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HEREDITARY VARIATION AS THE BASIS FOR SELECTING SUPERIOR FOREST TREES

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1. Report of the first southern conference on forest tree improvement. Atlanta, Ga., January 9-10, 1951. Mimeographed. U. S. Forest Service, Atlanta, Ga.

2. Proposal for a cooperative study of geographic sources of southern pine seed. Subcommittee on Geographic Source of Seed, Philip C. Wakeley, Chairman. Mimeographed. Southern Forest Experiment Station, New Orleans, La. October 25, 1951.

3. Standardized working plan for local tests of seed source. Subcommittee on Geographic Source of Seed, Philip C. Wakeley, Chairman. Mimeographed. Southern Forest Experiment Station, New Orleans, La. October 24, 1951.

4. Hereditary variation as the basis for selecting superior forest trees. Subcommittee on Tree Selection and Breeding, Keith W. Dorman, Chairman. Southeastern Forest Experiment Station, Station Paper No. 15. March, 1952.

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HEREDITARY VARIATION AS THE BASIS FOR SELECTING SUPERIOR FOREST TREES

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INTRODUCTION

The Southern states are now producing 50 percent of the Nation's annual production of pulpwood, 40 percent of its lumber, a larger percentage of the poles, railroad ties and other products, and all of the turpentine and rosin. The South contains 40 percent of the commercial forest land, although this region is only 27 percent of the gross area in the United States. Until recently there has been little attempt in general silvicultural or forest management work to improve the genetic quality of the forest crop. We are planting more than 200 million trees each year in the South--enough to cover more than 200 thousand acres--yet little seed is collected from selected trees or strains of high vigor, quality, and resistance to pests. Instead of collecting seed where it is of high quality, we tend to collect it where it is abundant and cheap. We have recognized wide variability in tree quality in natural stands, but we have used the knowledge to increase economic returns by harvesting the better trees instead of using it to reserve good trees to regenerate new stands. These practices are dysgenic: they lead to degeneration of the crop, and no farmer, orchardist, or animal raiser would use them.

Some of our unsound practices are matters of expediency, but they should not become habitual. We can maintain the genetic quality of the present forest and improve those of the future by adopting a three-point program of:

(1) Establishing new stands by planting or natural methods with seed from the best trees in the best stands.

(2) Making tests, with seed or grafted material, of the best trees, stands, and races to isolate the best types, so that superior seed can be produced in the future.

(3) Starting a program of tree breeding to create new types.

The first step in this program insures use of what we think to be the best stock at present. The second will provide us with good indications in the near future as to which of the selections are the best stock and some indication of how superior they are. The third will provide, at some time in the future, new types of proven superiority.

The first two steps in the above program assume that heritable variation occurs between trees, and that we can recognize it. Do we know this?

The answer is yes, and the proof lies in the results of many test plantings described in the following sections.

In his discussion of the basis of individual variation, Stebbins (1950) states: "The variation seen between the individuals of any population is based on three factors: environmental modification, genetic recombination, and mutation. Of these, environmental modification is the least important in evolution, although sometimes very conspicuous. As mentioned . . . . the first step in any analysis of natural variation is the performing of transplant experiments by which the effects of environmental differences are largely neutralized. Such experiments have shown that each genotype has its own genetically determined degree of modification or plasticity. The adult individual we see, therefore, is a phenotype which is always the product of the effect of a given environment on an individual with a particular hereditary background, or genotype. That this axiom of genetics disposes at once of many futile arguments as to the relative importance of heredity and environment, or 'nature and nurture,' has been pointed out by many geneticists. . . ."

The first step in studying variation in forest trees should be to review what is known about the influence of each of the three factors listed above. This should tell us how to look for variation, how to recognize it, and how to evaluate it by test plantings. Because this background is necessary, the following sections give in some detail the results of many studies in this and foreign countries. They also cover many species because what is common in one may be common in others. This summary gives us a basis upon which to build plans for studies of natural variation in local species, and the remainder of the discussion is concerned with this phase of the job. It gives the characters that are important in vigor, quality, and resistance to pests, and discusses what variation has been observed in studies up to this time. Also, there is a discussion of the qualities important in utilization for various products. We must be alert and recognize valuable material, because we don't know what will be found. If the limits of variation were known and we could set up final standards for superior trees, there would be no need for additional work.

Some of the variation between phenotypes of southern pines is illustrated by the photographs which follow in figures 1 through 16.

Figure 1.--A slash pine tree (Pinus caribaea Mor.) that is 55 percent larger in diameter than the average tree in the same section of the plantation. Its basal area is 2.4 times that of the average tree. The tree is 15 years old, 10.7 inches in diameter, 59 feet tall, and has good form.

Figure 2.--Fifteen-year-old slash pine with high vigor and good form. Although growing very rapidly, it has pruned itself well. The branches are not overly large and the trunk has little taper. The tree is 12.7 inches in diameter and 54 feet tall. This is an extremely good type, and it is suitable as a mother tree.

Figure 3.--Fifteen-year-old slash pine with high vigor but very poor form. It has been growing nearly an inch a year in diameter, but it is poorly pruned, the branches are large, and the stem has excessive taper. The tree is 13.6 inches in diameter, 48 feet tall, and it is one of the largest trees in the plantation. It is growing within a few feet of the good phenotype shown in figure 2.

Figure 4.--Longleaf pine (Pinus palustris Mill.) of good stem and crown form and high vigor. The tree is 30 years old, 13.5 inches in diameter, and 58 feet tall.

Figure 5.--Longleaf pine (on the right) with undesirable crown form. Poor natural pruning, branchiness, and excessive stem taper make this a poor mother tree. Trees of better form appear on the left.

Figure 6.--Longleaf pine with fastigiate form. This tree is 26 years old, 12.8 inches in diameter, and 65 feet in height. Although this is a very vigorous tree, and the crown is very slender, this type of branching habit may not be desirable, because natural pruning may be slow. However, some foresters prefer slender-crowned trees because they occupy a small amount of space.

Figure 7.--Longleaf and loblolly pine may cross in wild stands. The offspring are called Sonderegger pine, and they are usually poorly formed trees, although vigorous. This natural hybrid shows morphological characters intermediate with the parents.

Figure 8.--Shortleaf pine (Pinus echinata Mill.) of good form and high vigor. The tree is 25 years of age, 13.1 inches in diameter, and 62 feet tall. Although it is not growing under competition, the tree is fairly well pruned and branches are not objectionably large.

Figure 9.--Shortleaf pine of high vigor but poor form. The tree is 25 years old, 15.6 inches in diameter, and 62 feet tall. Although the crown is slender and the branches small, there is a strong tendency to crook, and the tree is poorly pruned.

Figure 10.--Shortleaf pine of good form and high vigor. It is 15 years old, 9 inches in diameter, and 26 feet tall. The small branches are nearly at a right angle to the stem, and with competition this type of tree would be well pruned.

Figure 11.--Shortleaf pine (center) of high vigor but poor crown conformation. The branches are long and large in diameter. The tree is 16 years old, 11 inches in diameter, and 34 feet tall.

Figure 12.--Loblolly pine (Pinus taeda L.) on the left, 26 years of age, 18.3 inches in diameter, and 69 feet tall. This fast-growing tree is the same age as the 10.4-inch loblolly pine on the right.

Figure 13.--Loblolly pines with wide variation in crown width. The crown spread of the tree on the left is 20 feet, that on the right 40 feet. Slender-crowned trees are preferred because the branches form small knots and are easily pruned.

Figure 14.--Loblolly pine 22 years of age, planted at Bogalusa, La., shows the effect of geographic source of seed on height growth. Source of seed in rows of trees, from left to right, Louisiana (local), Texas, Georgia, and Arkansas. Photo from Wakeley (1951a).

Figure 15.--Total merchantable pulpwood produced on 1/8 acre (a piece of four loblolly pine stocks) 22 years after planting at Bogalusa, La. Seed source, from left to right, Louisiana (local), Texas, Georgia, and Arkansas. Photo from Wakeley (1951a).

Figure 16.--Open-grown loblolly pine that exhibits poor natural pruning. The strongly ascending branches tend to persist for a long time. Horizontal branching is preferable.

THE HEREDITARY-VERSUS-ENVIRONMENT CONTROVERSY

It should be understood that all plant characters are heritable--the important thing is the rigidity of genetic control. If a character is loosely controlled (plastic in nature), then environmental changes can so alter the character that the genetic control becomes of little importance. Conversely, some characters are now so rigidly controlled genetically that the environment is of little importance. Some people have assumed there was no heritable variation in tree species, and they planted seed regardless of geographic source of seed until they found some sources were undesirable; they cut the best trees until they discovered most of the trees in succeeding stands were of generally lower quality. They collected seed indiscriminately until they discovered some poorly formed mother trees gave poorly formed progeny. Foresters who have encountered such experiences believe there is heritable variation within species of trees. The explanation that all observable differences are merely the effect of "environment" is no longer acceptable in the face of the growing volume of experimental evidence demonstrating heritable variation.

The breadth of heritable variation can perhaps best be stated by a quotation from Mather's (1949) book, "Biometrical Genetics." He states, "A great variety of characters is now known to show heritable variation. It includes gene and chromosome behavior, cell shape, gross morphology, physiological and biochemical properties, psychological characteristics, mating behavior, resistance to disease and toxic agents, ability to infect a host, ability to act as a vector in virus transmission, and antigen production. Indeed, few geneticists would question the proposition that no character of an organism would fail to show heritable variation were it subjected to adequate examination. Furthermore, the magnitude of the heritable differences shown in a character may range from the smallest that is detectable to the largest that is possible." The more one studies the complex nature of some of our important tree species the more he sees the spectrum of variations, many of which are doubtless inheritable. Stebbins (1950) expresses this very well when he states, "A thorough study of Nature's variation pattern reveals that fickle Dame Nature has very different ends in view from that of making neat hierarchies of species and genera which naturalists can file away tidily in cabinets with the least possible trouble."

The species concept in plant taxonomy does not imply genetic uniformity. Taxonomists or plant systematists who use the broad concept of the species are called "lumpers," and those using a narrow concept are "splitters." They disagree on the point of how "uniform" a species must be.

The geneticist, the ecologist, and the systematist has each developed terminology to describe categories below the rank of species. Some of these terms will be listed in passing because a full explanation of their derivation is beyond the scope of this paper. Stebbins (1950) gives a number of them in his discussion of variation patterns. He describes varieties and subspecies as units within species and the form as a unit within either subspecies or species as they are all used by plant systematists. Also, the biotype, pure line, clone population, and ecospecies or ecotype are explained as they are used by geneticists.

The biotype consists of all the individuals having the same genotype. Since even a small amount of cross-fertilization will produce heterozygosity and differences between genotypes for at least a few of the hundreds of genes present in any organism, the biotype in cross-fertilized organisms usually consists of a single individual. But in self-fertilizing plants the individuals may become completely homozygous and produce by selfing a progeny of individuals all with the same genotype, and therefore belonging to the same biotype. The offspring of a single homozygous individual is called a pure line, which therefore represents the appearance of the same biotype in successive generations. When asexual reproduction occurs, either through vegetative means or through apomixis, several individuals of the same biotype may be produced even if the parent is heterozygous. All asexually produced offspring of an original individual are collectively termed a clone. A population is a group of individuals among which interbreeding and gene exchange can occur. Usually plants interbreed with others of the same species that are adjacent to them in the population. Because of the distance, they do not mate with those in other parts of their natural range. Moreover, a difference in blooming time prevents them from mating with those in the same locality but at different elevations. Ecospecies or ecotypes are distinct races resulting from the selective action of a particular environment.

The lack of uniformity has led to many problems in describing species, such as Douglas-fir, ponderosa pine, European larch, and many others, as we will learn from the following discussion. Variation within a species creates opportunities for locating better types, and raises problems in avoiding undesirable types. It may be just as great an error in judgment to use the wrong race, variety, or variant of a species as it is to use the wrong species.

Between the growth habit exhibited by the prostrate juniper and the West Coast redwood--between the slender, fastigiate form of Lombardy poplar and the "weeping" willow--lie many intermediate types, and no one denies that the extreme type of form exhibited by these plants are heritable; no one should deny that smaller differences in crown or stem form can be inherited. We don't expect to change the inherent form of "weeping" and fastigiate types, or the dwarf and giant types, by growing them in different environments.

The tree that grows in the woods (the phenotype) is a product of the environment and genetic constitution (the genotype). While we can detect major genotypic effects which separate the species--the maples from the oaks, the pines from the cedars--there are other smaller differences in genotype, within a population, which can be accurately determined only by studying the tree's progeny. Such studies are made with offspring obtained by controlled pollination, showing traits passed on through inheritance in sexual reproduction. Progeny tests may be necessary in precise experimentation, or before making an investment to reproduce the stock as a superior variety. They are not a requisite for most silvicultural selection where a great many selections are made.

In contrast to the differences between individuals within a population there are differences between populations. These differences between groups of trees of the same species have been recognized by the plant systematists, ecologists, and geneticists, as discussed previously by Stebbins. They may be common in species with a wide geographic range where differences in minimum and maximum temperatures, length of growing season, and many other factors act through natural selection. These factors of natural selection acting upon generation after generation gradually eliminate those trees less suited to local conditions. Natural selection can be effective only if there are different genotypes within the population. These differences between individual trees may be caused by mutations or recombination of genes, and they will be discussed in more detail in following sections.

The argument of environment versus heredity should not be permitted to delay any longer the use of better parent stock of forest trees in the selection of outstanding trees to form the final crop or for a source of seed. Our obligation is to find out whether superior types exist, and if so, to use them. Foresters have yet to catch up with workers in other fields of agriculture in recognizing the opportunities furnished by variation within species.

THE BASIS FOR HERITABLE VARIATION

The improvement to be made by selecting superior single plants or races depends upon the amount of heritable variation. It will help in establishing a frame of reference for selection work if we review the three broad factors of variation that were listed in the introduction and the effects of each; also, if we assemble the results of studies showing the extent of this variation. With this groundwork we will be in a position to develop methods and preliminary standards of selection applicable to the South.

Studies of variation in forest trees are reviewed in three sections under the headings of variation through recombination, variation caused by mutations, and variation between populations. These divisions of subject material are not strictly comparable because only recombination and mutation actually cause variation, which then may be acted upon by natural selection to develop varieties. Recombination and mutations cause variation within populations, and natural selection causes variation between populations. Standard works in genetics should be referred to for a full discussion of these subjects, because space limitation prohibits adequate coverage here.

Variation Through Recombination

Heritable variation that causes differences between plants of the same species may be caused by various combinations of genes that control growth and form. We know from the tests made with cuttings, seed from controlled breeding, and seed collected from single trees exhibiting certain traits, that a good many of the visible traits may be truly hereditary. Because of its value and application to forestry practices at the present moment, the following discussion covers in some detail the results of tests where seed is taken from selected trees and the offspring compared with the mother tree or with those of other trees. This is the result of mother tree, or one-parent selection, and in general shows that traits both good and bad may be transmitted to some of the next generation regardless of the male parent.

One-parent progeny tests with softwoods.--In Australia, according to the Queensland Forest Service (1950), seed of loblolly and slash pine have been collected usually from selected trees of the best form and vigor. In order to know whether or not this was a desirable practice, controlled test plantations were made in 1942 and 1944 with seed from crop trees (the 160 chosen for pruning, out of an original planting of 680 per acre), from a more highly selected group of "plus" trees and with seed resulting from inbreeding a few of the selected plus trees. In 1948 the trees were measured and rated on the basis of form and growth. When the average results for the three groups were expressed as the number of stems per acre of form equal to or better than the best 160 per acre of routine source, they found the open-pollinated seed from the plus trees gave 350 stems and the inbred seed source 570. The progeny of 9 of the 11 plus slash pine trees was significantly superior to those from the routine collected seed from the 160 pruned trees. A similar test with loblolly pine seedlings showed 310 trees per acre from the plus seed equal to or better than the best 160 from the routine collected seed. The progeny of 12 of the 13 plus trees was superior to that of the routine seed source. The selection of both slash and loblolly pine was made in plantations where environmental conditions were fairly uniform. In all cases in the above experiment there was a range of types from good to poor in the progeny of each plus tree. By selecting open-pollinated seed from the plus trees, the Australians obtained more than twice as many top-quality trees. By inbreeding the best slash pine plus trees, they obtained 3.5 times as many top-quality trees and 15 percent were better than any from open-pollinated crop trees. These results may be conservative if a comparison is desired between plus trees and average trees, because these plus trees were compared with the offspring of crop trees which were the best 25 percent of the stand, instead of with average trees in the stand. The crop trees would be those regenerating the next stand unless they were removed to make a commercial thinning or as a result of naval stores chipping, both of which are sometimes done in the southern United States.

