SELECTION AS A METHOD OF TREE BREEDING[1]

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One objective of tree breeding is to provide trees of better genetic quality. The speed with which the breeder can do this is a good measure of his effectiveness. Therefore, he is inclined to produce new combinations of traits with just as few manipulations as possible, regardless of whether the traits come from individual trees, races, varieties, native species, or introduced species. The tree breeder is more anxious to make use of the opportunities that present themselves, irrespective of the method of breeding or combination of methods, than to follow each classical method, such as tree introduction, selection, hybridization, or polyploid breeding, to the complete exclusion of the others. The more he can work with familiar or local trees, varieties, or species the more certain he can be that some important undesirable traits will not interfere with his plans.

The South is very fortunate in that a fairly wide variety of genetic stock is available in various species, races, and individual trees. This might be called the hope of the tree breeder and the despair of the silviculturists. It is the hope of the breeder because he can create innumerable combinations of traits for various specialized strains without having to worry much about introducing undesirable ones. It is the despair of the silviculturist because no two trees are alike.

In order to appreciate how easy it is to introduce undesirable traits along with a foreign tree species or a hybrid of a native and non-native species, just add up sometime all the factors of soil fertility, soil moisture, temperature, temperature changes, insect pests, disease pests, day length, length of growing season, windstorms and competing vegetation under which southern pines grow fast, reproduce well, and produce a large number of valuable products. A different species or species hybrid, to be more valuable, would have to excell in many traits and have no really poor traits.

Genic action can affect morphological, physiological, or chemical traits. *We* can't do the optimum job in single-tree selection, hybridization, or racial selection, including

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analysis of progeny test data of any kind until we can define variation within species fairly well for all the southern tree species. It is up to the tree breeder and geneticist to make use of the skills of various specialists, such as wood technologists, pulp and paper technologists, plant plysiologists, and others to work on various traits. These people are competent in their fields of work, but need advice on how to work on the tree breeders' problems.

Forest genetics research need not be dictated by tree breeders, but it should be made to serve applied tree breeding, We have made studies in such fields as soils, botany, physiology, silvics, wood utilization, and others serve silviculture. Forest genetics should be no exception.

We should all make an effort to see that no gap exists between our basic forest genetics research and research in forest tree improvement or in applied forest tree breeding by research people or industry. Certainly it is profitable to seek out the basic laws with which we are to explain relationships, but we can exercise considerable judgment to choose the subject fields in which we want to search for "laws" and in the choice of tree species or other material with which we work. People other than foresters are concerned with the relationship between fields of research, as you will note from the following excerpt from the report of the Twentieth Century Fund by August Heckscher, Director (1961):

> " Of the responsibility of research in contribution to action I would speak in somewhat more detail. The discouraging fact seems to be that research is becoming increasingly divorced from deeds. The social sciences seem to have taken over from the natural sciences the old idea that any addition to human knowledge is of itself a boon, regardless of its seeming pertinence or relevancy. A new fact is expected to come in handy, like the missing piece of a jigsaw puzzle, when it is most needed, The trouble is, of course, that in the world as it actually exists, with its imperious necessities and its huge accumulation of books and surveys, the isolated fact is apt to remain isolated. Having been given no life or destiny by its first begetter, it is all too unlikely ever to be given life by another. It dies within its own solid covers, too remote or detached to influence the rapidly moving stream of events. Research which disavows any responsibility except that of being objective and nonutilitarian may well qualify as pure but it is a kind of purity which a society--particularly a society in an age of change--can overvalue."

When a man of the stature of Glenn I. Seaborg--physicist and chancellor of the University of California--in his report as Chairman of the Panel on Basic Research and Graduate Education of the President's Science Advisory Committee (1960) makes a statement like the following

Table 3. Average Survival, Height and DBH of Ten-Year-Old Loblolly Pine by Seed Origin and Planting Locations

