Juvenile-Mature Tree Relationships

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The best criterion for selecting geographic races, progenies, or individual trees will be their performance record based on periodic measurements from the time of planting through rotation age. Many years and great expense will be required to obtain this record. Our present individual tree selections are based on performance at maturity, which is a very valuable record in genetic evaluation, but these selections must be tested to reaffirm their superiority if this degree of accuracy is required. Tree breeders have recognized the opportunity for and have written much about speeding up this testing process by predicting mature tree performance from juvenile performance. Little concrete evidence has been presented yet to show the exact nature and strength of juvenile-mature tree relationships, but records being made now of juvenile performance in progeny tests will soon provide valuable information on them.

The objectives of this paper are: (1) to discuss briefly the problems presented by juvenile selection, i.e., how the stages of plant growth affect the reliability of juvenile evaluation, and (2) to outline some of the current information on juvenile-mature tree relationships for the southern pines.

The Problem

The Stages of Plant *Growth*

Sax (1958) has divided the stages of plant growth into embryonic differentiation, juvenile development, maturity, and old age. Excepting the end of embryonic development, there are no clear-cut distinctions between successive stages, and all parts of the plant do not change from one stage to the next simultaneously.

The existence of these stages in trees and shrubs has not always been recognized, and there are instances in taxonomy where mere juvenile forms have been erroneously elevated to specific or varietal status (Schaffalitzky 1954). Cuttings from plants in the juvenile stage typically root and graft more easily than cuttings from older plants (Schaffalitzky 1954, Sax 1962). Generally, trees and shrubs are sterile during juvenility, although some species and individuals within other species produce flowers as early as 1 or 2 years (Greene and Porterfield 1963). The wood near the pith of the tree has been variously referred to as "juvenile wood" or "core wood," and its properties differ from those of wood produced farther from the pith (Zobel et al. 1959). We are all familiar with the S-shaped height-growth curve and its typical trend during the years immediately following establishment.

Obviously, the stages represent varying physiological processes in the life of the tree. Many different gene complexes control these processes, and their expressions are in turn affected by environmental variations.

Reliability of Juvenile Evaluation

There are numerous factors affecting the reliance that we can place on the evaluation of juvenile performance. Among these are (1) the number of progenies being tested in relation to the accuracy required, (2) the strength of the offspring-parent heritability estimate, and (3) the age at which expression of a particular trait is critical.

Number of progenies in relation to *accuracy required.—Numerous* statistically significant differences among progenies and seed sources have been reported for embryonic and juvenile characters, such as embryo size (Vincent 1957), height growth (Wakeley 1961), rooting habits (Snyder 1961), photosynthetic rate (Reines 1963), and dry-matter content of needles (Schmidt 1957). However, sufficient time has not elapsed to allow many of these differences to be related to meaningful values near harvest age.

Furthermore, a statistically significant juvenile-mature tree relationship is not necessarily a useful one. If a small number of progenies are being compared for juvenile performance, a higher degree of accuracy is required and mere statistical significance may not be strong enough. However, if a large number of progenies are being compared, a statistically significant juvenile-mature tree relationship can be used but with the realization that some poor progenies will be accepted and some good progenies rejected.

Strength of offspring-parent *heritability.—Squillace* ' suggested that " . . . if parent tree evaluations are available, including good controls, such information can and should be used in genotypic evalu-

, Personal communication from A. E. Squillace, Apr. 29, 1963.

ation as well as juvenile performance." For traits exhibiting a strong offspring-parent heritability, careful measurements made on mature parent trees can add greater reliability to the evaluation of juvenile performance within 10 years or so after planting.

Age of *expression.-Certain* traits are critical during the juvenile stage and can be evaluated then on the assumption that they will exhibit a strong juvenile-mature tree relationship. Resistance to drought, brown spot, and fusiform rust are examples of such traits. Height growth and many other traits are expressed over a much longer period and will require continued scrutiny.