Minckler (1942) reported 5-year results of a one-parent progeny test with loblolly pine trees. The planting was then destroyed by a hydroelectric project. Although no criterion was discovered for selecting seed trees, the data did show highly significant statistical differences in both growth and survival of progenies from different mother trees. The mean growth in four randomized plots of the best progeny was 8.3 feet and the poorest 5.4 feet. The mean survival of the best progeny (from the standpoint of survival) was 96 percent and the poorest 53 percent. The 10 best progenies from the standpoint of growth grew 36 percent more in 4 years than the 10 poorest, and the 10 best from the standpoint of survival were 48 percent better than the 10 poorest.

Sherry (1947) has shown that both desirable and undesirable characteristics of Monterey pine (Pinus radiata) mother trees grown in South Africa may be passed on to their offspring. Seed was collected from 14 parent trees which exhibited marked character in regard to vigor, branch thickness, length of internodes, stem form, and crown form. At 7 years of age, the progenies, about forty trees from each parent tree, were measured and scored for morphological characters. The results are expressed as the percentage of each progeny which reproduce the characters of the maternal parent. Data from two of the progeny groups will illustrate the type of results obtained from the plantation. One mother was selected for high vigor, small branches, relatively short internodes, straight stem, and narrow crown. The progeny showed 89 percent with small branches, 91 percent with short internodes, 96 percent with straight stems, and 47 percent with narrow crowns. Another rapid-growing mother tree that had small branches, long internodes, crooked stem, and wide crown gave progeny 73 percent of which had small branches, 37 percent long internodes, 72 percent crooked stems, and 55 percent wide crowns.

The range in number of offspring showing the characteristics in stem form and crown shape of the mother parent is very interesting, although the number of examples cited is rather small. They are given by Sherry as examples, not averages, of the range that occurred from the 14 mother trees. Generally, about 45 percent at the lower limit (33 to 55 percent) to about 85 percent at the upper limit (72 to 96 percent) of the offspring showed the same traits as the mother tree. Sherry concludes that, "A surprisingly high percentage of trees in these progenies resembled the maternal parent in the characters which were scored, suggesting that these characters are genetically controlled . . . . There are indications from the data that characters such as slender branches and short internodes may be genetically dominant and that defects in the crown and leading shoot are heritable. The results, in general, suggest that mother tree selection in the collection of seed from P. radiata may effect considerable improvement in the form of resultant crops."

A number of studies in Europe show that in Scots pine the mother tree influences form and vigor of the offspring. Lubyako (1941) found significant differences in the average height and diameter of progeny of different pine trees at the age of 13 years, though there was great variation within each progeny, even the best containing over 20 percent of individual trees having a height below the average for the worst progeny group. In another investigation, 11-year-old progenies of first-quality stands averaged 1.8 times the height and over twice the diameter of those of third-quality stands. Behrndt (1935) reports results obtained by individual selection in three plantations, consisting of the progenies from single trees and seedlings obtained from certified seed. For the 7-year observation period all three plantations demonstrated differences in the height attained by the various progenies of the same age from single trees. These differences are regarded as being partly due to direct genetic causes and partly to differences in susceptibility to Lophoderium pinastri. Progeny on one tree in one of the three plantations exhibited remarkable resistance to this fungus throughout, as well as a particularly high growth rate.

Syrach Larsen (1937) has reviewed early European work with open-pollinated seed in forest tree-improvement programs, and cites several workers who claim that the characters of the mother tree are dominant in the offspring of the individual tree.

Arnborg (1946) describes a form of Scots pine called "broom" pine. It is characterized by fastigiate multiple stems formed in youth, and generally fused later into a composite stem from one to several meters long in old trees. No true main stem is formed. Cone setting is usually poor and cones small, but no distinct differences from type exist in the general morphology of leaves or cones. The form is practically confined to Uppsala and the adjacent counties in Sweden, but possibly occurs in several Norwegian localities. Seed from parents in a number of localities was sown in 1942. In the 4-year-old progeny only 23 percent had straight, single stems with short branches, 65 percent had single stems but long branches, and 12 percent had two or more stems. The difference in seedlings begins to show in the first to second years.

Differences were found by von Wettstein (1949) between the progeny from open-pollinated seed of selected Scots pine trees and that from mixed seed of all trees in the same stand when planted in alternate rows. The differences were consistent for yearly plantings over a 5-year period, and he suggests this method for separating elite trees from standard or average trees.

Johnson (1948) describes two cases of albinism in seedlings of Pinus nigra var. austriaca. In one case, seed was collected from an isolated self-pollinated individual tree. The other seed came from a group where some cross-pollination was likely to have occurred.

An unusual type of spruce, called "worm" spruce in Sweden, is described by Geete (1944). Treschow (1944) reports on progeny of spruce of this type. Of 400 plants raised from seed collected in 1922 from a single tree--the only one of its kind in the stand--most offspring appeared at 4 to 5 years of age to be ordinary Norway spruce. The remainder (16 plants) were planted out, and are still of a pronounced "snaky" type. Five or six of them are quite typical, with several annual shoots having no lateral shoots whatever, and have therefore stagnated in growth. The rest, though of the "snake" type, have formed almost normal leaders of late years and have grown fairly well; the largest is now 10.7 meters high and 21 centimeters in d.b.h.

In Wisconsin, Riker, Kouba, and Brener (1949) found that seedlings from wind-pollination of selected rust-resistant white pine trees had little more resistance to blister rust than commercial seedlings. Grafted trees, from the 163 parent trees that had been selected in natural stands because of their apparent resistance, were variable in resistance to the disease. About one-fourth of them had high resistance. Resistance to blister rust occurred in one or more of these ways: (1) infection negative or reduced in amount, (2) needle lesions reduced to small spots or flecks, (3) stem lesions corked out, (4) lateral stem lesions failed to reach the main stem before the twig died, and (5) cankers failed to form aecia.

<u>One-parent progeny tests with hardwoods</u>.--The earliest work in individual tree selection in hardwoods was in Europe with beech, about which Syrach Larsen (1937) states, "Cieslar and Opperman's works, published in the beginning of this century, were pioneer works in the recognition of the hereditary differences in shape in individuals of apparently the same geographical type. Both took a special interest in the so-called freak forms. Opperman's work was of the greatest importance to Danish conditions. His comparison between offspring of marked weeping beeches and other normal trees, and with offspring of isolated, particularly beautiful, individual trees, or whole growths of particularly fine specimens, give a strong impression of the necessity of seeking the best possible seed trees also within the individual districts. He created the word 'freak' as a forestal term denoting a tree with poor hereditary properties with respect to shape. At the Egelund nursery he demonstrated his experiments in such a manner that it was impossible to leave the nursery without feeling an urgent desire to apply these results. Opperman roused Danish foresters from indifference with regard to the origin of seed, and throughout his life he urged us to gather seed from the best possible trees only."

Selection of trees superior in latex production has been an important part in the development of improved rubber-producing trees of <u>Hevea</u>. Through a program of selection and controlled breeding with the use of bud-grafted superior types, the best stock is expected to produce about 2,000 kg. per hectare as compared with a yield of 460 to 640 kg. per hectare of the unselected plantations in 1926. Seed from superior trees does not always give high-quality progeny, and some average trees may have progeny that are superior to the parent tree. Practically no effort has been made to improve growth rate by selection, as hybridization seems more feasible. Maas (1948) states, "Thus far seed selection has already resulted in trebling the productive capacity, and further increases can be looked to in the future, now that sufficient information is available to extend the range of the recommendations. The difference in the productivity capacity of seedling plots as compared with bud-grafted plots has been smaller than had originally been expected, and this difference can still further be reduced by closer planting and selective thinning; methods better suited to seedling areas than they are to a monoclone planting. When a comparison is drawn between buddings and seedlings growing under conditions similar as regards planting distance and thinning out, the figures show that the rate of production does not exceed 15 percent in favor of the buddings, and in many cases it has proved to be a good deal less. . . . The planting of seedlings should be included in planting programs on a scale larger than hitherto, but the selection of the planting material should be referred to expert advice."

Open-pollinated seed of mimosa trees resistant to mimosa wilt produced trees about half of which were likewise resistant to the disease. Toole and Hepting (1949) found only a very few resistant seedlings when seed was collected without regard to resistance in the parent. Rooted cuttings from resistant trees show high resistance to the disease, and about half the seedlings were resistant when open-pollinated seed was collected from the trees developing from these cuttings.

Dilatush (1950) states that hollies grown from seed vary in the way leaves are retained throughout the year, leaf color, fruit color, permanence of fruit color, tree form, growth rate, and in the way the fruit is distributed among the leaves. Zimmerman and Hitchcock (1933) class seedling variation in holly under the following headings: (1) shape of plant, (2) fruitfulness, (3) color of fruit, (4) shape of fruit, (5) color of foliage (yellow to dark green), (6) shape or form of leaves (entire to very spiny or smooth to very twisted), (7) shedding of leaves, (8) winter hardiness, and (9) color of new leaves and stems.

Osborn (1931) was the first to make progeny tests with black wattle (Acacia mollissima Willd.). Between 1927 and 1930 he set out about 300 progenies from natural seed of selected trees in alternate rows with seedlings from commercial sources. He found that a remarkable degree of uniformity occurred within many of the progenies while others did not breed true to the same extent; that superior characters--mainly vigor, form, foliage, disease resistance--appeared consistently within a number of progenies; and that recessive lethal and developmental modifying characters appeared mainly in the seedling stage in some progenies. In some cases the standard deviation of basal area for the offspring of a selected tree was only about half that for a group of trees of commercial source. Osborn observed that isolated trees produced fertile seed and that recessive seedling characters occurred in natural progenies of plantation trees. This indicated that black wattle was not self-incompatible. He concluded that the studies of variation in vigor, bark yield, and tannin content provided sufficient evidence to recommend mass selection as a preliminary step in the improvement of the variety.

Black locust seed from fast-growing trees should be preferred over that of other trees, according to Cummings (1947). Seed was collected from 27 individual trees of different vigor classes, and after 6 years the seedlings averaged 9.1 feet in height for progeny of trees of good growth, compared with 7.0 and 7.7 feet for progeny of trees of fair and poor growth, respectively.

Esson (1946) reports that fastigiate oak reproduced from seed. Of three acorns collected in 1931 from a specimen of *Quercus robur* var. *fastigiata* growing at Great Neck, Long Island, two produced ordinary English oaks with spreading branches, and the third a fastigiate tree that is now 34 feet tall.

Much variation of individual tree characters has been observed in cinchona plantations (Ferguson 1946). Clones vary in height growth, stem form, and branching. Quinine content of the bark is also genetically determined. Ebes (1951) discusses results of selective breeding with *Cinchona ledgeriana*. An improved stem form was found in the first generation.

The point that stands out from this review of tests made with open-pollinated seed of both superior and inferior trees is that a large number of traits important to foresters in establishing, managing, and harvesting forest stands are heritable. Some of the characters are dominant and they are passed on to many progeny, while others are passed to a few progeny. This applies to both pine and hardwoods. Traits such as high vigor, good form, and disease resistance are most important to the practicing forester, and the case for selecting outstanding trees with these traits is well supported. These individual trees could be used as source of open-pollinated seed for large-scale planting, for grafting and cutting material with which to establish seed orchards, and for parent trees in controlled breeding. There is strong evidence for the careful selection of the best trees to form the final crop and for seed trees where this system of regeneration is used. There is a great need for additional studies in natural variation in commercial species of forest trees. We need progeny tests of the offspring of selected trees to show the proportion of variation contributed by environmental and genetic factors.

Variation Caused by Mutations

Another source of variation that may cause differences between plants of the same species is mutation. Mutations are sudden variations that are later passed on through inheritance and that result from changes in a gene or genes. Mutations in forest trees have been identified in both softwoods and hardwoods. A tetraploid (four chromosomal sets) has been reported in spruce from Sweden by Andersson (1947). The progeny resulting from wind pollination of the polyploid spruce show varying height growth, growth habit, and stomatal size. The Institute of Forest Genetics in California has what is believed to be a mutant shortleaf pine. It is characterized by slow growth, thin crown, and very short needles. Guinier (1944) describes a group of three branchless firs growing close together. The trees were very small and about one-half centimeter in diameter and 75 to 80 centimeters in height, although the trees were 30 years or more old, as indicated by the appearance of scars left by the fall of bud-scales. It is believed they were apparently the result of a mutation characterized by abortion of the lateral buds. Stebbins (1948) found the coast redwood was a hexaploid with 2N = 66 chromosomes. The dawn redwood recently discovered in China has 2N = 22 chromosomes, as does the big tree of California. Liese (1935) presents evidence for the hereditary nature of witches-broom on pine. Pine cones gathered from witches-broom yielded a progeny half of which showed the typical anomalous form of growth, while the other half of the progeny was normal. A second experiment gave similar results, except for the presence of a group of intermediate types. The author attributes the formation to bud mutation, asserting that the most careful investigation has never yet revealed the presence of a causal pathogenic parasite in the growth.

Chromosome counts have been made for a large number of hardwood species, and also in many unusual cases where anomalies were suspected. It is apparent that irregularities occur in both basic chromosome number and amount of natural polyploidy. Table 1 gives the chromosome number for several genera and some of the polyploid species or varieties. It shows the basic number is not uniform in Cornus, Ilex, Robinia, and Salix. Also, some very important genera, such as Acer, Betula, and Fraxinus contain many polyploids. Chromosome number has not been determined in some species and varieties of southern forest trees, and additional study of this important subject may uncover other examples of polyploidy.

In some genera of hardwoods polyploidy has formed the basis for separating species; in others the basis for separating varieties. Although the original specific and varietal classifications were made on the basis of external morphological differences, these classifications were later confirmed by cytological study. Some large genera like Quercus show no natural polyploidy. The genus Betula presents an interesting example of polyploid series. Darlington and Janaki Ammal (1945) list 19 species and 5 varieties in this genus. Twelve species have the diploid number of 28 chromosomes. There are seven polyploid species with 56, 70, or 84 chromosomes. Paper birch, Betula papyrifera, is a tetraploid species with 56 chromosomes, and varieties cordifolia and subcordata also have this number. However, variety kenaica has 70 and occidentalis has 84 chromosomes. Alnus, or alder, the other genus in the family, has 28 chromosomes and polyploid types with 42 or 56 chromosomes. It is easy to speculate how the present species in the Betucaceae may have developed from original forms with a haploid number of 7 chromosomes (diploid number 14). It should be pointed out that chromosome counts are often made on single trees, and more data is needed before we can be certain the published figures hold for a species or a variety.

A number of methods for inducing mutations have been in use recently, and have been particularly successful in aiding breeding programs with small fruit, vegetables, and ornamental flowers. The drug colchicine is effective in doubling or multiplying sets of chromosomes, while radiation by X rays may cause changes in arrangement. Trees with multiple sets of chromosomes may have special value for their increased vigor and size, as well as for the larger cell size. Duffield (1943) and Wright (1944) have suggested polyploidy may be responsible for the variation in wood quality of some of the hardwoods. Wright (1944) found the tetraploid and hexaploid white ash growing with normal types. Nilsson (1943) found that triploid aspens had cells 50 percent larger than those of diploid types, and yielded a higher percent of cellulose. Whether or not chromosome doubling, which results in increased cell volume, can be used to create types of hardwoods that grow rapidly and still produce

Table 1.--Some genera of hardwoods which show variation in basic number of chromosomes or whose species or varieties form polyploid series

Genera	Diploid species		Polyploid forms	
	Species with diploid chromosomes	Diploid chromosome number	Species with polyploid chromosomes	Chromosomes in polyploid series
	Number	Number	Number	Number
Acer (maple)	18	26	4	52, 78, 104
Aesculus (buckeye)	4	40	2	60, 80
Alnus (alder)	7	28	5	42, 56
Betula (birch)	11	28	9	56, 70, 84, 90
Carpinus (hornbeam)	7	16	1	32, 64
Carya (hickory)	5	32	4	64
Cornus (dogwood)	2	20		
Cornus (dogwood)	8	22		
Diospyros (persimmon)	5	30	2	60, 90
Fraxinus (ash)	5	46	1	92, 138
Ilex (holly)	1	34		
Ilex (holly)	2	36		
Ilex (holly)	4	40		
Magnolia (magnolia)	4	38	6	76, 95, 114
Populus (poplar)	12	38	5	57, 76
Robinia (locust)	6	20	2	30
Robinia (locust)	1	22		
Salix (willow)	22	38	20	76, 114, 152
Salix (willow)	2	44		
Tilia (basswood)	7	82	4	164
Ulmus (elm)	11	28	1	56

wood of light weight has not been proven. The possibility is indicated by Johnsson (1950), who found density of wood in alder was lower in a cross between a polyploid derived from colchicine treatment and a diploid type.