Origin of seed	Planted within native range a/			Planted outside native range			
	Alabama, Jefferson County	Alabama, Marshall County	So. Carolina, Union County	Arkansas, Newton County	Illinois, Hardin County	Tennessee, Anderson & Union Counties	Kentucky, Marshall County
				Survival, percent			
Atlantic Coast:							
Maryland	77	8	73	58	53	79	16
South Carolina, lot 2 b/	79	4	58	10	73	90	31
Virginia	71	10	69	65	49	76	56
North Inland:							
Alabama	94	61	94	75	63	95	88
Mississippi	75	46	66	75	59	67	56
Tennessee	94	73	67	92	85	87	60
South Inland:							
Alabama	96	62	94	73	79	93	68
Georgia	96	67	90	96	89	94	78
Mississippi	83	19	73	72	71	81	31
				Average height, feet			
Atlantic Coast:							
Maryland	27	22	24	26	20	26	17
South Carolina, lot 2 c/	26	25	28	20	19	29	18
Virginia	31	19	25	28	20	26	20
North Inland:							
Alabama	30	23	25	28	21	30	22
Mississippi	29	24	23	28	22	27	20
Tennessee	29	20	23	27	24	27	18
South Inland:							
Alabama	29	24	24	26	20	27	20
Georgia	28	23	23	28	23	28	18
Mississippi	29	20	24	27	21	26	14
				Average DBH, inches			
Atlantic Coast:							
Maryland	4.6	5.6	4.8	5.3	3.6	4.5	3.4
South Carolina, lot 2 d/	4.0	4.8	4.8	3.5	3.1	4.4	2.9
Virginia	5.4	4.6	5.1	5.5	3.7	4.3	3.4
North Inland:							
Alabama	5.2	5.1	5.4	5.8	4.1	5.4	3.6
Mississippi	5.2	5.3	4.9	5.5	4.2	4.8	4.0
Tennessee	5.2	4.6	5.0	5.7	4.5	4.8	3.6
South Inland:							
Alabama	5.0	5.6	4.9	5.3	4.0	4.9	3.8
Georgia	5.0	5.1	4.8	6.0	4.2	5.1	4.0
Mississippi	5.2	4.8	4.8	5.7	3.8	4.7	2.2

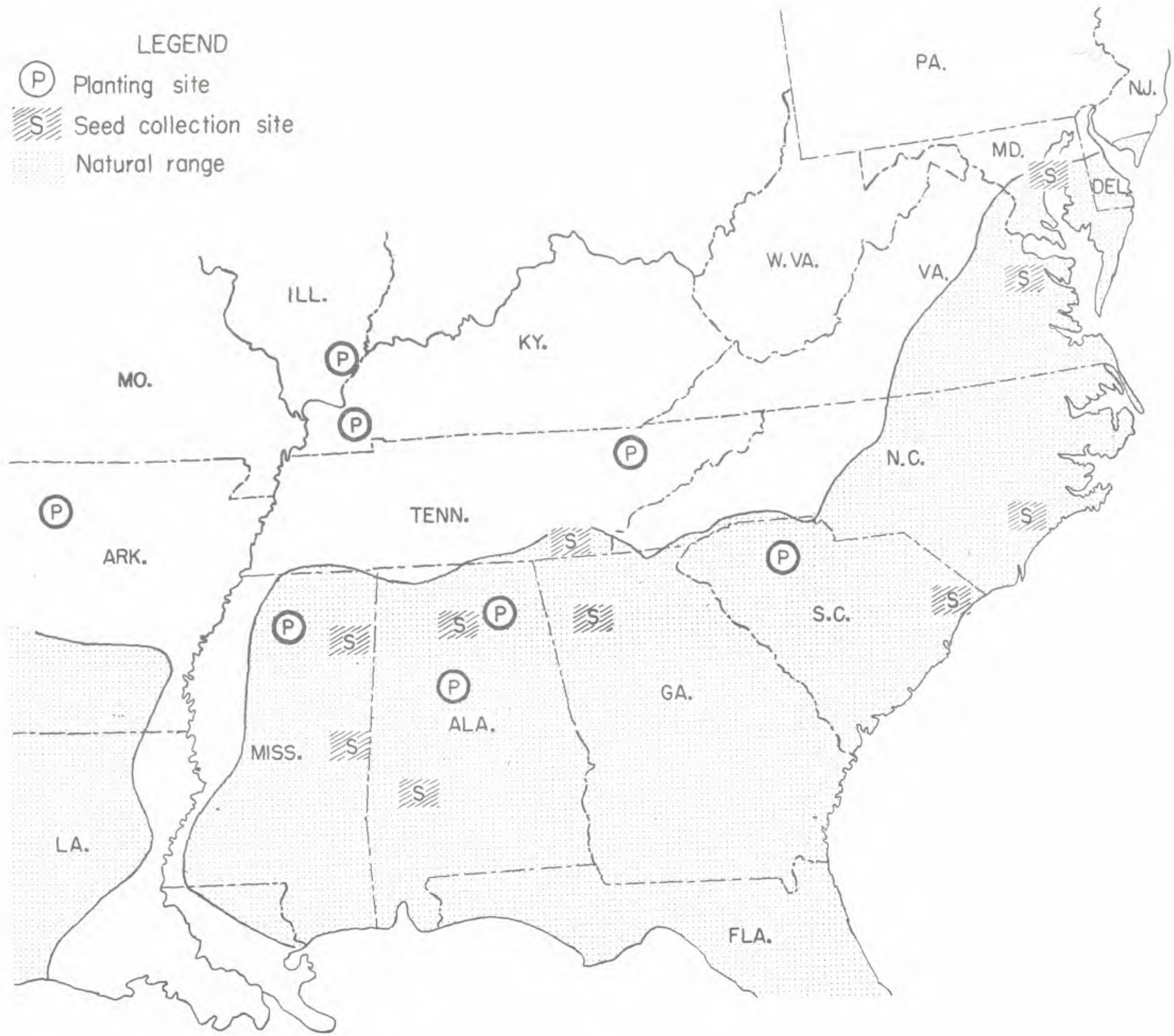
a/ Excludes the planting in Lafayette County, Mississippi, which was dropped as a failure after 5 years.

