How Much Is Forest Genetics Helping the Forester by, Increasing Growth, Form, and Yield?

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Today we are beginning to measure the increased yields from forest genetics, and we now have a basis for estimating the gains expected in the future. Until recently the principles of forest genetics had been consciously practiced very little, but good silvicultural practices incorporate many of the basic principles. Thinning from below, seed tree cutting, and shelterwood management are examples of practices that should leave the best formed, fastest growing trees for the regeneration of future stands. The recent developments in forest tree improvement have served to make foresters consciously aware of the importance of considering the individual tree in addition to species and race with the future in mind. We realize that we have to maintain a positive selection pressure to avoid retrograde. We have also become much more aware of the importance of individual traits in the ultimate use of the tree and recognize the intrinsic characteristics of the wood itself. We are learning how important characteristics like straightness can affect pulp quality and how small differences in specific gravity can mean important differences in pulp yield and in yield per acre.

Wakeley (1954) has shown that the choice of the wrong geographic source of seed can be disastrous in terms of growth and disease resistance. Perry and Wang (1958) have translated these volume differences into monetary values to demonstrate that we can afford to make large investments in controlling our seed to prevent the use of wrong sources. There are numerous similar references covering various species, but let us leave geographic origin with the assumption that good land managers are going to use the best geographic source available; they will be using local seed when they do not have reliable data on which to base their selection of geographic source of seed. For the remainder of this paper, I will be speaking with reference to individual trees and local stands.

We haven't begun to realize many of the gains from our tree improvement work, but the material we are now planting and using from seed production areas and, on a limited scale, from seed orchards is earning its way in added growth and quality that will be havested in the not-too-distant future. In fact, the Ida Cason Callaway Foundation sold for pulpwood last winter the rogues from a seedling seed orchard established in 1955. This is probably exceptional, but it does show that we don't have to wait a lifetime to see some of the fruits of our labors.

The available data on growth, form, and quality of individual trees and progenies are limited to rather young age classes. Charlie Webb will tell you how confident we can be in projecting our juvenile data and using them as a basis for selecting our best trees and progenies. With some degree of conservatism, here is some current information and what I think we might realize based upon it.

Growth

Squillace and Bengtson (1961) reported heritabilities of 8 to 16 percent for height and 29 to 58 percent for diameter in 14-year-old slash pine. I have calculated ' heritabilities of 20 to 30 percent for height and 6 to 34 percent for diameter in l- and 8-year-old slash pine progenies.

There are numerous reports in the literature of significant differences among open and control-pollinated progenies of our southern pines. Considering only the older of this material, we see differences of 10 to 20 percent among means for both diameter and height. If we use a selection differential of the top 5 percent of a stand (2.06 standard deviations) and apply a heritability of about 30 percent for height and diameter, we can expect our future crop to exceed the present stand average by about 10 percent. So you see, we can translate our present knowledge into a rough figure to show what we might expect in the future by immediate control of seed source. Gain heritability x selection differential, thus both, are of great importance. As you realize, our selection level for seed orchard clones is much higher than mentioned and though the heritabilities may be slightly lower when applied to selections in natural stands, we can expect greater increases in growth-

[1] 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.

possibly up to 12 or 15 percent in height and diameter.

In the first selection cycle from natural stands, the selection differential can be at a maximum for all traits because we have the entire population to choose from. In subsequent cycles of selection, we will be selecting from progenies of only a few hundred trees at most and will be limited in the selection differential that we may use.

Our data on the southern pines is supported by studies in several other species. Callaham and Hasel (1961) have estimated heritability of height growth from 15-year-old ponderosa progenies of about 39 percent. These progenies averaged about 26 feet in height. Toda (1958) has reported broad-sense heritabilities of 68 percent for height and 58 percent for girth in Cryptomeria from seedling (42 years old) and vegetatively propagated (39 years old) trees. He concluded that where vegetative propagation could be used, selection of the top 1 percent of the stand would show gains of 17 percent in height and 28 percent in girth. In another study, Toda et al. (1959) worked with 20-year-old progenies of *Cryptomeria* averaging 26 feet in height and found narrow-sense heritabilities of about 26 percent for both height and diameter. He also worked with some data from Europe on Scots pine and found a narrow-sense heritability of 24 percent for height.

Form

One very interesting aspect of form is the proportion of the wood produced by a tree that is in the stem where it can be harvested. Fielding (1953) determined the volumes of several Monterey pines by trunks and branches. Two of his trees were almost identical in total volume (9.59 and 9.75 cubic feet), but one had 48.9 percent of its total volume in the trunk and the other 62.6 percent—a difference of about 1.5 cubic feet or 28 percent more stem wood in one tree than the other. As we select for smaller, shorter limbs we may also select for a higher proportion of total wood in the stem.