However, there is some indication that weight of wood increases with increases in sets of chromosomes where polyploid species occur in the same genera. No data are available for polyploid forms of the same species. Table 2 contains the average weight of dry wood, as given by Markwardt and Wilson (1935), for several species of magnolia, birch, and hickory that form polyploid series. There are many factors that affect weight of wood, and they may be more important than chromosome number. However, the effect of polyploidy on wood quality is a field of work that could profitably be studied.

Table 2.--Relationship between number of chromosomes in magnolia, birch, and hickory, and weight of wood

Species	Diploid chromosomes	Annual rings per inch in test samples	Weight of dry wood per cubic foot
	Number	Number	Pounds
Magnolia fraseri	38	15	31
Magnolia acuminata	76	14	33
Magnolia grandiflora	114	15	35
Betula lenta	28	27	46
Betula populifolia	28	-	35
Betula papyrifera	56	6	38
Betula lutea	84	16	43
Carya cordiformis	32	11	46
Carya laciniosa	32	19	48
Carya ovata	32	19	50
Carya alba	64	18	51
Carya glabra	64	20	52

Although it is difficult to ascertain if their origin is by mutation or through recombination, many variants in softwoods and hardwoods have been described, and, in some cases, have been widely utilized in landscaping where unusual form or coloration can be effectively used. Rehder (1940) lists seven varieties of Scots pine that are distinctive in needle color, needle length, width of crown, and angle of branch to trunk. In addition to these he lists four geographical races that differ in morphological characters. Nine varieties of Austrian pine are listed that vary widely from each other. Among them is a dwarf globose form and a prostrate form. Wyman (1949) comments there are about 40 forms of Norway spruce and Rehder (1940) lists 32. The latter divides them on the basis of forms differing in color of the leaves: columnar and narrow, pryamidal forms; pendulous or sparingly branched forms; and dwarf forms. Seven varieties of white spruce are listed. Five forms of white pine are recognized. There is a form with light bluish green needles, and another with ascending branches forming a narrow, pyramidal head.

One is a dwarf or somewhat conical compact bush with short needles, another is a dwarf, umbrella-shaped bush with short needles, and one has a dwarf, decumbent form with diffuse trailing branches. Probably many of these variants are mutations. Inasmuch as the horticulturists have been so successful in selecting horticultural forms, there seems good reason to believe that quite as good results might be obtained by selecting for economically valuable characters of interest to the forester.

Hardwoods contain many varieties and offer a fertile field for selection. Rehder (1940) lists four varieties of yellow-poplar. One type, Liriodendron tulipifera fastigiatum, is a tree with upright branches forming a narrow, pyramidal crown. The other three have leaves of distinctive shape or color. Sweet gum has a variety (Liquidambar styraciflua pendula) that is characterized by the deflexed pendulous branches forming an almost columnar crown. Another variety has leaves with three to five short, rounded lobes. Magnolia grandiflora lanceolata has leaves of distinctive shape and a narrow, pyramidal habit. Varieties of many other species have been described, and some of them may be of value to the forester. However, some are described on the basis of a morphological difference of little economic importance. Those that have distinctive and superior form may be superior to wild types for planting. These should be carefully studied with this in mind.

In summarizing this review of the variation caused by mutations, the main point is that some extremes of form may occur through changes in one or more genes and that these desirable or undesirable traits will occur in future generations. Small mutations may cause slight differences between plants that could not be distinguished from the effects of recombination and segregation, while other mutations would cause much larger differences. The effects of mutation may be expressed in many forms because of the large number of ways in which they may take place. Some forms may be valueless for most forestry work while others could be the foundation of valuable types. These types may breed true from seed or some of them might require vegetative propagation. Selection of superior mutants is one way of obtaining better types of trees, and those available now should be studied by foresters.

Variation Between Populations

A number of terms, such as cline (a pattern of continuous genetic variation in geographic space), topocline, and ecocline are used to identify groups of plants in which the differences in one or more characters are graded in a definite direction, often with topography or with changes in ecological conditions. Loblolly pine planted in South Africa showed clinal variation in height growth according to latitude of origin (Sherry, 1947). After nine years, the most growth had been made by stock of southern provenance, and total height decreased gradually for the other provenances toward the north. Clinal variation is often associated with altitudinal zones. Cold resistance and photoperiod responses often show clinal variation.

Another set of terms is used to identify groups of plants in which the variations are generally not graded continuously in any definite direction; these are variously called ecotypes (geographic races), varieties, subspecies, and a whole host of others. Such plant groups may vary either physiologically, morphologically, or both, but in any case the variation is not great enough to cause the group to be called a separate species. Ecotypes, varieties, etc., are developed under the influence of natural selection, although occasionally characters are developed that, on the surface at least, have no direct relations to environmental factors. Commonly these variations are thought to be distinct from clines, but usually there is a definite overlap and the two cannot be distinctly separated. The terms used in the above paragraphs are defined in more detail in the glossary.

A number of important conclusions can be drawn from the studies in the United States and foreign countries of seed source effects on growth, form, and other characteristics of forest trees. A summary of these is given in the appendix. The conclusions of most importance are (1) source of seed may have an important effect on growth and yield of pine and hardwood plantations, (2) our knowledge of best sources is insufficient to guide the forestry work in the South.

Other brief conclusions are as follows: Some species have more strains than others; material of southern provenance often grows poorly in the north because of frost damage; some sources are more disease resistant than others because of differences in time of flushing or other traits that hinder infection; it is necessary to determine proper provenance for various climatic areas because material that does well in certain areas or on certain sites may not do as well in others; different races may occur within a few miles of each other and show as much difference in growth as more widely separated areas; the growth of trees from seed collected at lower altitudes may be greater than that collected from higher altitudes; seed of some foreign provenance may grow better than local races; some variation is continuous and the change is gradual over long distances, while others are discontinuous and wide variation occurs within short distances.

The problem of determining which races or strains give the highest volume growth in each of the broad planting regions of the South is a large and important one. With our present knowledge we can use stock of local origin and expect returns that are about average for that area, or we can use seed of some other source and expect to get either average returns, greater returns, or lesser returns.

SELECTION IN TREE IMPROVEMENT

Selection has a definite place in forest tree improvement, and can be carried out in different ways. Hayes and Immer (1942) have outlined the major types of selection as follows:

1. Mass Selection
    a. In self-pollinated crops
    b. In cross-pollinated crops
    c. In dioecious crops (selection of both male and female plants for the characters desired)

2. Individual Plant Selection
    a. In self-pollinated crops
    b. In cross-pollinated crops without control of pollinations
    c. In controlled self-pollinated lines of cross-pollinated plants
    d. In dioecious crops
    e. In crops normally clonally propagated

According to Richens (1945) the methods of selection used in forestry are mass selection, mother tree selection, and individual plant selection. This is essentially the same as given by Hayes and Immer, but with more emphasis on selection of seed from superior mother trees because of the importance of this method in forestry practice. In mass selection, seed from a number of superior trees is collected and planted for several successive generations. No attempt is made to keep the seed separate by individual trees. This is the least precise method of selection because there is no strict control of parentage on either side and the population remains genetically heterogeneous. Roguing nursery seedbeds and immature stands, when making intermediate cuts, eliminates inferior stock and favors perpetuation of the better types. Selection of superior seedlings from nursery beds is a form of mass selection. It has not proven very effective in a test at the Institute of Forest Genetics and other tests in Europe. This technique has not been adequately tested with southern pines, and data applicable to these species are needed.

Mother tree selection consists of choosing satisfactory trees, after progeny tests, and planting the open-pollinated seed for several generations. Seed of each tree is kept separate. There is no control of the male parent in this type of selection, but there is more emphasis on superior individual mother trees than there is in mass selection.

Individual plant selection followed by controlled pollination, using pollen from selected trees, is the most efficient method of improvement because both parents are known. It is the most expensive method, but if precision is required in improving certain traits, it is the most practical.

Selection of superior trees in wild stands and after hybridization is a part of tree-improvement programs in Sweden, Denmark, Canada, Australia, South Africa, Great Britain, and the United States (Sylven, 1939; Lindquist, 1948; Syrach Larsen, 1949; Place, 1951; Fielding, 1948; Philp and Sherry, 1946; Mathews, 1950; Curry, 1943; U. S. Forest Service, 1948; Brink, 1949; Anon. 1950; Ibberson, 1950; and Scanlon, 1951).

Hazel and Lush (1943) discuss the efficiency of three methods of selection, as follows: "The 'tandem method' is to select for one trait at a time until that is improved; then for a second trait; later for a third, etc., until finally each has been improved to the desired level. The 'total score method' is to select for all the traits simultaneously by using some index of net merit constructed by adding into one figure the credits and penalties given each animal according to the degree of its superiority or inferiority in each trait. In the method of 'independent culling levels' a certain level of merit is established for each trait, and all individuals below that level are discarded, regardless of the superiority or inferiority of their other traits." In discussing the features of each method, Hazel and Lush state: "In all three methods there is always the danger that selection will fall below its maximum efficiency because too much attention is paid to some characteristics and too little to others. In the tandem method that would take the form of selecting first or in too many generations for unimportant things while postponing or selecting too briefly for more important things. In the total score method that would take the form of using too high values for some characteristics and too low values for others, or making mistakes in estimating the heritability so that some characteristics would be thought more highly heritable and others less highly heritable than they actually are; or of failing to consider properly the effects of genetic and environmental correlations between traits. In the method of independent culling levels, the culling level might be set too high for one characteristic, too low for another." They conclude that: "Selection for a total score or index of net desirability is much more efficient than selection for one trait at a time. . . . Selection for several traits by using independent culling levels for each is more efficient than tandem selection for each trait one at a time, the relative efficiency increasing with the number of traits and intensity of culling."

Selection for an index which gives proper weight to each trait will probably be the most fruitful in obtaining improved varieties of trees. Generations of trees are too far apart to select for one trait at a time, as in the tandem method. However, in selecting for disease resistance it may be advisable to attach the most importance to this one character. Before selection will be most effective we will have to obtain data on the economic importance of each trait and its heritability. Selection can then be made for combinations of traits with a high value as indicated by the product of its heritability and its economic value. The total value is the sum of these products.

Hazel (1943) discussed the genetic basis for constructing selection indexes. He reviewed the use of the discriminant function for wheat selection as used by Smith (1936). Hazel presents a multiple correlation method of constructing selection indexes having maximum accuracy for swine breeding. The following constants must be known in order to solve the simultaneous equations:

1. Relative economic values for the different traits
2. Phenotypic constants
   a. Standard deviations for each trait
   b. Correlation between each pair of traits
3. Genetic constants
   a. Heritability of each trait
   b. Genetic correlation between each pair of traits

Other studies in methods of selection are those by Simlote (1947), discussing application of discriminant function for selection in durum wheats, and Robinson, Comstock, and Harvey (1951), who propose a method of separating genotypic and phenotypic variation and construction of a selection index for corn.

Mather (1949) has listed the various factors affecting the speed of the selective progress. Selection may not have the significance within a short period of time in improving succeeding generations of forest trees that it does with annual crops, but the factors that control progress are of interest because they indicate some of the variation we may find between species. We know the genetic make-up of some species is quite different from that of others, and accordingly we should expect some differences between species in the type of improvements that can be made. The speed of selective progress will depend on:

1. Rigor of selection
2. Number of genes, as organized into effective factors
3. Variation in magnitude of action of the genes or factors
4. Their dominance relations
5. Their linkage relations
6. The size of the contribution of nonheritable agents to the F_2 variation
7. The sampling variances of the genotype frequencies in progeny

It has been indicated that selection of superior plants from wild stands and in successive generations of control-bred plants is considered an important part of plant-improvement programs. However, as far as selection of trees is concerned, practically no work has been done toward developing techniques for selection. There is need for studies in natural variation to establish the range of variation for traits of economic importance in commercial species, and, also, to learn the proportion contributed by the environmental factors as opposed to genetic factors. Well-designed progeny tests with material from known parents will provide data on the latter.

Some of the variation in traits of economic importance for commercial species is discussed in the next section.

SELECTION FOR SINGLE TRAITS

Selection will be used by practicing foresters in seed collection and timber marking for both intermediate cuts and the regeneration cuts. In all of these the primary consideration will be for the best traits in combination. In other words, the silviculturist evaluates the entire tree in relation to others in the stand. Other foresters, such as those working in tree improvement or studying natural variation, may be primarily concerned with evaluating individual traits of which there may be a great many, as well as combinations of traits that make trees worth more. These two objectives require somewhat different approaches and will be considered separately. Single traits form the basis for combination, so they will be discussed first.

Selection of superior trees for single traits as well as for combinations will be necessary in tree-improvement work. Selection plus hybridization, involving different species as well as the same species, provides an opportunity for combining a number of superior traits that would never occur under natural conditions. While desirable combination of traits, such as vigor, quality, and resistance to pests, is of some importance, it is not critical. It is much easier to find individual trees that have the extreme of one character than of two or three desirable ones. If found, the latter should be used of course, but to deliberately search for them may be a time-consuming job and not very productive in comparison with results from methods of improving trees by a program of controlled breeding along with selection. In forest stands cross pollination usually occurs between trees that are fairly close to each other. Wind-borne pollen may travel for long distances, but usually the volume is insufficient to cause widespread pollination. Thus, single, outstanding trees, if widely spaced, aren't apt to cross pollinate and produce seed in volume. Buell (1947) collected pollen at distances up to one-quarter mile from a shortleaf pine stand and found at a quarter of a mile about a tenth of the pollen falling within the forest itself can be expected. For the first tenth mile the amount drops rapidly and beyond that distance, gradually. The Northeastern Forest Experiment Station (1950) found that spruce, fir, oak, and pine yielded little viable seed except where trees of the same species were growing close by. For white pine, production of viable seed was only 0.3 to 1.8 per cone on trees isolated from pollinating neighbors by 200 feet or more. Isolated trees may produce seed, but much of it may be empty.

Selection for single traits as part of research permits more choice of areas in which to work, the standards are higher, and the variety of traits studied will be much broader. Careful choice of areas in which to work is of primary importance, and it should be possible to eliminate much of the phenotypic effects by careful selection of stands. The physical features of the area, such as topography, soil, moisture condition, and exposure, should be as uniform as possible. Likewise the stand should be even-aged, and the trees should be evenly spaced. Wider spacings are desirable because competition has less effect on any one tree and also a better estimation of crown form is possible. Planted stands with rather wide spacing on level, old fields are about the best places in which to work. It is realized that conditions such as these don't occur very often, particularly with hardwood species, because few have been planted. However, there is usually a choice of areas so that the best under local circumstances can be used. If racial variation occurs within the species, the better races should be scouted for superior individual trees to determine the best trees in the best race.

Construction of frequency distribution curves to establish the limits of natural variation is an important part of selection work, until experience is gained in selecting by eye. These curves will reflect mostly genetic variation if the data for them are taken in stands where environmental factors are uniform. Distribution curves indicate the proportion of the population that will fall under various levels of selection, and also the rate of advance under selection if they are skewed. Hazel and Lush (1943) state: "When the population is skewed with the long tail of the distribution toward low merit, progress is faster with mild selection and less rapid with very intense selection than in a truly normal curve. If the long tail of the distribution is toward high merit, the reverse is true--progress is a little less with light selection, but a little more with intense selection."

If the field selections are to be verified, they should be followed through with progeny tests for the final estimation of the genotype. Such tests are expensive and usually only the very best trees can be studied in such detail. Thus, the standards by which trees are selected should be very high. Usually it will be desirable to make a survey of the range of natural variation in the particular characters to be studied so the upper limits will be known. Also, it is possible to reject some trees because of undesirable secondary traits.

Selections may be made for a large number of single traits, especially in the field of wood quality and resistance to fungi and insects. Such studies will require special planning to meet the immediate objectives in regard to species and utilization. The discussion by Koehler (1939) of heredity versus environment in improving wood in forest trees will be helpful to those planning to make selection for quality.