At this point, the true value of juvenile performance may be stressed by coining the phrase "juvenile rejection and mature tree selection." The juvenile performance of progenies and races is an integral part of a test. If a progeny or race does not perform well for traits critical at an early age, then it can be eliminated quickly from further costly consideration.

But what are the risks involved in using juvenile performance to predict traits critical at a later age? Many of us are faced with making decisions that cannot wait for the 20-year results. A review of current information on some traits may partially answer this.

Current Information

Current information on juvenile-mature tree relationships will be discussed primarily from the standpoint of evaluating progenies or groups of individuals rather than selecting individual trees within progenies. Callaham and Duffield (1963) postulate that "juvenile-mature correlations in height growth (of ponderosa pine) may be quite significant for predictions of growth of progenies but not for predictions of growth of individuals within progenies." This will probably be true for other traits as well as height growth.

For the purpose of this discussion, most of the traits in which we are interested can be grouped into two broad classifications: those affecting volume per acre, and those affecting wood quality.

The variables affecting volume per acre are:

1. Height
2. Diameter breast height
3. Form class
4. Competitive ability
   a. Photosynthetic efficiency
   b. Crown form
   c. Root competition
5. Disease and insect resistance
6. Drought, heat, and cold resistance

The variables affecting wood quality are:

1. Straightness
2. Specific gravity
3. Tracheid and fiber lengths
4. Cellulose content
5. Percent summerwood
6. Self pruning
   a. Branch angle
   b. Branch diameter
   c. Number of branches
   d. Photosynthetic efficiency
7. Oleoresin yield

Volume Per *Acre*

Height growth.-The juvenile-mature tree relationship for height growth has received more attention than any other characteristic, but an exact relationship has not been established. Numerous juvenile-mature correlations have been reported for height (table 1), but r' provides a gauge for

TABLE 1.—*Juvenile-mature correlations for height*

Material studied	Authors	Ages correlated	r[1]	r^2	n
Races:					
Ponderosa pine	(Squillace and Silen 1962)	2-30	0.85	0.72	10
		3-30	.75	.56	10
		4-30	.48	.23	10
		5-30	.65	.42	10
		6-30	.69	.48	10
		11-30	.86	.74	10
		20-30	.86	.74	10
Scotch pine	(Schreiner et al. 1962)	2-13	.61	.37	25
European larch	(Genys 1960)	4-12	.74	.55	36
Progenies:					
Slash pine	(Squillace[2])	8-14	.79	.62	8
		8-14	.82	.67	8
Individual trees:					
Slash pine	(Barber 1961)	1-7	.53	.28	1058
		2-7	.72	.52	1058
		2-8	.67	.45	1433
		3-8	.78	.61	1433
Ponderosa pine	(Callaham and Duffield 1963)	12-20	.83	.69	--
		12-20	.75	.57	--
		12-20	.65	.42	--
		12-20	.67	.45	--

[1] All values of r are significant at the 1 percent level except those for progenies, which are significant at the 5 percent level.
[2] Squillace, A. E. Unpublished data of the Southeast. Forest Expt. Sta. on file at Olustee, Fla. April 1963.

the reliability which can be placed on these correlations. Although the correlation coefficients are statistically significant, the amount of the variation in mature height which is accounted for by juvenile height is still relatively small. Some of the authors cited presented several correlations at different ages but only the earliest ages showing a significant juvenile-mature tree relationship are given.

Dorman has expressed the opinion that the length of time required to reach a height equivalent to two logs (i.e. 32 feet) may provide a usable compromise for some purposes to long-term evaluation of height growth and tree quality. By 8 to 12 years the tree has attained a height which will represent a majority of its final volume. This will probably be more applicable for short-rotation predictions than for sawtimber, although there seems to be no generally accepted rotation age for southern pines.

Personal communication with Keith W. Dorman April 29, 1963.

