives

Weevil resistance among co-dominant trees in an old field white
pine stand in Maine.                          Less than 33 percent

Blister rust resistance of eastern white pine in Wisconsin
                                        More than 50 percent

Growth form of Scotch pine along a wind-swept coast of Norway
                                    Probably less than 25 percent

Height growth of loblolly pine              25 to 50 percent
(presumably based on comparison of uniformly spaced, dominants)

Needle color in blue spruce                 Nearly 100 percent

These estimates fall within the same range found in well-kept herds of livestock for such characters as rate of gain in swine, milk production in cattle, and laying ability in hens. For the present we would be overly optimistic if we assume heritabilities greater than 50 percent for most of the quantitative characters in which we are interested. As rapidly as possible we should find out what the actual heritabilities of a number of characters are in order to plan our work better. In the meantime we can get rough estimates from data already on hand. For example, if a forester finds that he can account for 90 percent of the variability of branch size in a stand because of variations in spacing, height, type of competition, etc., we have a maximum heritability estimate of 10 percent and should avoid that character and that stand. On the other hand, we can profitably devote attention to characters on which the field forester is stumped..

Stand selection.--We have geographic races in most widely ranging species. Several authors have reasoned that if the differences between a Maine climate and an Ohio climate were enough to cause the formation of a Maine race and an Ohio races, why wouldn't the equally great climatic differences that we get between some hilltops and adjacent valleys be enough to cause the formation of hilltop and valley races? Nearly always, however, they have forgotten that hilltop and valley trees in the same area continuously cross with each other whereas Maine and Ohio trees do not. They have neglected to consider the isolation factor, and this factor is important.

In discussing the possibilities of improvement through the selection of superior stands as seed orchards or as material for cross-pollination, we have

Table 1.--Genetic improvement obtained with phenotypic selection

of a character controlled by many genes showing no dominance

| Heritability (percent) | Genetic superiority[1]/ of selected trees over un-selected trees in same stand, if the select tree is the best of-- | | | Percentage of the selected trees that are elite[2]/, if the select tree is the best of-- | | | Minimum number of selected trees that must be tested to prove heritability, if the select tree is the best of-- | | |
|---|---|---|---|---|---|---|---|---|---|
| | 6 | 40 | 600 | 6 | 40 | 600 | 6 | 40 | 600 |
| 0 | 0 σ | 0 σ | 0 σ | 10 | 10 | 10 | | | |
| 10 | 0.07 σ | 0.11 σ | 0.15 σ | 11 | 11 | 12 | 410 | 167 | 90 |
| 25 | .19 σ | .29 σ | .39 σ | 12 | 14 | 15 | 55 | 24 | 13 |
| 50 | .41 σ | .64 σ | .87 σ | 16 | 21 | 27 | 12 | 5 | 4 |
| 75 | .70 σ | 1.1 σ | 1.5 σ | 23 | 39 | 67 | 4 | 4 | 4 |
| 90 | 1.0 σ | 1.5 σ | 2.1 σ | 41 | 67 | 99 | 4 | 4 | 4 |
| 100 | 1.4 σ | 2.2 σ | 3.0 σ | 59 | 100 | 100 | 4 | 4 | 4 |

1/ σ is a statistical measure of variation; it may apply to any character. To compute the actual improvement gained, we determine the value of σ and proceed as in the following example. If the average dominant white pine reaches a height of 60 feet in 30 years on a given site, and the σ of this 60 feet is 5 feet, an improvement of 1.0 σ means that the average dominant white pine will reach a height of 65 feet in 30 years on the same site.

2/ An elite tree is here defined as one which is genetically in the upper 10 percent of the population.

to consider this local race question.    What chance is there that this stand, which is growing on a good soil, has become adapted to this good soil over a period of generations and is genetically better than a stand on a nearby poor soil?    The chance is slim if the stands adjoin each other and exchange seed and pollen regularly.    For each generation the results of selection would be nearly wiped out by migration from the other stand.

But our species do not have actually continuous ranges.    The pollen of most of our trees doesnt travel far; most of it settles within a few hundred feet of the source. Gaps of 1/2 to 1 mile are probably enough to permit the formation of local races. Here around Williamstown it would be easy to find a gap that large in the range of red spruce but difficult in the range of sugar maple. The exact size of the necessary gap also depends on the number of trees per acre. The more common the species, the larger the gap needed. Gaps must have existed for several generations.

 If we are thinking of single genes or groups of a few genes, there is another side to the question.    In most of our species hundreds of small muta- tions have arisen and more are arising constantly.    Since most single muta- tions spread rather slowly it is doubtful whether these mutations are spread uniformly through a population.    There are probably many that are common in some areas and uncommon nearby.    The white pine work in northern Idaho fur- nishes an example.    Some drainages have not yet furnished a single rust-re- sistant white pine whereas other nearby drainages have furnished 8 or 10 such trees. (If we want to speak of these drainages as having local races we have to say that the races are very slightly differentiated; more than 99 percent of the trees in a "resistant" drainage are susceptible.)

For immediate practical purposes there would seem little genetic advant- age in selecting the best stand in every town ship or every county and collect- ing all seed from it. But from the theoretical standpoint we cannot treat every stand in a township as containing the same genes. For our future breed- ing work we shall have to combine individual tree and stand selection.

How far do we have to go to get appreciable differences between stands so that we can practice stand selection? The only information we have is from the geographic racial studies mentioned earlier, which indicate that in some cases 100 miles may make the difference between one race and the next. It is very likely that in some species 50 miles or even 20 or 30 may suffice in some areas.

We are going to see a great deal about stand selection in Europe in the near future.    In many instances the results will not be the same that we should expect here.    For in Great Britain and in the Low Countries the selec- tion is being done on planted stands grown from introduced seed.  It will not be unusual for two adjacent stands to show pronounced differences because of differences in geographic origin. However, we probably shall be able to in- terpret the results from Scandinavia in terms of our own conditions.

How does the selection of individual trees and stands and subsequent mating of the best with the best stack up with hybridization of races and species as an improvement measure? There is no one answer for all species. In white pine and sugar maple it looks as if we should combine the two methods. In red pine and white ash the outlook for interspecific hyoridiza- tion is dim whereas the outlook for the selection of individual trees is good.