Selection for vigor.--One of the first steps in selecting trees for vigor is to study the range in growth rates for the particular species. There are not many data of this type because in the past the emphasis has been on determining average growth for a stand or area rather than the extremes. The curves for planted stands of slash pine are examples of data of this kind. Figures 17 and 18 show the diameter and height frequency distribution for plantations 8 and 16 years of age. In both cases maximum diameter is about 50 percent larger than the average. Basal area of the largest trees is about 130 percent (2.3 times) greater than that of the average tree. There is also a rather wide variation in total height. Frequency distribution curves such as these are useful to show variation in plantations of southern pines because there is not much variation in soils, as compared with mountainous areas, and spacing is relatively even. All the variation may not be from genetic causes, because planting technique may have been faulty in some cases.

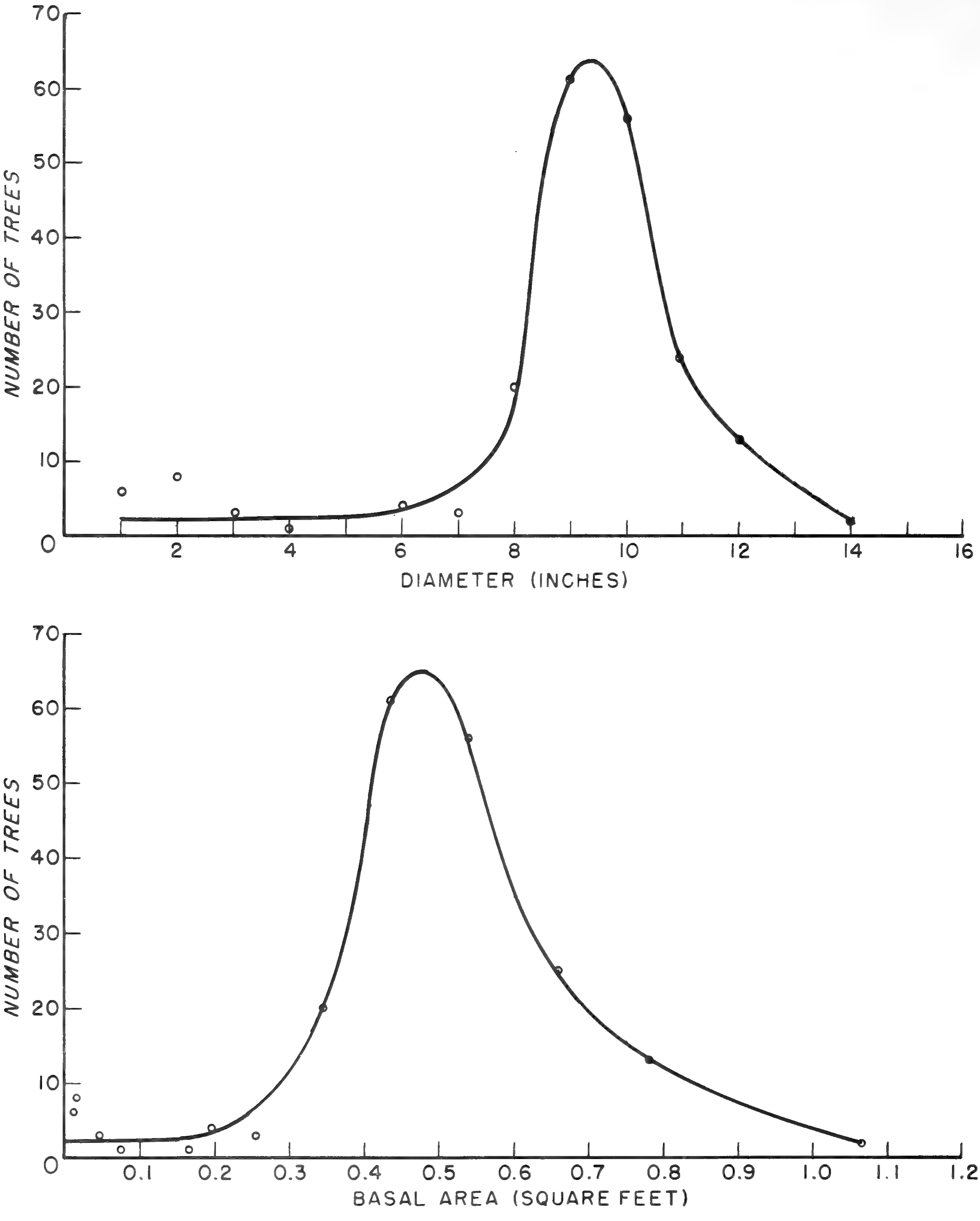

Figure 17.--Frequency distribution curves for plantation slash pine after 16 growing seasons. There are 202 trees on a 1-acre plot. The diameter curve (upper) shows that most of the trees are between 6 and 14 inches, and average 9 inches. The largest trees are 55 percent larger than the average tree. The basal area curve (lower) shows the largest trees are 130 percent larger than the average tree.

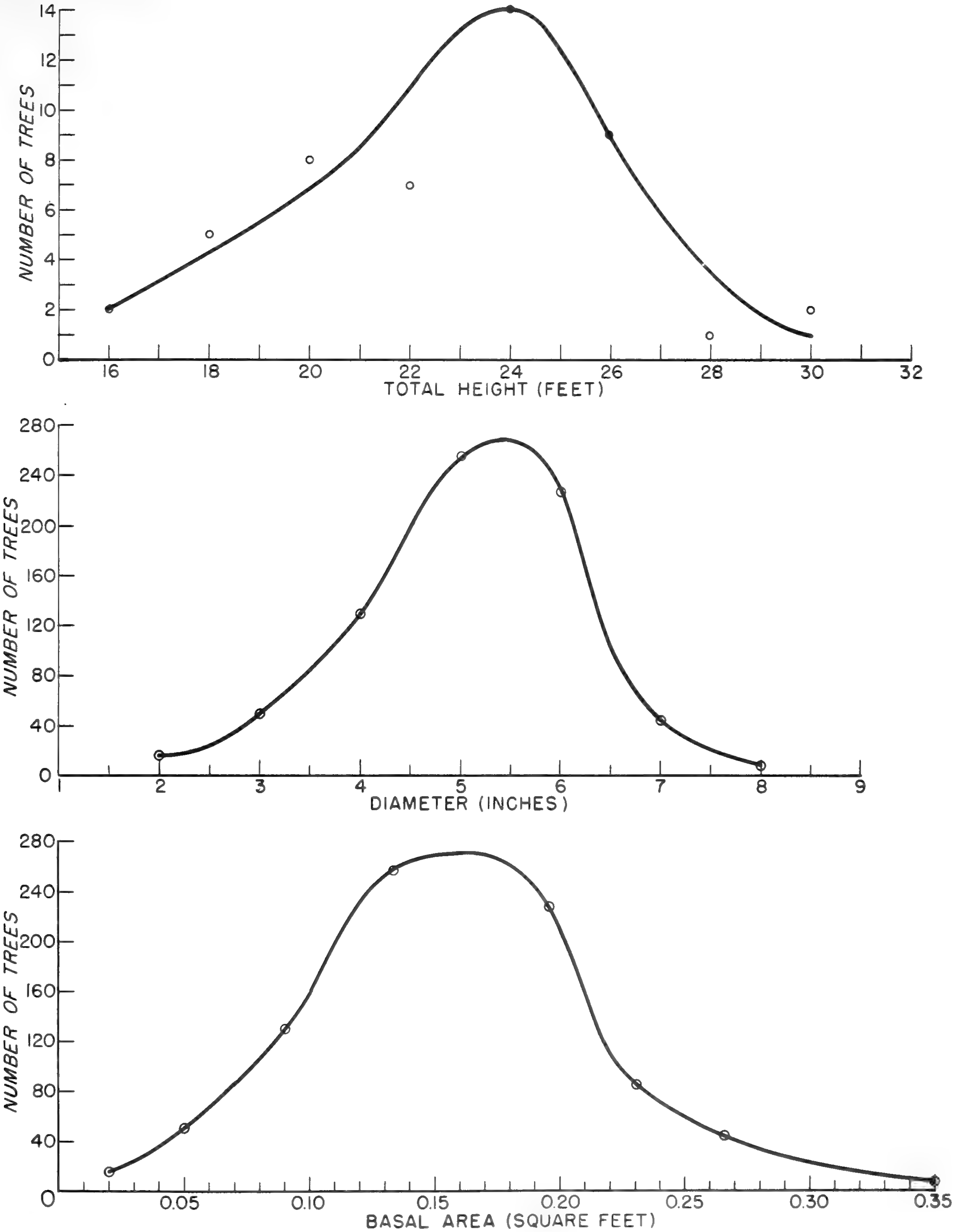

Figure 18.--Frequency distribution curves for slash pine in a 5-acre plantation on a uniform site after 8 growing seasons. The height curve (upper) shows the tallest trees are 30 percent taller than the average tree. The diameter curve (center) shows that some trees are 60 percent larger than the average tree. The basal area of some trees (lower curve) is 130 percent larger than average.

In uneven-aged stands or in areas where site changes rapidly in short distance, other standards for selecting plus trees may be desirable. In Sweden, Scots pine is selected for form and vigor. Some of the requirements, according to Lindquist (1948) are: "As regards the cubic contents, experience has shown that elite stems should have at least 50 percent more volume than the average of the three next biggest trees in the immediate vicinity. In selecting such trees, the slenderness of the branches should be balanced against the vigor of growth, but in such a way that no trees are chosen outside the slender-crowned type, and no selection of extremely slender-branched trees is done outside the fully dominant type." Lindquist also lists requirements for superior hardwood trees of several species.

Regardless of species, the plus trees should be rated on the basis of their superiority over average trees, and the more trees used to determine the average the better, if the site remains uniform. A comparison with 20 or 25 trees on the same site is more reliable than many times that number scattered over a large area where the site varies.

The standards for selecting trees for vigor will be much easier to set up after some progeny tests are made for each species; until then it is a matter of judgment. Standards for superior trees should be high and chosen after some field study of the species has been made. Only a relatively few trees can be used in progeny tests, so only those that are very outstanding should be selected.

Foresters should not expect a tree-improvement or tree-breeding project to remove the need for silvicultural treatment. These two fields of work should supplement each other, but are not interchangeable. Regulation of growing space plus judicious pruning and roguing in thinnings by removing undesirable types are very practical methods of controlling both vigor and quality. This applies particularly to the slow-growth versus rapid-growth controversy. Arthur Koehler of Forest Products Laboratory had this in mind when he wrote: "Wood of very rapid growth of some species has been found to have some very undesirable properties, but that was true for trees that had a large amount of growing space, at least, while young. In a nearly fully stocked stand, I don't think that we need to worry about too rapid growth of individual trees so far as wood quality is concerned, provided the stand is kept well stocked from the beginning. There may be a tendency in managed stands to keep the stand somewhat understocked, so as to get a greater amount of growth per tree. It is there where a question may come up whether too much quality is sacrificed for quantity, and that depends on the species and what the wood is to be used for. Another important factor is to keep the rate of diameter growth fairly uniform within a tree, since wide rings around the center and narrow ones toward the outside do not make for the best kind of wood. So far as breeding timber is concerned, it seems to us that there need be no goal or limit for rate of growth. The faster it will grow per acre, the better; the width of rings and coordinated properties can be regulated by density of stocking."

Selection for quality.--Improvement in quality may be divided into two fields of work. One is that concerned with external characteristics, such as branch size, crown width, stem taper, stem straightness, and pruning ability. The other is concerned with the wood itself where characters such as density, fiber length, grain straightness, chemical composition, and many others are important. Improving the quality of wood by selection and breeding is an important field of work, and at the same time a rather complicated one. However, it lends itself very well to specialization, and it is here that perhaps the most may be accomplished. It may be easier to separate forms from the wild species that will be better adapted to certain products than the run-of-the-mill wild stock. This will not remove the need for types suitable for all-round use, but there is need for both. It is difficult to imagine one type of hybrid corn that would be as suitable for popping, table use, and fattening livestock, as the three types which we now have, each of which contains many varieties. Specialty woods are probably of more importance for furniture or veneer, pulps or wood derivatives than for lumber.

Not many studies have been made of natural variation in wood quality in the pines, and others will be necessary before much selection or breeding can be done for anything other than volume growth. The demands of the pulp industry may have a bearing on this because of the variety of products they make. The yield of pulp obtained from southern pines ranges from about 95 percent by weight for groundwood pulp to 45 to 48 percent for sulfite and sulfate pulps. The requirements of a superior pulp tree depend on its use. For example, for the production of pulps to be made into paper requiring good formation and smoothness of surface, a good bursting strength and tensile strength, but not high-tearing strength, pine wood containing a relatively high volume of springwood is likely to be more satisfactory than wood containing a high amount of summerwood. On the other hand, for papers and boards in which low porosity and high resistance to tearing are desirable, and smoothness and bursting strength not so important, wood containing larger amounts of summerwood may be expected to give better results. For mechanical pulping and sulfite pulping, fast growth is preferable to slower growth, particularly if the latter contains an appreciable amount of heartwood. Since the yield of pulp on a volume basis increases with the density, it is desirable to produce a wood with as high a specific gravity as possible, commensurate with the other properties desired. Whether or not strains of trees that inherently produce wood of these types, combined with suitable silvicultural practices, can be developed remains to be seen. The veneer industry, under present standards, prefers fast-grown wood with little difference between springwood and summerwood.

The breadth of the field of work in wood improvement is indicated by the summary prepared by Arthur Koehler, of the Forest Products Laboratory, at the request of the division of forest genetics of the Northeastern Forest Experiment Station. The list is repeated in full and gives the characteristics to aim for in breeding certain species.

Straight stems Minimum butt flare Early self-pruning Resistance to decay within an economic rotation period Rapid height growth for volume and distance between knots Rapid basal area growth per acre Straight grain (except where figured wood is desired)	all species

Wide sapwood - Abies, Acer, Betula, Fraxinus, Tilia

Narrow sapwood - Juglans, Pinus (white pine particularly), Quercus

Long fibers - Abies, Picea, and Pinus (This is not so important for paper making as some think it is, because the fibers are broken up more or less in the beater. An increase of 10 percent in fiber length would mean little.)

Figured wood - Acer, Betula, and Juglans (The value of figured wood is so much more for certain species that it should be a lucrative field for tree breeding.)

Density - High density for Abies, Acer, Betula, Fraxinus, and some Quercus (This could be obtained largely automatically in stands kept growing vigorously by thinning, except in Abies, Picea, and Pinus, in which the density of the wood decreases in rapid growth.) Low density is desirable in Liriodendron, Juglans, Prunus, and some Quercus, on account of ease of working and low shrinkage. Low density and rapid growth per tree in these species usually do not go together. It would be a question as to which is more important.

Strength - High strength for Acer, Fraxinus, Pinus, and some Quercus

Durability of heartwood - Pinus and Quercus (white-oak group only), compare difference between ordinary and shipmast black locust

Ease of surface finishing	all species
Low shrinkage	
Freedom from excessive warping (sweet gum particularly)	
Rapid drying without serious degrade	
Ease of penetration with preservatives	
Ease of pulping and bleaching	

Branching habit may be important in determining spacing of plantations, rate of natural pruning, and the volume of the clear wood in the tree. Slender crowns are preferred over broad, and small branches over large. The reasons are rather obvious and probably not worthy of further discussion. We should remember though, that branch habit should be considered as secondary, and important only as it affects the economic yield of the tree. We don't want to sacrifice vigor or seed production for the sake of having small knots in the wood unless smaller knots will raise the value of the wood product. On the other hand, there is little point in having a lot of volume in large, massive branches if we can obtain good growth without it.

The angle of the branch with the horizontal is of some importance. Where it is large and the limbs extend upward and outward, they do not prune as quickly as horizontal branches that become shaded much earlier. Loblolly pine has this undesirable type of branching and it probably could be improved by selection. The tree in figure 16 is an example of a fairly open-grown tree that is very poorly pruned. Crosses of loblolly pine with longleaf pine usually show the branch habit of loblolly pine, as far as number and form of the branches are concerned, but, in addition, the branches are large in diameter, similar to those of the longleaf parent. Segregation of more desirable types may occur in the F_2 generation which could be observed by growing seedlings from open-pollinated seed of natural hybrids.

There may be an opportunity to select strains that give higher than average yields of pulp because they have less lignin in the wood. Nilsson (1943) cites cases of variation between trees in the amount of lignin of Scots pine and spruce, and also spruce from different parts of Sweden. In spruce and pine he found differences in chemical composition of the wood, and a big difference in yield of sulphate and sulphite pulp. Resin, lignin, and cellulose varied from 0.52 to 2.73 percent, 26.3 to 31.2 percent, and 48.1 to 55.5 percent. There was some difference in the wood between ramets (see glossary) of some aspen clones, but not as large as between clones. Fiber length was found to vary also. The samples were selected at random, and wider extremes may occur.