b/ Eighth year survival. The original planting from North Carolina seed failed and was replaced the following year by South Carolina seed lot 1 which also failed. The South Carolina seed lot 2 planting was established in the winter 1951-1952.

c/Adjusted to 10-year heights; average 8-year heights were four-fifths of the values shown above.

d/ Adjusted to 10-year DBH; average 8-year diameters were four-fifths of the values shown above.

FIG. 1 COOPERATIVE LOBLOLLY PINE SEED SOURCE STUDY



we should pause to consider it. He says, "Because basic research is aimed at understanding rather than at practical results, the layman sometimes assumes that it is entirely abstract and theoretical, and that only when it becomes a matter of industrial development does it 'come down to earth'." This is a false notion, and its falsity becomes increasingly clear with time. Indeed one striking characteristic of our scientific age has been the disappearance of the barriers between pure and applied science." Later in the same section he says, "Part of the strength of American science stems from close intellectual intercourse between basic and applied scientists. . . . We do not believe in any artificial separation between basic and applied research or between science and engineering. The fact that a scientific advance is useful does not make it unscientific."

The alternative to research in the more important fields of forest genetics with important tree species is work in unimportant fields or with unimportant species. We don't need to go overboard and everyone work on the same problems, It would be ridiculous for all of us to work on variation and inheritance in slash and loblolly pin. It would be equally ridiculous for all of us to work with holly, Chinaberry, or Arizona cypress. However, everyone should take the responsibility for directing his own work to make it effective.

With the objective of service to the tree breeders and silviculturists in mind, the work of the geneticist is often simplified because the subject fields and the species are more accurately delineated. If we accept the fact that genetics is the study of variation and inheritance, then we can pursue studies in these fields with the most important species at different locations. This may seem a narrow definition, yet it is the type emphasized in many publications. The 1936 Yearbook of Agriculture defines genetics as: "The science of heredity, variation, sex determination, and related phenomena." Crane and Lawrence (1952) in their book, "The Genetics of Garden Plants," state: "The study of uniformity and variation, of resemblances and differences between plants and the frequency in which the characters constituting these resemblances and differences appear from generation to generation is the business of the geneticist." Andrews, Warwick , and Legates Rice et al (1957) in their book, "Breeding and Improvement of Farm Animals," say that genetics "can be defined as the science which seeks to explain the resemblances and the differences which are exhibited by related organisms." Montagu (1960) in his book, "Human Heredity," says that "genetics is the branch of biology concerned with the manner in which inherited differences and resemblances come into being between similar organisms."

Since species, racial, and individual tree variations are of such great importance to the tree breeder, strong effort should be directed toward their study. In the southern pine, particularly the major ones, species differences are fairly well defined. Studies of geographic variation are under way in the major southern pines as well as racial variation studies

Racial variation studies in the South are, in many cases, racial selection studies also, since races of trees are grown under various conditions in which they could be planted on a commerical scale. Numerous studies of variation between individual trees have been made as well as studies of inherent variation. A great many more are needed, however, particularly of wood quality and physiological traits. If we don't select for a trait, we may in our ignorance of variation, select against it.