Diameter breast height.—Although differences in diameter growth are significant among young slash pine progenies, evaluation cannot be considered reliable until after the base of the crown has progressed above 4.5 feet and crown competition has begun.' Squillace ' reported correlation coefficients of 0.72 and 0.96 between d.b.h. at 8 years and d.b.h. at 14 years for slash pine progenies. These were significant at the 5 and 1 percent levels respectively (df = 6).

Form class.—I have found no references that mention the juvenile-mature tree relationship for form class, absolute or Girard. Certainly absolute form class will mean little until crown closure has been in effect for some time, and measurement of Girard form class should be delayed until the base of the live crown is above the first 16-foot log.

Competitive ability.—Competitive ability is a composite character, and it will be difficult to ascribe to it a juvenile-mature tree relationship. Yet, it may eventually be possible to relate competitive ability to maturity with demonstrated juvenile differences among progenies in photosynthetic rate (Reines 1963; Wyatt and Beers') and crown form (Barber; Trousdell et al. 1963). Root competition will be one of the most complicated and difficult components of competitive ability to determine. Unless differences in rooting habits of seedlings can be related to mature tree performance, root competition cannot be practically evaluated.

Disease and insect resistance.—Southern forest geneticists are interested in combating diseases and insects that are critical early in the life of the tree; e.g., fusiform rust, brown spot, and tip moth. Because they are critical in the juvenile stage, the mature tree performance may be relatively unimportant.

In contrast, littleleaf disease usually does not appear until a later age. Although Zak (1961) found differences in susceptibility of loblolly and shortleaf seedlings to Phytophthora *cinnamomi* Rands, his laboratory tests have not yet been related to actual field performance.

Drought, heat, and *cold resistance.—Resistance* to drought, heat, and cold are among the characteristics which are critical during the juvenile stage. The short-term approach can be taken to test the ability of progenies to become established in spite of drought, heat, and cold. However, testing for growth rate under adverse conditions, especially drought and heat, will probably require the long-term approach.

Of the variables affecting volume per acre, the very important factors of resistance to certain diseases and insects and to drought can be evaluated at an early age, if the proper environmental conditions exist.

Wood Quality

There is more room for optimism in early testing for wood quality than is presently evident for volume per acre. The ability to correlate wood produced in early years with mature wood has provided an excellent opportunity to establish reliable relationships.

Straightness.—Perry (1960) reported striking differences in straightness and crook among loblolly pine progenies as early as 2 years in the field. Barber ' found the same to be true for slash pine up to 8 years of age. However, for all the southern pines, straightness probably can be evaluated best on young trees around 30 feet tall, representing ages from 8 to 12 years. As mentioned with respect to height growth, this height is the first two 16-foot logs, and represents a major part of the volume of the tree. If a tree is straight up to around 30 feet, it will very likely continue to be straight to maturity. However, slightly crooked trees may smooth out and apparently become straighter by eccentric growth with resulting compression wood.

Specific gravity.—The juvenile-mature tree correlation for specific gravity is complicated by the presence of compression wood in seedlings. However, Brown and Klein (1961) found highly significant differences in specific gravity among 2-year-old seedlings of loblolly pine produced by crossing various combinations of high and low specific gravity parent trees. These seedlings reflected, to a high degree, the specific gravity of the parent trees. Zobel et al. (1960) reported highly significant correlations between juvenile or core specific gravity at breast height and the specific gravity of whole loblolly and slash pine trees. Forty slash pines showed a correlation coefficient of 0.798 and 14 loblolly pines showed a correlation of 0.890, both being significant at the 1 percent level. Together, these results indicate that a rough screening of progenies for specific gravity can be carried out on young seedlings, and a fairly accurate evaluation of specific gravity in progeny tests can be obtained at about 10 years of age.

Tracheid length.—Kramer (1957) presented data on loblolly pine that strongly discouraged the use of breast height tracheid length at two or three rings from the pith for evaluating the tracheid length of the mature tree. He suggested using the 10th or a later ring from the pith to denote the tracheid length of a particular tree. This means that progeny tests should be at least 10 years of age before any rough screening for tracheid length is attempted. Preferably, tracheid lengths should

Barber, John Clark. An evaluation of the slash pine progeny tests of the Ida Cason Callaway Foundation (Pinus elliottii Engelm.). Ph. D. Diss., Univ. Minn. 206 pp., illus. 1961.