Selection or creation of polyploid forms of hardwoods may be desirable. Cells of certain plants which have double the usual sets of chromosomes may be 50 percent larger than in normal types. This has been advanced by Duffield (1943) as a possible cause for some of the variation in wood of red maple and by Wright (1944) for white ash, which contain polyploid types. Johnsson (1950) found in a polyploid-diploid cross of alder that the specific weight of the dry wood was lower. Also, Nilsson (1943) found the cells of a triploid aspen in Sweden were 50 percent larger than those of diploids. Thus, changing the number of sets of chromosomes may be a technique for obtaining types of hardwood trees that form relatively light wood even though they grow rapidly. Unlike pine, rapid-growing, ring-porous hardwoods produce heavier wood than slow-growing trees.

Sylven (1942) reported results of analyses of annual ring breadth, the autumn wood percentage, the volume weight, and the content of resin, lignin, and cellulose of 149 different 70-year-old central European spruces in Sweden. Spruces of different branching types gave similar values, but the breadth of annual ring was demonstratively greater in comb spruce variety than in the brush spruce or the "plane" spruce varieties. The analysis showed the existence of large differances between trees which might well be of importance in breeding for quality. In comb spruce, for example, the resin content varied from 0.74 to 2.14 percent (on a dry-matter basis), the lignin content from 26.3 to 29.9 percent, and the cellulose content from 49.3 to 54.8 percent.

Selection for durability of the wood may be important in species such as the oaks and black locust. From a study of the decay resistance of four white oaks (white oak, Oregon white oak, chestnut oak, swamp chestnut oak) and three red oaks (northern red oak, scarlet oak, black oak), Scheffer, Englerth, and Duncan (1949) concluded that: "Individual trees of the same species, of approximately the same size, and in the same locality differed markedly from one another in resistance. This was true of all four species examined, but especially so of white and swamp chestnut oak. This variability in resistance among trees appeared to be attributable more to genetic differences than to differences in the environment of the trees. The possibility presents itself, therefore, of selecting and propagating oak trees with wood having not only a longer but also a more uniform service-life expectancy." Hopp (1941) has emphasized the importance of selecting black locust for wood quality. Scheffer and Hopp (1949) tested the decay resistance of shipmast locust, a variety called Flowerfield, and common locust. They found on the average that the Flowerfield strain decayed the least, the shipmast somewhat more, and the common locust considerably more. Black locust has several varieties, and the genus Robini itself is variable in its cytology. Some species have 10 diploid chromosomes, two are triploids with 15 diploid chromosomes, and one race has been reported with 11 diploid chromosomes. Selection should be very profitable in a species where such wide genetic variability occurs.

From a study of the wood from 23 yellow-poplar trees, Erickson (1940) found indications that specific gravity decreased as rate of growth decreased, but rate of growth was not closely correlated with specific gravity. Only 23 percent of the variance of all the samples could be explained by the variation in the rate of growth. For 20 of the trees the regression coefficients were negative values and for the other three they were positive. Thus, it may be possible to select strains of yellow-poplar that grow rapidly and yet produce light wood.

Selection for resistance to disease and insect pests.--Selection for resistance to common enemies of forest trees should have an important place in plant-improvement work. Damage of this type not only causes loss of individual trees but reduces quality and growth and complicates marking for intermediate cuts. Resistant strains would reduce the loss of seedlings in the nursery and throughout the life of the stand, and would result in an increase in total yield of wood per acre. Resistance to certain insects and diseases has been demonstrated to be heritable, and, in some cases, like mimosa wilt, some individual trees developing from open-pollinated seed of resistant mother trees are themselves resistant.

A number of diseases cause large losses in southern pine. Probably most important is *Cronartium fusiforme*, the rust canker. It is particularly damaging to slash and loblolly pine. Some slash pine trees may be resistant, because disease-free trees have been observed in plantations where 75 percent of the trees are infected. Some of the disease-free trees may be the largest and most rapid-growing trees in the stand. This is in contrast to observations which show that, in general, fast-growing trees, or those fertilized or cultivated, are more susceptible to this disease than slow-growing trees. Rapid-growing trees that have escaped infection in heavily damaged stands should be tested for resistance to the disease.

Selection and breeding for disease resistance has been common in horticulture, and with certain tree species such as chestnut and white pine. The techniques that have been worked out vary somewhat according to the nature of the disease because testing progeny for resistance is a specialized job. In his book, "Principles of Plant Infection," Gaumann (1950) makes the following statement concerning inheritance of resistance in plants: "The innate infection and disease-resistance capacities depend on a number of very heterogeneous conditions. Only seldom do they depend on a single factor, but mostly they are the result of the interplay of heterogeneous elements, such as resistance to attack, penetration, or spread, anti-infectional and anti-toxic defense reactions, and induced tolerance. Accordingly, their mode of inheritance is very complex. Certain factors associated with resistance are inherited, as also are certain functional capacities associated with the defense reactions; the final result (the resistance to disease as measured experimentally in laboratory and field trials) is produced by spatial and temporal cooperation of all these factors. The following facts are basic:

1. Resistance to any one disease is usually inherited as a unitary, genetic complex, entirely independent of resistance to any other disease.

2. For specialized pathogens (and these form the overwhelming majority) the resistance to each single strain is, as a rule, inherited as a unitary, monovalent, genetic complex, more or less independent of the resistance complexes against other strains of the pathogen."

Selection for resistance to temperature extremes.--This is an important factor in choosing strains or races for use outside their natural range or near the northern limits. Damage from freezing may occur when seed of southern provenance is grown in northern areas or at higher altitudes. Shortleaf pine from areas in the southern part of its range is injured in Pennsylvania, while trees of local sources are uninjured. We may find that generally in this hemisphere plants may be moved toward the north or from lower to higher elevations and grow more rapidly than local plants, provided they are not moved so far that they suffer from frost damage.

Selection for secondary products.--Some tree species, particularly those producing edible nuts or valuable oils, may be as valuable for these products as for the wood. There are good opportunities for selecting superior types because of the wide variability in the wild stand. The TVA has selected some 42 varieties of black walnuts. The Stuart variety of pecan is a selection that is still popular after many years. Honey locust trees have been selected for higher sugar content in the pods, which are suitable for cattle feed. Sugar maple trees have been selected for high sugar content in the sap.

Selection of slash and longleaf pine for high oleoresin yield is important in the naval stores region, and individual trees producing 2.5 times the average have been found (Dorman, 1950). Laurie (1941) lists 24 species of Indian trees, some of which exhibit individual or racial variation in yield of oil, resin, or other minor products as well as in yield of timber, growth form, and hardiness.

Usual procedure in selection is to itemize the factors of most importance, such as flavor and ease of cracking nuts or kind and quality of certain oils. Individual trees that produce the best are then sought out in wild stands, and the progeny tested to insure that traits are inherent. There is some evidence of physiological races in forest trees, although the subject has not been exhaustively studied. Scheffer, Lackmund, and Hopp (1944) found differences between trees in the amount of hot-water extractives in black locust wood. In Australia, Penfold and Morrison (1948) found only small quantities of the aliphatic aldehyde citronellal in the essential oil of certain trees of *Eucalyptus citriodora*, where it is usually present to the extent of 65 to 85 percent. The Queensland Forest Service (1950) summarized additional work to determine the reason for the variation in oil yield and oil quality. Some samples showed a range in yield from 0.2 to 2.0 percent. Normally, the oil is of excellent commercial quality, but that of a few trees showed such a low aldehyde content that it was practically of no commercial value. Guinier (1926) found differences between individual maritime pine trees in composition of resin. Spaven (1949) described the work in Vermont to develop better strains of maple. Certain trees have been found that have 7 percent sugar in the sap as compared with 2 percent of average trees. Also, some trees produced four times as much sap. These are the results of study of sap from 4500 trees. Ferguson (1946) states that quinine content in the bark of Cinchona trees is genetically determined. Chittenden (1950) states that breeding work with rubber trees is directed toward development of types giving a stable latex, and especially a white latex suitable for crepe production as well as high-yielding types with good secondary characters.

APPLICATION OF SELECTION TO SILVICULTURE

The three traits of most interest to the forester in silvicultural work such as timber marking or seed collection are (1) vigor, (2) quality, and (3) resistance to pests. They are the important features of each tree that are discernible in the woods. Also, they are the most important in determining volume and grade of the products which govern financial returns. Quality is used here to indicate form of crown, branchiness, stem taper, straightness, general wood quality, and self-pruning.

Selection for vigor.--Volume growth is probably more important in determining returns than is quality. But inherent vigor is not as easy to manipulate through silvicultural practices as is quality. In this discussion vigor will be considered as a characteristic of the individual tree and not of stands.

Selection of the most vigorous trees in timber marking consists merely of choosing the largest trees consistent with quality. These are the trees that have made superior volume growth in comparison with the average trees on the same site. More variation is to be expected in natural than in planted stands and in mountainous or uneven topography, where soil fertility or moisture conditions may vary within short distances. Spacing of the selected trees to be left in the stand is important, of course, and trees of average growth will be left in many cases because of this requirement. It may be desirable to choose outstanding trees from within a group where comparisons of growth are possible, rather than larger trees in small openings where competition has not been a factor and where it is difficult to compare them with the average because there are few trees in the immediate vicinity. The forester is in a position to rate the individual trees in each particular case because of his knowledge of the effect of superior site or other conditions on the tree growth and development. In each instance, if he chooses the outstanding individual tree on the basis of average growth of a number growing under the same conditions, he won't go far wrong.

When selecting pine seed trees, the requirements or standards can be much higher because only 6 to 10 trees may be left on each acre. In these stands the trees are much older and larger. And because these are the trees that will regenerate the stand, they should be chosen with some care. The same requirements apply that they be the best trees available when compared with others growing under the same conditions, and they should not achieve this superiority at the expense of seed production. The presence of abundant cones from recent crops indicates good producing ability.

In selecting trees from which to collect seed, spacing is less important, and about the only consideration is to keep the collector's travel to a reasonable distance. Also, it is possible to choose the stands from which seed will be collected. Thus, the selection work can be done where it is possible to make comparisons between trees. Fruitfulness of the tree is a requirement in addition to vigor, quality, and resistance to pests. Von Wettstein (1937) observed that trees of low growth rate frequently produce more abundant cones than rapid-growing strains. The same condition has been found in teak (Laurie, 1936), oak (Anon. 1943), and yellow-poplar (Perry and Coover, 1933). Indiscriminate seed collection favors perpetuation of these mediocre types. Even-aged, uniform stands or plantations in areas where soil conditions are least variable are the best places in which to work.

A few really superior trees are not enough to supply the demand for seed. Moreover, collection from standing trees is not widespread. But over a period of time as the practice increases, it should be possible to have enough outstanding trees selected and marked to supply each year a larger proportion of the annual seed requirement.

Selection for quality.--Quality goes hand in hand with vigor, but on this point foresters and geneticists sometimes disagree because of the close relationship between them. Selection for a combination of traits is most important and comprises the most difficult to make. It is not enough to have fast-growing trees; fast-growing trees must also have high quality. The key to the problem is that we must remember to concentrate on the genotype by estimating and subtracting the environmental effects wherever possible. Open-grown trees are often squatty and limby. The same trees might have grown tall and slender with well-pruned trunks had they been crowded by others of the same species. This means nothing as far as selection value is concerned. If the same individual trees, while in the open, had grown tall and slender with small branches and some natural pruning, it would be a different matter, as this would indicate that they are inherently a good type.

If we select trees in stands without regard to their individual crown size, branch size, crown width, straightness and pruning ability, we are not selecting superior trees; we are selecting trees that are merely big. If we select the most slender trees that have small, narrow crowns and long, well-pruned stems, we may not be selecting superior trees; we may be selecting trees that are merely poor competitors. A superior phenotype is a tree with exceptional vigor, good crown form in proportion to tree size, straight stem, and good natural pruning in proportion to the size of the branches. This is the tree that has demonstrated its superior efficiency by producing the most wood with its proportionate share of light, moisture, and growing space.

Foresters are often hesitant about choosing the largest trees in the stands for crop trees. Many of the large trees present a rough appearance in comparison with other trees which may be much smaller. It should be kept in mind that trees with two to three times the volume of average trees could have proportionately larger branches. The dead branches may not prune as promptly as the smaller branches of other trees, which gives the impression that the crowns of the large trees are much longer than they really are. Good pruning practice prior to the time selections are made will make the large trees very attractive. Inherently vigorous strains are very desirable and should not be sacrificed in favor of quality that can be obtained through good silvicultural practice.

The important external factors in tree quality are:

1. Clear length of stem
2. Taper of stem
3. Straightness of grain
4. Diameter of branches
5. Diameter of bole
6. Forking
7. Straightness of stem
8. Amount of natural pruning
9. Apical dominance (strong central stem in the crown)
10. Flare of the butt
11. Sprouting of epicormic buds

As far as we know, all these are inherent traits, and only trees with the most desirable combinations of them should remain in the stand. The relative importance of each item will vary with species and with the major product the stand is being managed for. The forester can evaluate them in accordance with the local situation. He is better qualified to judge quality than anyone else. If the final product is to be some specialty with unusual requirements, the traits governing them should be of first importance; otherwise the factors that promote high value in trees for saw logs would be paramount.

Selection for resistance to diseases and pests.--This is a relatively simple procedure in the woods. Wherever possible, only healthy trees should be left in the stand. This is true of intermediate as well as final cuts. It is not always possible to remove all the damaged and diseased trees, but they should be discriminated against. Resistances may be phenological, such as those concerned with the period when the tree flushes or begins to grow in the spring. If the new growth of some individual trees or strains and races either precedes or follows the main period of spore discharge of a disease or the emergence of a brood of insects, the new shoots will escape heavy damage. Physiological or morphological differences give rise to other types of resistance.

In summarizing this section on the application of selection, it should be emphasized that a forester in the woods has to work with what he has on the ground at the present time. He can't be, and shouldn't be, concerned with minutiae. If he strives to maintain or improve the vigor and quality of the stock and to reduce loss from disease or pests, he is fulfilling his obligation as a technician. The point is that all variations in form and vigor are not (as foresters so often say) a result of differences in site conditions. Many a poor tree on good soil is the result of poor parents. It is thus unwise to harvest all the best trees and leave the worst to produce the next generation. You can't expect genetically poor mother trees to produce good offspring.

PLANS FOR SELECTING SUPERIOR TREES

Before going to the field and attempting to choose superior trees of any species, it is desirable to take time to plan the operation. The important factors of quality which are influenced by tree form will vary between species. Also, the utilization, or the products made from the tree, will determine what traits are important in superior trees. The important items to be considered in a plan for selection can be listed as follows:

I. Species

II. Products for which the tree is utilized and which may require certain characteristics of form or quality

  A. Lumber or poles (good natural pruning, little taper, small knots, thin bark, good central stem, etc.)

  B. Pulpwood (heavy pine wood for kraft, light for newsprint, yield of cellulose, low percent waste from lignin, knots, and bark)

  C. Furniture or veneer (straight grain, good central stem with little taper, desired sapwood-heartwood ratio, bark thickness, figured grain, etc.)

  D. Other products (fruit, nuts, oleoresin, seed)

III. Important pests

  A. Diseases (foliage, bark, or wood)

  B. Insects (foliage, bark, or wood)

IV. Important uses other than manufacture

  A. Ornamental

  B. Erosion control or soil building

  C. Windbreak

V. Other traits characteristic of the species or the use

  A. Cold resistance

  B. Drought resistance

  C. Fertility of seed as well as volume produced

  D. Growth habit of seedlings

VI. Best areas in which to search

  A. Areas in which best races occur

  B. Plantations

  C. Old-field stands

  D. Virgin stands or second growth

VII. Traits of which little is known about range of variation

After such a list has been prepared, it is apparent that for most purposes and species, there are only a few major points to rate superior trees. An example of a plan for selecting slash and loblolly pine and yellow-poplar is about as follows:

Slash pine.--(When used for lumber, poles, pulpwood, and naval stores; possible future use for softwood veneer.)