The one thing that held up study of within-species variation is the mistaken belief that it could be done only with sexually produced or vegetatively produced material. In other words, progeny tests or clonal tests were required. This is, of course, true if we are measuring hereditary variation; and measuring hereditary variation is very important, but it is only a part of the problem. By definition (Yearbook of Agriculture, 1936) variation is: "In biology, the occurrence of differences among individuals of the same species or variety." Rice et al., (1957) in their book on animal breeding quote this definition also. Allard (1960) in his book, "Principles of Plant Breeding," defines variation as: "The occurrence of differences among individuals due to differences in their genetic composition and/or the environment in which they were raised." Hayes, Immer, and Smith (1955) in their book, "Methods of Plant Breeding," discuss variation in connection with methods of plant breeding. So does Lerner (1958) in his book, "The Genetic Basis of Selection," Montagu (1960) defines variation as: "The occurrence of differences in characters; Discontinuous variation, graduations of differences are perceptible in the phenotype; Continuous variation, graduations of difference are imperceptible in the phenotype." Other authors use "qualitative" and "quantitative" rather than "discontinuous" or "continuous" to describe the two types of variation.

The important thing about the definitions of variation is that little if anything is said about variation being only hereditary variation or that it has to be determined by clonal or progeny tests. Allard specifically states variation is influenced by genetic composition and/or environmental factors, The basis for studying variation between plants in place is well established.

Selection and hybridization within species, as a method of tree improvement, is being used extensively with southern pines in breeding specialized varieties and in our clonal seed orchards. Based on the studies of variation and the heritability data obtained to date, some of which will be discussed in the following papers this afternoon, the rewards will be impressive. To me, this means we should hit hard by using selection and within-species hybridization as a method of breeding for still other traits, and we need to refine our techniques in breeding for traits which are now included in breeding plans. This simple breeding method is a "bird in the hand" so to speak. More elegant methods of breeding can be attempted later.

Undoubtedly, clonal and progeny tests give valuable data on variation and inheritance, and we have to have this information, but tests are slow and tests are expensive. Because they require a lot of space, rarely can they include test trees with a large number of different traits that may occur in a species. Also, to be most useful and productive, they should be based on information about variation so that the selection of traits to test is good and the design of the study is adequate, especially in regard to plot size and number of replications. In other words, to be good the progeny tests should be based on some of the data that they are now being designed to produce.

Studies of variation should be made in a logical sequence to be of the most help in applied breeding. We need them first for the economically important species at different locations over the South. We need studies of important traits of high utility and we need them for waste products, such as bark and lignin. It is common practice in research circles to make a study of a certain subject using one or two species. After the results are reported the tendency is to not follow up with more detailed studies or other species because it would seem to be repetitious. From the standpoint of forest genetics research it might be sufficient to show that trees in fairly uniform stands vary in certain traits. From the standpoint of the tree breeder, this is not adequate, because he wants to know the range of variation in each of a large number of traits, for each species, under some different environmental conditions, particularly on different sites. This is a job for research people, but in the past, most of the data on variation and inheritance has come from applied breeding projects instead of the fundamental or basic research projects.

Studies of variation can be planned to progress in an orderly manner, increasing in cost and precision as the subject merits. Probably the most simple is to sample or measure trees under conditions where most of the factors thought to affect the trait are held as nearly constant as possible. For example, we could work with trees of the same diameter, height, and crown class in a uniformly spaced, even-aged stand on a level site where the understory is nonexistant or very uniform, It is true that this measures phenotypic variation, but it is variation where the environmental effects are as small as it is possible to make them, If no variation of economic importance is found, it certainly would not encourage anyone to test for it further in different environments or with clonal or progeny tests. If the trait does vary widely, however, additional study is warranted. This could be done with trees of different size on the same site, or then, in other studies, with trees of different sizes on different sites. If variation is still present and can't be explained by measurable environmental factors, and it occurs in economically important traits, clonal tests and others with sexually produced progeny are warranted to give information needed in seed orchard or applied breeding work. As stated earlier, these methods of studying variation put the physical effort and cost in studies where the most precision and most useful results to silviculturists and tree breeders are needed. There is little point in studying environmental effects or inheritance of traits that don't vary.