' Squillace, A. E. Unpublished data of the Southeast. Forest Expt. Sta. on file at Olustee, Fla. April 1963.

Wyatt, W. R., and Beers, W. L., Jr. Growth chamber analysis of wind-pollinated plus tree progeny—slash pine **(P.** elliottii Engelm., var. elliottii). Unpublished manuscript. 1963.

Op. cit.

Ibid.

be measured from several rings to account for year-to-year environmental variations.

Cellulose content.—For the present use of tree improvement, the complex field of cellulose chemistry can be divided into water-resistant carbohydrates and alpha cellulose. These are two important constituents used to characterize wood chemically in pulp and paper manufacture (Forest Biology Subcommittee 1960). There was a significant correlation between water-resistant carbohydrates in the core wood zone at breast height and water-resistant carbohydrates for the whole tree (Zobel et al. 1960). However, the relationship between core wood alpha cellulose and alpha cellulose for the whole tree was consistently non-significant. This indicates that a rough screening for high producers of water-resistant carbohydrates might be attempted at 10 years of age, but evaluation of alpha cellulose must be delayed until later.

Percent summerwood.—Measurements of percent summerwood during the juvenile stage have little meaning because of the erratic and poorly defined summerwood in the core wood zone (Zobel et al. 1959). The seventh or eighth ring is probably as early as this characteristic can be meaningfully measured, and measurement should extend over several rings. Consequently, evaluation of a progeny test for percent summerwood will have to be delayed until 12 or 13 years of age.

Self-pruning.—Self-pruning is another complicated composite character, and the juvenile-mature tree correlations of its components are still uncertain. Photosynthetic efficiency was mentioned earlier. It is very obvious in the field that 3- to 7-year-old progenies differ widely in branch angle, diameter, length, and number of branches (Barber;" Trousdell et al. 1963). This may be the best age to evaluate these traits, but their exact relationship to self-pruning remains unknown. The existence of an auxin gradient is suggested by Barber's report" that certain slash pine progenies begin to show self-pruning well before crown closure. This is further indicated by the results of VanHaverbeke and Barber (1961) showing that branches bent to a horizontal and to a downward position showed 50 percent less elongation than branches left in their normal upward position.

Oleoresin yield.—Oleoresin yield is included under wood quality because it is closely related to certain anatomical variations. A micro-chipping method, developed for determining oleoresin yield on young trees, shows heritabilities of yield ranging from 45 to 90 percent based on 14-year-old progenies (Squillace and Dorman 1961). Results should soon be available to show the relationship between yield at various ages according to this micro-chipping method.

Summary

Selection for mature characteristics on the basis of juvenile performance cannot be as accurate as selection based on the mature tree. Yet, indications are that certain time-saving and essential information can be obtained from juvenile development. The fact that plants pass through different stages of growth affects the reliability that we can place on juvenile performance. In comparing a small number of progenies, a strong, accurate juvenile-mature tree relationship is needed, but a weaker relationship can be successfully used in screening larger numbers of progenies. Characteristics exhibiting a strong offspring-parent heritability can be selected for or against fairly soon, and other characteristics that are critical at an early age can also be evaluated at an early age.

Current information on factors affecting volume per acre indicates that resistances to certain diseases and insects and to drought, which are critical at an early age, can be evaluated during the juvenile stage. Other components of volume per acre such as height, diameter, form class, and competitive ability will require scrutiny for a longer period of time.

Of the variables affecting wood quality, the very important traits straightness and specific gravity offer encouragement for testing on the basis of juvenile performance. Other traits, such as tracheid length, cellulose content, percent summerwood, self-pruning, and oleoresin yield, will require evaluation at 8 to 10 years of age or later.

Ibid.
Ibid.