I. Items upon which to rate trees

A. Traits to improve quality for lumber and poles

1. Less taper in trunk
2. Narrower crowns with small branches to give small knots
3. Fewer branches per lineal foot of trunk
4. Less buttswell
5. More ability for natural pruning
6. Thinner bark on fast-growing trees
7. More rapid growth--50% greater in diameter at least--than average

B. Traits to improve quality for pulpwood

1. Same as for lumber except items 1 and 4 above
2. For kraft pulp, high density wood (over .54 specific gravity, high percent summerwood)
3. For newsprint, low density wood (less than .38 specific gravity, low percent summerwood)
4. Higher yield of pulp, lower waste per ton of pulpwood
5. Looser bark

C. Traits to improve quality for naval stores

1. Same as for lumber
2. High oleoresin yields (250 percent or greater of average)
3. Gum of uniform quality throughout the season
4. Less scrape
5. Thinner, softer bark to make chipping easier
6. Ability to produce well on first streaks

D. Traits to improve quality for veneer production

1. Same as for lumber
2. Less variation between specific gravity of summerwood and springwood
3. Better gluing properties
4. Looser bark

E. Traits to improve pest resistance

1. Resistance to fusiform rust, cone rust, pitch canker, needle diseases
2. Resistance to bark beetles and Nantucket pine tip moth

F. Other important traits to select for

1. Drought resistance

II. Best areas or stands in which to search for plus trees

A. Any area near where trees are to be planted (there is not much evidence of racial strains, but the problem has not been adequately studied)

B. Planted stands of good racial stock should have first priority, and even-aged old-field stands second

III. Traits for which little is known of natural variation and which may be important in improving this species

A. Quality of oleoresin (uniformity of yields over different seasons of the year, proportion of important components, such as turpentine, alpha and beta pinene, tendency of gum to form scrape on the tree)

B. Wood density range (between trees and between springwood and summerwood of same trees)

C. Yield of pulp, lignin, and waste products (variation within trees under 20 years of age has been studied) Little known of pulping qualities of south Florida variety of slash pine.

D. Bark tightness (bark should come off very easily; it is not known to what extent this is a variable trait and whether it is genetically controlled)

Loblolly pine.--(When used for lumber, poles, and pulpwood)

I. Items upon which to rate trees

A. Traits to improve quality for lumber

1. Less taper in trunk
2. Narrower crowns with small branches to give small knots
3. Fewer branches per lineal foot of trunk
4. More ability for natural pruning
5. Thinner bark on fast-growing trees
6. More rapid growth
7. Stronger, more pronounced trunk in crown region (strong apical dominance)
8. Larger angle between branch and trunk (branches more nearly at a 90-degree angle with the trunk should be preferred; this is to aid in natural pruning)

B. Traits to improve quality for pulpwood

1. Same as for lumber except item 1
2. For kraft pulp, higher density wood
3. For newsprint, lower density wood
4. Higher yield of pulp, lower waste per ton of pulpwood

C. Traits to improve quality for veneer

1. Same as for lumber
2. Less variation between specific gravity of springwood and summerwood
3. Better gluing properties
4. Looser bark

D. Traits to improve pest resistance

1. Resistance to fusiform rust, cone rust, needle disease, littleleaf
2. Resistance to Nantucket pine tip moth, and the bark beetles

II. Best areas or stands in which to search for plus trees

A. Areas in which best strains occur for planting in designated areas
(Many racial strains occur in loblolly pine, and it is important that selection be made within the best races. If best races are not known, make selection near where seed is to be used.)

B. Plantations of good racial stock even if original source is unknown
(Knowing the source is important, but not an absolute requirement if the plantation is of good quality.)

C. Even-aged second-growth or original old-growth stands

III. Traits about which little is known of natural variation and which may be important in improving this species

A. Wood density variation
(between trees and between springwood and summerwood within the same tree)

B. Yield of pulp and waste materials per ton of pulpwood for various age classes of merchantable trees

C. Bark tightness

Yellow-poplar.--(When used for lumber and furniture veneer)

1. Items upon which to rate trees

A. Traits to improve quality for lumber

1. Figured grain
2. Less epicormic sprouting
3. More rapid growth
4. More ability for natural pruning
5. Both high and low density of wood

B. Traits to improve pest resistance

In this species, susceptibility to major pests is not yet an important factor.

C. Other important traits to select for

1. Higher fertility of the seed

II. Best areas or stands in which to search

A. Plantations of good racial stock

B. Second- and old-growth stands

III. Traits of which little is known of variation and which may be important in improving this species

A. Wood density
(In natural stands density varies widely and the causes are unknown. Paul and Norton (1936) have stated the wood is about twice as variable as that of hard maple. This may be a result of a more heterogyzous nature or from polyploidy which is thought responsible for variation in ash. The occurrence of polyploid types has not been studied.)

MARKING SELECTED TREES

It is very important that selected trees be marked and their location accurately described so they may be easily found again. In addition, they should be described in such a manner that comparison of good and poor traits can be made in the office. One of the most desirable features of a uniform numbering or identification system is that it can be understood by different workers.

The individual tree will be the common unit in selection work. They can be marked temporarily with white cloth and later on by light-colored paint or metal tags. Bands around the trees are easily seen from all directions, although they may be unsuitable for trees near inhabited areas. Several bands may be used to indicate the relative value of the tree or the degree to which it has been used in the tree-improvement work. One band may indicate a first selection, two bands those tested with open-pollinated seed, three bands those used in controlled breeding, and four bands those proven to be genetically superior trees.

Some Swedish tree breeders refer to selected trees as "plus" trees until the genotype has been determined. If they prove to be superior genotypes they are called "elite" trees. A more precise method would be to call untested superior phenotypes "phenotypically elite," and progeny tested trees that are indeed superior genotypes "genotypically elite."

The Institute of Forest Genetics uses a simple and effective system of numbering trees. Metal tags carry the data and are nailed to the tree with long nails driven only part way in to allow for tree growth. The tag gives the abbreviated Latin name of the species, the county and state, the plot number, and the tree number within the plot. Trees more than a quarter mile apart are given different plot numbers, and a plot can be one tree or several trees. In local studies or projects the plot and the number would be sufficient for identification, but if seed or grafting material is sent to other sections the full code should be used. The designation "PC, Harris, Ga., 3A, 4" would mean "slash pine, Harris Co., Ga., plot 3A, tree number 4." If metal tags are unsatisfactory, paint can be used.

Southern pine species abbreviations used by the Institute of Forest Genetics:

	Abbreviation
Pinus caribaea (slash pine)	PC
P. clausa (sand pine)	PCla
P. echinata (shortleaf pine)	PE
P. glabra (spruce pine)	PGl
P. palustris (longleaf pine)	PPa
P. rigida (pitch pine)	PRi
P. serotina (pond pine)	PSe
P. Sondereggeri (Sonderegger pine)	PSon
P. taeda (loblolly pine)	PT
P. virginiana (scrub pine)	PV

Abbreviations for the 90-odd species of pine are available from the Institute, while those for other species will have to be prepared by workers in the South. New symbols should be added only by joint action of all agencies with the Institute.

A detailed set of notes on the characteristics of each tree should be taken. The attached form can be used to suggest the points to be noted. A sketch map of location can be made on the back of the form. If possible, a photograph or sketch of the tree should be included. If progeny tests are made, a record of seed collection, outplantings, and performance of seedlings can be included. Standardization of a record-keeping system will avoid confusion among workers. If additional data can be taken, a sketch can be made showing summer-wood and springwood in the increment core; also, descriptive data for average trees in the stand, so that a comparison can be made between the study trees and others. Bark thickness, stem taper, branch length, branch thickness, crown length, crown density, and crown width will be useful items of information.

A somewhat similar form can be used in recording data for phenotypically elite stands. The characters of form, vigor, or others that vary from average in the species should be recorded; also the location of the stands so they can be found by other workers. If a large number of selections are made, it may be advisable to transfer the data to punch cards.

CATALOGUE OF SUPERIOR TREES

Species ______________________________

Local number ______________________________
(Plot and tree number)

Description of tree:

Age ______________ Height ______________

Diameter ______________ Sex ______________

Is there evidence of flower or seed production? ______________

Superior traits:

Vigor ______________________________
(Percent taller, larger diameter, or greater volume than average)

Branches ______________ Crown ______________
(Larger, smaller, or average thickness) (Wider, narrower, or average width)

Straightness of grain ______________ Specific gravity of wood ______________

Percent summerwood ________ Angle of branches from horizontal ______________
(Larger, smaller, or average)

Pest resistance ______________________________
(Damage by insects, diseases, mechanical breakage)

Other traits ______________________________

____

Location:

Section, township, range, lot, etc. ______________

County and state ______________

Name and address of owner or others ______________

____

Elevation ______________

Identification marking on the tree ______________

____

Name and address of reporter ______________

____

Record of seed collection: ____________________
(date and seed lot number)

____

____

____

____

Progeny tests or tests with grafts or cuttings: ____________________
(date, location, experiment number)

____

____

____

____

Photograph or sketch

(show form and size in comparison with adjacent trees)

Map of location

NAMING IMPROVED STRAINS

Tree breeding and selection projects will probably develop plant material that will be difficult to name under the present methods of nomenclature. Also, it will be undesirable to give formal names to many varieties, variants, or hybrids that may be of value only in experimental work and which will never be used commercially. The book, "Standardized Plant Names," discusses the nomenclature of plant material other than species, varieties, and races, and it should be used as a reference.

At present, races of trees are not given formal names but they are called by a common English name which is usually descriptive. Examples would be the "red-barked" or the "pointed-crowned" races of Scots pine. Natural varieties have been recognized by adding a Latin varietal name to the specific name (see "form" and "variety" in the glossary). Some taxonomists prefer to limit recognition of varieties to those cases where the plant is found over some geographic area rather than to one plant. The way to avoid confusion is to identify a selected strain or variety by the name of the individual, or a number, and avoid Latin names altogether. A strain of slash pine selected by John Doe would be known as Doe's slash pine. This system could also be applied to lots of controlled pollinated seed of superior strains. Some plant breeders prefer to call vegetatively propagated strains by English names and sexually propagated strains by number.

"Standardized Plant Names" suggests some terms for identifying vegetatively propagated clones. A clone is defined as a group of organisms composed of individuals propagated vegetatively from a single original individual. An ortet is the one original plant from which a clone ultimately derives. A ramet is an individual member of a clone. These terms apply to grafted plants or rooted cuttings and not to sexually reproduced types. The term "polybrid" is used as a group name for hybrids from crosses between two particular species, varieties, or genera.

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APPENDIX

Summary of Studies in Racial Variation

The following sections summarize some of the published data regarding clinal and other types of racial variation in the tree species of the United States and in foreign countries.

Races of trees in the United States.--In a 22-year-old test planting at Bogalusa, La., loblolly pine of local source produced a much higher volume per acre and was injured less by disease than that from other provenances (Wakeley 1944, 1951). The native Louisiana stock produced 41.8 rough cords of merchantable pulpwood per acre in trees 4 inches and larger in diameter at breast height. Texas stock had produced 22.7 cords, Georgia 17.7, and Arkansas 15.4 cords per acre. Thirty-seven percent of the trees from Georgia seed had rust cankers on the stems, while only 4 to 6 percent of those from other sources were infected.

From the preliminary results of a test begun in 1935 in South Africa with loblolly pine of different provenances, Sherry (1947) states there were several latitudinal topoclines. Growth of trees from southern latitudes was the most rapid, and was slower from northern sources, but the form of the slower growing trees was better.

The height of the trees in relation to latitude of the provenance is given in figure 19. The three seed sources between latitude 30°N and 31°N were Leon County, Fla., Montgomery County, Texas, and St. Tammany Parish, La. The northernmost seed source was Wisconsin County, Md., which is at 38.4°N.

Seedlings of the same sources were also planted at several places in the United States. At Athens, Ga., the average heights were between 31 and 35 feet, showing much less variation with provenance. At Jasper, Texas, they were between 29 and 34 feet (Wakeley, 1951). Thus, in South Africa, Texas, and Georgia the least adapted stock made 57, 85, and 89 percent, respectively, of the height growth of the best adapted.

In this same study of geographic races, in loblolly pine, infection by fusiform rust was associated with seed source. Wakeley (1951) states, "The North Carolina stock had 22 percent of all living trees infected at both Athens, Ga., and Jasper, Texas. The South Carolina stock had 8 to 16 percent infected at the same two places. Two western strains, those from the Kisatchie National Forest in Louisiana and from Trinity County, Texas, showed only 3 and 1 percent infection, respectively, at Athens, and 7 and 2 percent at Jasper. These results parallel those from the Bogalusa study, in which the one eastern strain of loblolly (Georgia) was more heavily infected than the 3 western strains (Louisiana, Arkansas, and Texas). But strains from northeastern sources, which were not tested in the original Bogalusa study also proved relatively unsusceptible in the 1935 study. Virginia stock was infected only 4 percent at Athens, only 6 percent at Jasper, and Maryland stock showed no infection at either place."

Slash pine has given rather uniform results in the tests made up until now with seed of different provenances. This species has a more limited range than the other major southern pines. If the south Florida type of slash pine

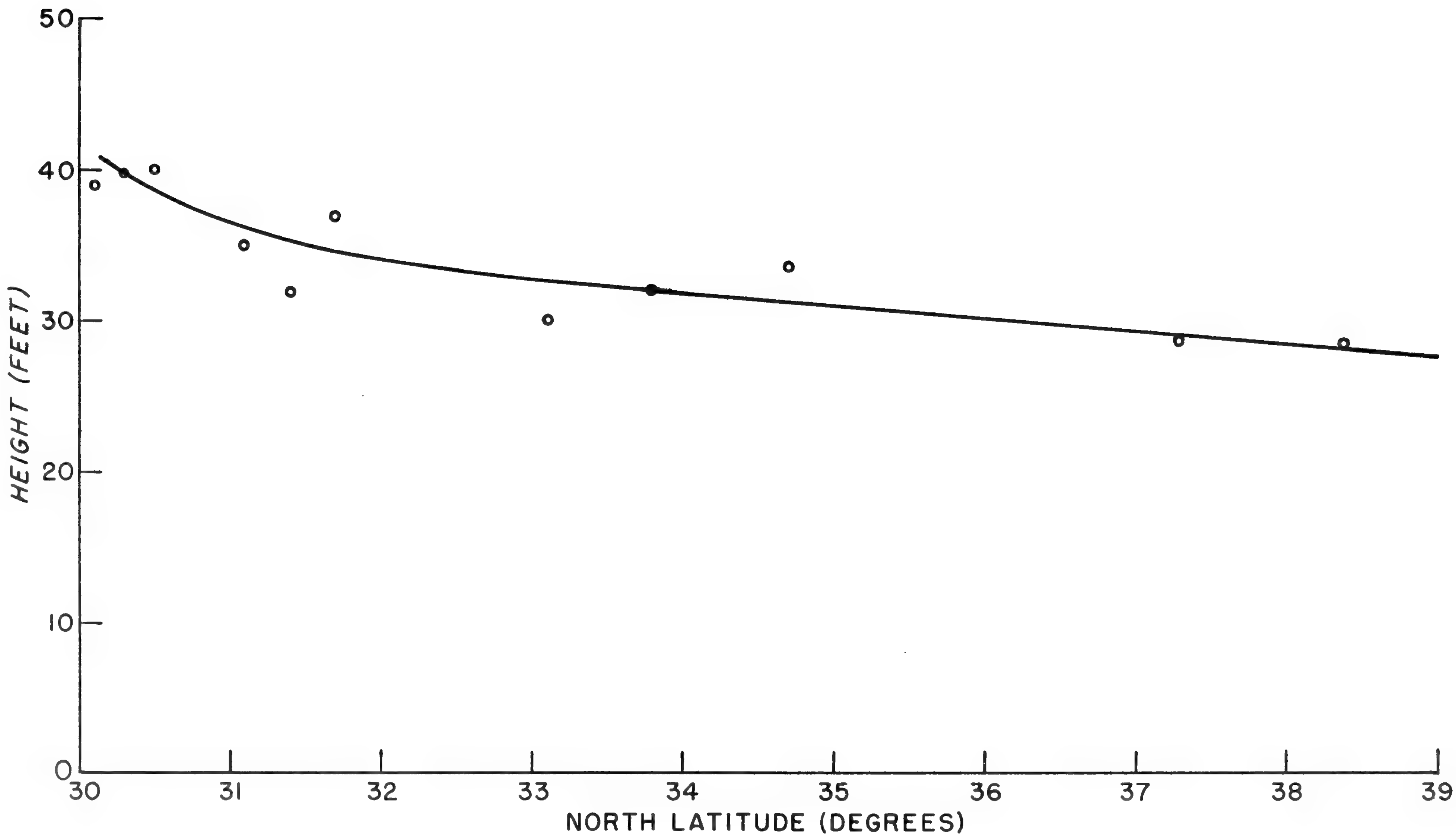

Figure 19.--Height of loblolly pine (growing in Africa) in relation to latitude of seed source (United States).

is excluded, the natural range of the species is between latitudes 27°N and 33°N. Seed from sources between the latitudes 30.1°N and 31.0°N were tested with loblolly pine in the South African study. The results as found by Sherry (1947) for the 9-year-old test show the average heights of plots of different provenance were between 35.7 and 37.4 feet.