Figures on variation and inherent variation are important in many fields besides selection. Their importance in silviculture, wood technology, wood utilization, insect research, disease research, and forest survey is obvious. They are important, too, in planning interspecific and intraspecific hybridization and in analyzing and interptreting progeny test data from this work. A knowledge of variation within various species is of vital 'importance in carrying out geographic variation, racial variation, and racial selection studies.

Some work could be done profitably in the field of biometrics in developing methods of studying variation, and interpreting as well as reporting the results. Statistical methods should be made to serve the geneticist and the tree breeder, not the reverse. This means that methods of study used should be those that apply to southern trees and the products of southern trees, and the results should be expressed in terms that not only are understandable but useful to the tree breeder. We need to study genetic variability as well as genetic plus environmental effects. So far, silviculturists haven't been able to grow trees without an environment of some kind. Thus we must have data on the sum of both factors.

We should remember that the silviculturist does not grow only one trait of a tree or just average trees; he has to grow the whole tree and the below-average and above average trees as well, He can't tell which tree is which until they have grown awhile. Therefore, the trees that aren't average in various progeny groups or populations need to be defined as well as the average. This is useful data. Falconer (1960) in his book, "Quantitative Genetics," deals with population data of different kinds and shows how to present it with frequency distribution curves.

In the gum yield progeny test at Lake City, Florida the interim results of which were reported by Mergen and others (1955) , the average gum yield of three progeny groups of plus trees after wind pollination was about 25 percent more than that of average trees. If, in a thinning, the average and below-average trees in gum yield in a population were marked, about 60 percent of the trees would come out. The gum yield of the remaining stand of trees of this size, however, would be about 75 percent, instead of only 25 percent, above that of average trees. For gum yields, the shifting in yield level of this magnitude, through silvicultural treatment, is possible because of the wide range in gum yield within progeny groups. Yield per individual tree of below 50 grams to over 450 can occur within a progeny group and is the result of genetic plus environmental factors. If the spread for a trait is less, silvicultural treatment would be less effective but still could be important. Thus, population data, trait by trait, is important for offspring of various types of mating. The man with the marking gun may become the most important "selector" of all where traits are inherited in a quantitative manner.

Industrial and public foresters, and particularly those in charge of seed orchard projects and nurseries, should keep pressure on geneticists and tree breeders to give them the kind of research data they need. Often there is a difference between what dirt foresters need and what researchers think he dirt foresters need. Most researchers are nearly human and can be reasoned with so that such contacts between people can be productive.

The silviculturist needs help with his problem of computing cost in relation to returns. Costs are difficult to determine in some types of free breeding work, but we can probably do better than we do now. Also, the silviculturist can be reasonable in asking for cost data because the sky seems to be the limit when it comes to the way various companies are organized and the way costs: and returns can be figured. Although it is difficult for researchers to figure the returns from a new method, it may be equally difficult for silviculturists to justify not making a change. For example, seed production areas obviously will not produce the ultimate in improved strains, but the geneticists and tree breeders don't know what the ultimate is nor do they know when they will produce it. In the meantime, foresters should do the best they can to obtain seed of good genetic quality. No one can say how much better is the seed from seed production areas than average or below-average seed that may be obtained from other sources, because no two seed production areas may be alike, but it is highly probable that it is better than what is being used now, and this is the important point. There is a lot of southern pine seed being used every year that doesn't come from good trees, to say nothing of the best trees. I realize there are problems, but I don't think they are all unsolvable for every individual, for every situation, in every state, for every species. The use of seed production areas is a way that selection pressure can be applied now. Seed from seed orchards of various types can be used when it becomes available. In the meantime we can do the best we can to keep seed quality high. Seed from one poor-formed southern pine tree may produce enough seed to plant 20 to 30 acres. Can tree planters afford to deliberately plant stock of poor genetic quality? The sum total of bad genetic traits plus bad environmental factors visible in some plantations of southern pine is shocking.

We should never underestimate the ability of researchers to make simple things complicated. Often this is merely the result of searching after details so that the main points become lost in mass of material, but sometimes we get carried away by the opportunity to work around the periphery of a problem rather than concentrate on the heart of it. If we continue to concentrate on studies of variation and inheritance in southern trees, use simple, effective methods to actually breed for better combinations of traits, and raise the genetic level of seed used to establish new stands, the forest geneticists and tree breeders in the South will have carried out their responsibilities well. The results of their work can then be defined in terms of trees as well as words.

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