Slash pine showed less variation in height growth between tests in four different locations in Africa than did loblolly pine. This may be site effects, but slash pine was remarkably uniform over the entire range when planted at 25°S, 28°S, 29°S, and 31°S. At two locations it was planted at elevations of 150 feet and at the fourth at 3,000 feet. The stock of Liberty County, Fla., provenance differed in height only 1.9 feet between the 4 areas. Stock of Osceola National Forest in Florida varied 5.3 feet, which was the widest range. The average of all 6 sources was 3.7 feet. The average for loblolly pine planted at the same location was 9.8 feet. Variation was less for southern provenances, averaging 7.7 feet for the three sources and 13.4 feet for the two northernmost sources. This indicates loblolly pine stock of northern provenance was more sensitive to local conditions than stock of southern provenance.

Both slash and loblolly pine were rather similar in one other respect in that there was little difference in their rating according to total height at the four test areas. The provenances showing highest average height growth were superior in all test areas--the provenances showing poor growth were poor on all four test plots. No data concerning volume, wood density, or pulp yield are available. Complete data will give a more accurate evaluation of the sources, and these will no doubt be available later.

When shortleaf pine from southern parts of its natural range was planted in Pennsylvania, which is near the northern limit, survival was low and growth very slow in comparison with stock of local origin (Aughanbaugh, 1950). The data for the stock of six sources is given in table 3, as follows:

Table 3.--Survival and growth after 14 years of shortleaf pine of different provenance planted in Pennsylvia

Source of seed	Trees living	Average height	Average diameter
	Number	Feet	Inches
Morgan County, Tennessee	57	14.3	2.7
Stone County, Arkansas	21	11.4	2.3
Houston County, Texas	6	11.3	1.7
Sabine Parish, Louisiana	1	10.0	1.5
Adams County, Mississippi	2	9.5	1.0
Edgefield County, South Car.	5	9.2	1.6

The seed germinated well, but survival was low. Growth of the 80 trees in each lot was very slow and they suffered from frost injury. Trees from seed of Morgan County, Tenn., which has the climate closest to Pennsylvania conditions, showed definite superiority over others from lower latitudes and altitudes. There were some differences in form of stem between Arkansas and Texas stock. The heights of both were nearly the same, but the diameter of the Arkansas stock was 2.3 inches and the Texas stock 1.7 inches. Results to date indicate that local seed is much the better for planting in Pennsylvania.

There is some additional evidence of racial variation in shortleaf and loblolly pine as indicated by variation in size of pollen grain and strength and weight of the wood. Cain and Cain (1948) measured pollen grains from 27 samples of shortleaf pine collected at various points between Texas and New York. The grains had an extreme variation from about 42 to 70 microns. They state, "The study of Pinus echinata shows what is coming to be expected of size characteristics of morphological features in general, that is, a considerable intraspecific variability. Some collections from stations considerably removed from one another may be very similar. Other material from one locality may be significantly different."

In shortleaf and loblolly pine, weight and strength of the wood varied with the locality where it was grown, but in slash and longleaf pine they did not, according to Johnson and Roth (1896). In shortleaf pine, wood from the southern coast and Gulf region and even Arkansas was generally heavier than wood from localities farther north. Very light and fine-grained wood was seldom found near southern limits of the range, while it is almost the rule in Missouri, where forms resembling the red pine are by no means rare. Concerning specific weight, Johnson and Roth state, "Though occasionally some very exceptional trees occur, especially in loblolly and shortleaf pine, the range in specific weight on the whole is generally within narrow limits."

Racial variation in spruce, pond, sand, Virginia, and pitch pine has not been studied. These are minor species in the South and planted only rarely. Races may occur because most of them have rather broad geographical ranges. Sand pine that grows only in Florida seems to vary in the date cones open. In January, most of the trees in the western part of the State had open cones as compared with only a few in the southern part.

Growth of red pine varied somewhat between provenances in a 16-year-old plantation in northeastern Minnesota, reported by Rudolf (1948). Seed of 37 origins throughout the Lake States and including two localities in New England were planted in the Superior National Forest. It was concluded that: "For best assurance of success, collect red pine seed from inland northeastern Minnesota localities, avoiding trees with thin foliage. Do not use red pine seeds from New England, lower Michigan, central Wisconsin, or the south shore of Lake Superior. If northeastern Minnesota red pine seed is unobtainable, second choice should go to northwestern or north-central Minnesota or northeastern Wisconsin." White spruce planted in the Nicolet National Forest in Wisconsin by the Lake States Forest Experiment Station(1947) showed difference in growth between the 6 seed sources tested, and seedlings of three provenances in Ontario, Canada, were best. This is interesting because northern provenances planted farther south did better than the local provenance.

In a test of ponderosa pine (Weidman, 1939), seed from 20 origins were planted in northern Idaho. The sources of seed were in western United States and Canada. The best strains made more than twice the height and diameter growth of the poorest. Two introduced strains, one from the Lolo and one from the Bitterroot National Forests in Montana, grew better than local seed. Munger (1947) reported results after 20 years' growth of ponderosa pine. No systematic observation of the morphological differences in the several lots was made, but even casual comparison revealed marked differences. Some lots were bushier than others, and the color of the foliage, time of needle retention, and the angle of the needles to the twig varied. Needle length ranged from 4 inches in one lot to 7-1/2 in another. On the basis of total height on all six plantations three sources appeared to be best. These three were not consistently best on all plantations, nor were they superior in the plantations most like their locality of origin. Two lots, one from western Oregon and one from western Washington, which are considered the same physiographic region, ranked quite differently. Lorenz (1949) found differences after 5 years of growth between 10 different seed sources of ponderosa pine planted in Illinois. Major differences in color and texture of needles and slight differences in general over-all form could be observed.

Douglas-fir is an important tree in this country, and it has been widely planted in Europe for a long time. Consequently, much has been observed of its variation throughout the natural range. As early as 1913 Zon (1913) reported differences in height growth and form of plantations of different seed source planted in Europe. Since that time, as indicated by Bornebusch (1939), European foresters are very careful to plant Douglas-fir from sources known to produce seed suitable for their area. Peace (1948) discusses the literature of racial strains and the various species and varieties set up by taxonomists. As a result of his own study of the variation within the species, he states, "One is faced, therefore, with two alternatives: either to split Douglas-fir into a very large number of species or varieties, whose ranges would be completely overlapping, or to admit that the tree is a complex of variables between two extreme types approximating to the former conceptions of P. douglasii and P. glauca, and to make no attempt at further botanical distinction. The author is entirely in favor of the second alternative." In summarizing his review of the studies of racial variation in Douglas-fir, Isaac (1949) states: "Various wild strains of the tree have distinct climatic and soil limitations; seed from such strains should not be used beyond these limits. There is also ample proof that superior growing strains exist and it pays to plant the best seed that can be obtained for a given area."

Hardwood species may show racial variation throughout their natural range in this country, as indicated by a number of studies. White ash is one of them, as reported by Wright (1944). On the basis of his study of the progeny of 155 trees from 28 localities in eastern United States and Canada, grown at Petersham, Mass., white ash shows at least three ecotypes:

1. The northern ecotype, which grows from Michigan to central Pennsylvania and New England, and northward; trees are diploid, show little winter killing, have a bushy root system, and lack any pronounced pubescence or anthocyanin development.

2. The intermediate group, which is found in a narrow belt through southern Pennsylvania, northern West Virginia and Ohio, trees

are characterized by a moderate amount of winter killing, bushy root systems, high incidence of pubescence, and lack of anthocyanin development.

3. The southern ecotype, which is found from Maryland to southern Indiana and southward; trees are very susceptible to damage from winter cold, and have tap roots, reddish petioles and leaves which are glossy above and pubescent below.

Of 54 trees of intermediate or southern origin for which chromosome counts or stomata measurements were made, 33 were diploids, 8 were tetraploids, and 13 were hexaploids.

Considerable variation was found in red ash, but the variation within the progeny of any one parent was much less than in white ash (Wright, 1944a). The progeny of 20 trees from 9 localities showed the species to be composed of at least three ecotypes:

1. The northern ecotype is found in Maine, Michigan, Wisconsin, and Minnesota, U.S.A., and Ontario, Canada, and presumably throughout the species range to the north; its southern extent is unknown. Progeny were slow-growing and winter-hardy, and lost their leaves early in the autumn.

2. The southern Coastal Plain ecotype was represented by collections from Virginia, North Carolina, and South Carolina. The seedlings were very subject to winter killing, were significantly taller at the end of the second year than those of 1, and were relatively more susceptible to deer browsing than the rest of the species.

3. The New York ecotype is intermediate between 1 and 2, with respect to winter hardiness and height growth.

It is believed all ecotypes are diploid. Also, Meuli and Shirley (1937) collected seed of red ash from 83 localities in the Great Plains region and grew the seed in northern Minnesota. They found the young trees to belong to three genetically different populations. Each was distinct as to geographic range, drought resistance, growth rate, number of leaves per plant, and leaf coloring.

A biometrical study was made by Anderson and Hubricht (1938) of the leaves of sugar maple (Acer saccharum Marsh) from groves in various parts of the United States. The New England population seemed to vary about a single plexus, A. saccharum proper; those of southwestern Michigan had two almost discontinuous centers of variation, A. saccharum proper and A. nigrum Michx. f., while groves in southern Missouri and southern Illinois either resembled those in Michigan or else had no recognizable centers of variation. Wright (1949) observed local genetic variation in silver maple. Seedlings from open-pollinated seed from nine wild trees in four different localities of Indiana after 2 years showed no significant differences in height or diameter, but did show marked variation in branchiness and frost tenderness.

Black locust has been known for its variability for a long time. Inasmuch as two-thirds of all the hardwood planting in the Southern states is of black locust, it is important that seed of good source be used. Morrison (1935) and Raber (1936) describe a variety known as shipmast locust, growing on Long Island, New York, that is tall and of good form. It differs in bark, stem, and flower characters, and in the exceptional durability of wood in contact with soil. It produces very few seed, however, and is usually propagated by root cuttings. The Central States Forest Experiment Station, Schreiner (1938), started work with 22 strains in a search for strains resistant to locust borer. Minckler (1948) reported that the shipmast strain showed no superiority in growth and form to local common black locust when planted in the uplands of southern Illinois. Hopp (1941) found wide variation in the form of open-grown trees in eastern United States. He divided them into pinnate, spreading, and palmate growth forms. Two or three forms may grow side by side within short distances. A distinctive strain has been found in Randolph County, West Virginia (Anon. 1948). The trees are in scattered stands of tall, straight trees superior to others in the county. They produce seed, while the shipmast strain is very poor in this respect. They come true to seed even when grown in other localities, and have been named West Virginia locust.

In *Populus* species of various geographic origins, Pauley (1950) found marked variation between clones, which he attributes to genetic differences. Many variations concerned time of certain physiological functions, especially leaf emergence in spring and growth termination and leaf fall in the autumn. *P. trichocarpa* clones from Alaska finished growth in the latter part of August at the latitude of Boston, whereas those of southern Oregon origin remained in active growth until the middle of October. All clones of far northern origin were uniformly dwarfed when grown in the shorter day of the Boston latitude. Other apparent ecotypic variables include growth rate, branching habit, stem form, leaf and bark colors, leaf shape, and resistance to *Melampsora* rust.

Races of tree species in (or from) foreign countries.--Many provenance studies have been made in Europe and other areas because of the importance of planting in their forestry work. This is particularly true of countries that have few native species and have to import seed of other desirable species. Experience has taught that success of these plantings depends upon obtaining seed of correct provenance. It is for this reason that during recent years foresters from Australia, Sweden, Denmark, and Norway have traveled in the United States studying racial variation and individual tree variations. They hope to obtain the best stock for planting in their countries.

Scots pine has been studied for a number of years and has shown itself to be extremely variable. These studies are reviewed because of the value they might have in planning similar studies in this country. Dengler (1938) studied Scots pine of foreign provenance in the second generation. Although the source of pollen had been impossible to establish with any degree of probability, the second generation showed a good general agreement with the first, and the several races continued to differ among themselves in the characters mentioned. In addition, the second generation varied in straightness of stem, needle characters, and anomalies of bud formation. According to Dengler, Munch was unable to find evidence of acclimatization in the first generation, and according to the present study no such tendency is observable in the second. In New York, Littlefield (1939) found 5-year-old trees of Scots pine showed marked differences in height growth between trees of Belgian, Baltic, German, and Nebraskan provenance. Gavris (1939) reported on selection of rust-resistant forms of Scots pine in Russia. Seedlings grown from the seed of mother trees that produced comparatively heavy seed were relatively immune, and the degree of immunity was generally higher in seedlings with six to eight cotyledons than in those with four to five. In two lots of seed where weight of 1,000 seed was about 4,000 grams, infection was 44 and 39 percent; where weight was 5,700 and 5,780 grams, infection was 12 and 19 percent.

Lindquist (1940) describes two main races of Scots pine in Sweden: a narrow-crowned race that predominates in the north and a broad-crowned race occurring more commonly in the south. Tiebe (1940) studied specific gravity and crushing strength of the wood of Scots pine from eight countries in Europe. Frequency curves for specific gravity were constructed for a large number of samples. It was shown that the curves for individual stems were mostly the same or at least similar within a race and differed from those of other races. Two subraces occurred in both material of Scottish and Belgian provenance. Specific gravity was shown to be a function of the assimilation capacity of the crown. Heavy and light stems were found within a race. Wood from the French and one subrace of Belgian trees was the heaviest, and varied little within individual stems; that from the Brandenburg, Belgian (the second subrace), Scottish and East Prussian races was medium heavy but varied within individual stems; that from the Perm race was also of medium weight, but varied less; and that from the Kurland and Perm races was the lightest and varied little. The investigation showed that the difference in the specific gravity of wood from individual stems was not traceable to the influence of the habitat. Comparison of figures for crushing strength indicated that in spite of individual variation there were considerable differences between the races in this respect, also. Burger (1941) found differences in specific gravity between races in a test of 32-year-old Scots pine trees of different provenance grown at three different elevations in Germany. When the weight of fresh needles required to produce a cubic meter of stemwood was computed, it was found that pines of different provenance grown on the same site required different amounts of needles to produce the same increment. The density of oven-dry wood grown on the same site varied with the race. Sylven (1940) reported a latitudinal topocline in Scots pine in respect to photoperiodic response. Wagenknecht (1939) investigated a north-east, south-west topocline concerning bark; the north-east forms had a smoother bark than the south-west ones.

In the Vosges mountains in France (Anon. 1941), two forms of Scots pine have been observed. One is a mountain form and the other an intermediate one. Imported strains are grown on the plains. Jacques (1941) describes a very superior race of Scots pine found in the Forez mountains of the Central Massif. Francois (1947) describes the superior race of Scots pine of St. Die in the Vosges. It can be divided into three varieties, distinguished by different types of bark. Hess (1942) describes a gray-barked and a red-barked race. The former occupies chiefly the dry slopes of the Rhone Valley up to 1,000 meters' elevation, and is characterized by slow height and diameter growth, strong branchiness, a flat crown, and very narrow heartwood. The red race is widely distributed at elevations of 1,000 to 2,000 meters. The trees reach a height of 25 meters, and a d.b.h. of 60 centimeters, have clean boles, a pointed crown, and the stems contain wide heartwood. The growing stock often exceeds 300 cu. m. per hectare, as compared with 100 cu. m. per hectare of the gray-barked race. The gray race is fit for firewood only, whereas the red race furnishes good timber.

Schmidt (1943) gives the results of experiments, based on observations of 3 million Scots pine from all the German regions of provenance planted in 12 large plots. The various provenances were compared on the basis of sensitiveness to light, disturbances in racial development caused by climate or human agency, plant-substance production capacity, length of trunk, density of stand, resistance to needle shedding, branchiness, faulty and oblique growth, and wound-healing capacity. Meyer (1944) reported on the narrow, pointed-crowned forms of Scots pine in Prussia. Heimburger (1945) found that for direct use under the conditions at the Petawawa Forest Experiment Station in Ontario, the best strains of Scots pine are those from East Prussia, Latvia, and Poland. Rudolf (1948a) examined Scots pine plantings in the Chippewa National Forest during the winter of 1947-48, and found winter injury to foliage varied greatly according to seed origin. Trees grown from seed native to localities in the same climatic zone as the Chippewa National Forest were largely uninjured, but those grown from seed originating in milder climate had a large part of their needles killed.

Van Vloten (1949) gave results of measurements on 21-year-old Scots pine of different provenance. They reveal great differences in growth among trees of different provenance, Dutch as well as foreign. Some imported strains were equal in quality to the better home-grown strains and may be useful for selection and tree-breeding purposes. Scamoni (1950) analyzed the F_2 of artificial crosses between Scots pine of different regions and varieties. The height growth of the trees of the crosses showed in the F_2 the same behavior as in F_1. Crosses of different origins, which in the F_1 showed a certain heterosis in growth, did not maintain this heterosis in F_2, but they tended to occupy an intermediate state between the parents. The bent-stem form of the southwest German pine was dominant in crosses with the straight stem forms of east German origin, whereas the better stem form of the French pines showed an intermediate behavior.

In Europe, Austrian pine (Pinus nigra) has been found to consist of several varieties, as reported by Delevoy (1950), who analyzed sample plot data of several provenances at different stations in Belgium and found small differences in height. The Corsican provenance is somewhat the more productive on good soils, but the Austrian provenance should be very profitable on poor marginal soils.

Norway spruce has been found to have a number of geographical strains. Rubner (1941) found spruce of the plate type--having a layered crown structure because the branches of the first order extend rigidly at a right angle to the stem--growing at two localities of the Bavarian Alps. Burger (1941) gives the results of a 40-year-old plantation of spruce of two provenances grown at two locations. At one location one of the races had much better height and diameter growth, but at the other the two races showed the same increment. One test planting was at an elevation of 470 meters and the other at 1,600 meters. Bornebusch (1941) gives data for 22 years of growth of Norway spruce plots of eight provenances planted in Denmark. Minimum growth was made by the Steinkjer, Norway, provenance and was 109 cu. meters, or 5 cu. meters per year. Best was Ghuringia, Germany, 220 cu. meters or 10 per year. The Danish Grib Sko provenance is relatively late in flushing and less susceptible to night frost in spring than other strains. It is recommended for districts with comparatively severe climates, whereas for the middle regions the Ghuringian provenance is preferable, though seed of good Danish or central European provenances can also be used. Average height data for spruce of different German provenances grown at Tharandt, after 7 years ranged from 40 to 88 cm., Rubner (1944). The height growth of seed from the higher elevations was relatively less than that of seed of other provenances in the same forest area. It appears that the elevation line, dividing fast- and slow-growing races, varies for the different mountain regions, being relatively higher in the more southern mountains of Germany. There was no evidence of a gradual decrease in height growth with increase in elevation of the provenance. Heimburger (1945) found that at the Petawawa Forest Experiment Station in Ontario, the best strains of spruce were those from Valea Mare, Roumania, from northern Germany and the Black Forest, besides the progeny of selected trees of a plantation already established at the Station. Baldwin (1949) reported differences in growth of Norway spruce of a number of European provenances planted at Fox Forest, New Hampshire, in 1933 to 1938.

In studies of European larch of different seed origin, Rubner (1941a) reported on a study of a 10-year provenance trial in Germany. Seed was obtained from various regions of the Alps, eastern Sudeten country, higher and lower Latra, Poland, and Scotland. The fastest early growth was made by the Sudeten race. Larches from the lower altitudes in the Alps made good growth, those from intermediate elevations made slower growth, while those from high altitudes were distinctly slow growing. Von Wettstein (1942) found, in small-scale investigations with larch seed from different altitudes and aspects of the Gschnitz valley in northern Tyrol that seed from over 1,500 meters' elevation produced at the end of one growing season stock having on an average about half as many needles as that grown from seed from 1,300 to 1,500 meters' altitude. Seed from southern aspects produced stock having a higher dry-matter content than did seed from northern aspects. Dengler (1942) gives an account of investigations on 7- to 9-year-old trees of seven provenances of European larch. Two Sudeten provenances and one from Silesia gave the best height growth. The stem form was good in all provenances, but best in the Weiner Wald. The color of the female flowers of the two Sudeten provenances and of the Silesian and Schlitz provenances was frequently green instead of red or rose. Schreiber (1944) found differences in bark percentage and heartwood formation in local races of European larch. Auer (1946) from his studies in Switzerland found that the present results show--in addition to the unexpectedly large differences in growth, at least in youth, reported by previous workers for larches from different geographical regions--that there is a considerable variation in the increment of larches from different sites within the same general area of distribution. In general, the wider the difference in climate between the localities of origin, the more pronounced are the racial differences. Auer concludes that the species Larix decidua Mill. (L. europaea Lam. et D. C.) must be considered a very complex aggregate of varieties, subvarieties, local types and races, very closely adapted to their stations. It is impossible as yet to indicate the race that will suit a particular site in all respects. The chief conclusion is that so far as possible seed should be collected from the immediate vicinity of the area to be regenerated.

Baldwin (1949a) reported on growth of European larch after 4 years of growth at Fox Forest, New Hampshire. Seed from 47 sources in Europe were planted. Indications are that seed collected at the higher elevations and at the colder localities in the lowlands resulted in slower growing plants than those from medium elevations in central Europe. Seed from Poland and medium elevations in Austria and Czechoslovakia have so far exhibited the most rapid growth. In Wales, Varma (1949) found that the race of European larch, called Darnaway, from Scotland, proved to be the best, and the race from Inn Valley, Austria, the worst. He found the length of branches is a morphological character which distinguishes the race; the angle of branching does not. Height growth is also a racial character and may be used to separate races under similar soil and vegetation conditions. There are significant differences between provenances in respect to straightness of stem and liability to lose the leading shoot.

Of maritime pine, Duff (1928) reviewed the varieties and geographical forms in Europe and South Africa. Perry (1940) recognized four races: (1) Landes (French Atlantic coast), (2) Portuguese (forests of Leiria and Marinha Grande), (3) Corsican, and (4) Esterel (Esterel and Var regions, southern France, or Lucca in northern Italy). Under western Australian conditions the Portuguese strain is faster growing than any others, exhibits particularly good form, and is now being planted almost exclusively. The strain designated as Esterel has not only a very slow rate of growth but also poor form. The Portuguese race is superior to others when planted in South Africa, according to Rycroft and Wicht (1947). Plantings were made in 1934 to 1936 with six races.

Laurie (1936) discussed seed origin and its importance in Indian forestry. He reported (1938) four different types of branching seen in teak plantations and the probability of their being due to hereditary factors. It appears that varieties arising from seed from dry localities may have considerably exaggerated characteristics when raised in damper and more favorable conditions. He emphasized the necessity for ascertaining that the seed comes from a good origin when making teak plantations. Sen Gupta (1941) also discussed the importance of seed origin in teak. For ease of establishment and early development, it seems that seed of local origin is superior to that of distant origin within the natural range of teak, but it is probable that for growth, form, timber quality, branchiness, and crop increment per acre, different origins will show trends independent of their early behavior. Kadambi (1945) reported it has long been observed by forest officers in Mysore that teak seed from the Kabakote (moist) district of Mysore, when used in plantations, produces stunted, relatively low, branchy trees with a relatively large number of insect galls. Trees of this origin are also more susceptible to defoliator attack, shed their leaves earlier, and sprout later than do those of Shimoga (Mysore, dry) origin. Teak has been raised in Trinidad from seed imported both from southern India and Burma; seed from the latter source provides much the better growth under the prevailing conditions (Beard, 1943).

A considerable amount of selection and breeding has been done with poplars in the United States and abroad, because of its value as a pulpwood species. The status of this work has been summarized in an excellent manner by Pauley (1949), including the results of selection. Selection of desirable variants and races has been carried on in Sweden (Lindquist, 1948). In France two races of Populus tremula have been described by Silvy-Leligois (1949). One is a mountain race which grows on well-drained slopes, and the other a plains race which grows on the valley bottom and even in the river. The mountain race is straight and well formed, with large, smooth leaves, and shows early and active self-pruning. The plains race is inclined to be crooked, with flattened crown, small leaves often tomentose on the lower side, and dead branches that often persist for a long time.

A Glossary of Genetic Terms[1/]

Allelomorph--Mendelian characters are inherited in alternative pairs (or series). These alternative forms of a gene, which are located at the same point on each one of a pair of chromosomes, are called allelomorphs. Examples: Albinism (recessive), normal pigmentation (dominant); horns (recessive), hornlessness (dominant). Allel, allelic (adj.)--variants.

Amphimixis--The union of maternal and paternal elements in gametic fertilization. See apomixis.

Apomixis--Reproduction in which the sexual organs, or related structures, take part, but in which there is no fertilization, so that the resulting seed is of vegetative nature. See amphimixis.

Backcross--Cross of a hybrid to one of the parental types.

Biotype--A group of individuals all of one genotype.

Blending inheritance--Inheritance in which dominance of either parental character is lacking. Genetic and biometrical methods have shown that this is due, in many cases at least, to the interaction of several multiple factors independently inherited.

Character (a contraction of characteristic)--A term used, often rather vaguely, to designate any form, function, or feature of an organism. The mendelian characters of genetics represent the end product of development in which a definite gene, or genes, have a decisive effect. The constant and unchanging thing, therfore, is the factor (gene) itself rather than the character, and the unity which Mendel observed lies rather in this underlying factor than in the visible, and perhaps variable character, which it produces.

Chromosomes--Dark-staining bodies visible under the microscope in the nucleus of the cell at the time of cell division. The chromosomes carry the genes, lineally arranged, which control the development of mendelian characters.

Cline--A pattern of genetical variation in which the differences of a character or characters are graded in a definite direction of geographic space.

Clone--A group of organisms composed of individuals propagated vegetatively, not by seeds, from a single original individual.

Cytoplasm--The protoplasm of a cell exclusive of the nucleus.

1/ These terms have been adapted from the glossaries in U. S. Department of Agriculture Yearbook for 1936 and Forest Tree Breeding and Genetics, by Richens; also from the Dictionary of Genetics, by Knight.

Dihybrid--An individual from a cross between parents differing in two genes or differing in two specified genes.

Diploid--Having two chromosome sets only.

Dominant--A character possessed by one of the parents of a hybrid, which is manifested in the hybrid to the apparent exclusion of the contrasted character from the other parent (the recessive). Thus in a cross of green- and yellow-seeded peas the first generation has yellow seeds. Yellow is dominant and green is recessive, being transmitted but not appearing in the presence of the factor for yellow.

Dysgenic--Tending toward racial deterioration, in particular toward a loss of vigor and productiveness.

Ecocline--The graduations of variation produced within a species by its reaction to the different ecological zones in which it occurs.

Ecospecies, ecotype--A distinct race resulting from the selective action of a particular environment. More strictly "ecotype" is "used as an ecological sub-unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat" and "ecospecies" is "the genotype compound narrowed down to the ecological combination limit."

Eugenics--The science which deals with influences that improve inborn or hereditary qualities of a race or breed, especially of the human race.

F_1--The first-generation offspring of a given mating.

F_2--The second filial generation. The first hybrid generation in which Mendelian segregation occurs. Produced by intercrossing or self-fertilizing the F_1. F_3, F_4, etc., denote later generations from a given cross.

Factor--A unit occupying a fixed chromosomal locus and governing, or affecting, the transmission and development of a heritable character; gene.

Factor-pair--Allelomorphs.

Form--A subdivision of a botanical variety distinguished by some minor character. In systematic botany, forms are represented by quadrinomial Latin names.

Gene--The unit of inheritance which is transmitted in the germ cells, and which by interaction, with the genic and cytoplasmic complex and the environment, controls the development of a character. The genes are supposed to be arranged lineally in the chromosomes.

Genetics--The science of heredity, variation, sex determination, and related phenomena.

Genotype--The entire genetic constitution, expressed and latent, of an organism. The term can also be used in dealing with the genetic constitution of an individual with respect to any limited number of genes under examination. A group of organisms all with the same factorial constitution. (See phenotype)

Genotypes, number of--The number of distinct genotypes expected in F_2 is given by calculating 3^n where N is the number of factor-pairs involved. In a backcross, the number of genotypes is 2^n.

Haploid--Having one chromosome set only.

Heritable--Capable of being inherited.

Heterosis--The manifestation in a hybrid of a degree of vigor superior to that exhibited by either of the parents.

Heterozygous--Containing both genes of an allelomorphic pair, or two genes of an allelomorphic series. Heterozygous individuals usually either resemble the individuals homozygous for the dominant character or are intermediate with respect to this character. They transmit the recessive gene to half their offspring.

Homozygous--1. [An organism] formed by like germ cells. 2. An organism is said to be homozygous for a given character when all its germ cells transmit identical genes for this character. This is the most frequently used meaning of the term.

Hybrid--The offspring of two parents unlike one another in one or more heritable characters.

Interspecific selection--Selection which operates to improve the competitive power of one species in relation to other species, as distinct from intraspecific selection, q.v.

Intraspecific selection--Selection which operates as between individuals within a species, as distinct from interspecific selection, q.v.

Mass selection--Selection of a group of superior individuals for breeding purposes. The progeny are not kept separate according to individual female parents.

Mendel's law--Mendel enunciated three basic principles of heredity: (1) Inheritance of character determiners (genes) as allelomorphic units, not as a blend; (2) dominance; (3) independent random segregation of allelomorphs in the formation of gametes and their random recombination at fertilization. As a consequence of these conditions, a given allelomorphic pair of unit characters appears in a certain definite predictable ration (3:1; 1:2:1; 1:1) among the progeny of a given mating.

Mother tree selection--Selection of mother trees without controlling the pollen parent. The progeny are kept separate by individual mother trees.

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Multiple factors--Two or more pairs of factors having a similar supplementary, complimentary, or cumulative effect. In a broader sense, any factors working together to produce a single result.

Mutant--An individual which has suddenly acquired a heritable variation not present in the parent form, and, by extension, the offspring of such an individual as "mutant race," "mutant strain."

Mutation--A sudden variation that is later passed on through inheritance, and that results from changes in a gene or genes.

Ortet--The one original plant from which a clone ultimately derives.

Phenotype--The organism as exemplified by its expressed characters, as contrasted with its genetic constitution (the genotype).

Phenotypic--Appertaining to the physical makeup of an organism or group of organisms as distinct from their genetic makeup. The phenotypic effect of any particular gene on an organism is its outward measurable quantitative or qualitative effect on that organism.

Polybrid--A group name for hybrids from crosses between two particular species, varieties, or genera.

Polygenic character--A character whose inheritance is controlled by many genes each having an effect which is small compared with nonheritable variation.

Polyploid--Having more than two sets of chromosome (see diploid and haploid).

Population--A group of individuals among which interbreeding and gene exchange can occur.

Provenance--Place of origin.

Pure line--A strain of organisms that is genetically pure (homozygous) because of continued inbreeding or self-fertilization, or through other means.

Race--A naturally occurring variety.

Ramet--An individual member of a clone.

Recombination--The rearrangement of linked genes due to crossing-over.

Roguing--Elimination of unsatisfactory plants in selection.

Segregation--Separation of the genes of a pair in the formation of germ cells, the two genes going to different gametes. Segregation is manifested in the F_2 (and later hybrid generations) as a separation and distribution to different individuals of the Mendelian characters in which the parents of the F_1 hybrid differed.

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Selection--The choice (for perpetuation by reproduction) from a mixed population of the individuals possessing in common a certain character or a certain degree of some character. Two kinds of selection may be distinguished: (1) natural selection, in which choice is made automatically by the failure to reproduce (through death or some other cause) of the individuals who are not "fit" to pass the test of the environment (vitality, disease resistance, speed, success in mating, or what not); and (2) artificial selection, in which the choice is made consciously by man, as by a plant or livestock breeder, for characters of value to man.

Sport--A mutation; an abrupt deviation from type.

Strain--A group within a variety which constantly differs in one or more genetic factors from the variety proper.

Subspecies-- The subspecies or geographic race is a geographically localized subdivision of the species which differs genetically and taxonomically from other subdivisions of the species.

Topocline--A cline in respect of topographical factors.

Trait--A term often used as a synonym of "character."

Variant--An organism differing slightly from the type.

Variation--In biology, the occurrence of differences among the individuals of the same species or variety.

Variety--A group of strains or a single strain which, by its structural or functional characters, can be differentiated from another group. They are usually represented by trinomial Latin names.