Bob McElwee will give you the details of wood quality, but I want to mention the part that some aspects of form play in the production of compression wood. Zobel and Haught (1962) reported a study made of loblolly pine compression wood. There are two important aspects to their work, the effect of stem straightness on the production of compression wood and the compression wood associated with knots. Their "straight" trees had about 6 percent compression wood, the "average" trees had 9 percent, and their "crooked" trees about 16 percent. These differences are not only statistically significant—they are meaningful. Mergen (1955) reported on the inheritance of crook in controlled crosses of slash pine where he found 76 percent of the offspring from one parent were crooked. Perry (1960) has reported similar data on loblolly pine resulting from crosses made among crooked parents. He obtained 88.5 percent crooked trees when both parents were crooked and 51.8 percent when both trees were straight. Reversing these figures, we see that the straight trees produced more than four times as many straight progeny.

McWilliam and Florence (1955) discussed stem form of slash pine in Australian plantations. Using "routine seed" from the best 160 crop trees per acre as their control, they found that open-pollinated progenies of selected trees contained twice as many acceptable trees. Controlled crosses among selected trees produced four times as many as "routine seed." The best open-pollinated progenies produced 7 to 10 times as many plus trees per acre. The best control-pollinated progenies produced 20 to 25 times as many plus trees. These trees were picked at a lower level of selection than we are using in our seed orchard programs; consequently, we can expect substantial improvement in stem form.

Open-pollinated slash pine progenies at the Callaway Foundation varied from 30 to 90 percent crooked stems at 7 and 8 years of age.' These were subjective ratings but very critical. Many of the stem deviations considered as crook or sweep will probably be masked by eccentric stem growth with its associated compression wood before the trees reach harvest age.

From these few studies we can see the opportunity for improving stem form to produce straight logs, poles, and other products. The accompanying reduction in compression wood will improve pulp quality and reduce problems in drying lumber.

As mentioned earlier, Zobel and Haught (1962) reported on the compression wood surrounding knots. They found that each knot was surrounded by an approximately equal volume of compression wood. Here we have the opportunity to reduce not only the size and amount of knots but at the same time to reap the benefits of a parallel reduction in compression wood.

Many foresters are inclined to think that stand conditions are of primary importance in determining branch size and limb retention. Undoubtedly, stand conditions are very important in controlling crown length, but sampling of natural stands or plantations of our southern pines will show great variation in branch size and number in trees of the same crown length. Our data on the inheritance of branching characteristics is limited because most of our progeny test are relatively young and have not had an opportunity to exhibit these traits under closed stand conditions. I have already mentioned Fielding's (1953) work on the relative volumes of stem and branches which emphasizes the importance of branching habits.

Kiellander (1957) showed that branching and quality in spruce could not be controlled entirely by plantation spacing. Finely branched trees planted at 4.9 feet retained their good branching and quality while a course source planted at 3.9 feet

[2] Ibid.

remained course branched and of poor quality. Fielding (1960) has described the number of whorls as highly heritable in Monterey pine, and they appear not much influenced by site.

Detailed crown examinations of seven 25-year-old slash pine trees in a plantation in Georgia showed that the average basal area of branches varied more than 100 percent from the finest to the coarsest.' A similar range was found among their open-pollinated progenies, but data were too limited to establish a reliable parent-progeny regression. Differences in crown width from 39 to 51 percent and heritabilities of 16 to 19 percent have been reported in slash pine (Barber 1961). Squillace and Bengtson (1961) reported heritabilities of crown width in slash pine of 12 to 48 percent. Trousdell et al. (1963) have recently published data on crown differeneces in 7-year-old loblolly pine open-pollinated progenies with heritability estimates of 17 to 34 percent. Although we cannot translate these differences into dollars or quantities harvestable at maturity, we can expect the gain in form to represent appreciable value not only to the manufacturer of primary products but also to the landowner in increased volume and value and to the harvesting crew in reduced labor for limbing.

Yield

These differences in growth and form add up to increased yield in quantity and quality. Also, improvement in wood quality and disease and insect resistance will add further increases in forest productivity.

Let's translate some of our height and diameter values into volume. In Queensland (1962) the best crosses among slash pine gave 30 percent more volume at 10 years and showed a "substantial superiority in stem straightness." Squillace and Bengtson (1961) reported volumes among 14-year-old progenies of 6.0 to 8.4 cubic feet; the fastest growing contained about 40 percent more volume than the slowest. From these data they estimated heritabilities of 31 percent from control-pollinated material and 18 to 35 percent from open-pollinated progenies.

Peters and Goddard (1961) arrived at an estimate of heritability of "vigor" in slash pine. This was the ratio of progeny superiority in height to parental superiority in volume. Based on controlled crosses and open-pollinated progenies, they arrived at a heritability of 15 percent.

Fielding and Brown's (1961) report on tree-to-tree variations in health of Monterey pine and response to fertilizers showed very sharp contrasts in growth and response. They worked with both seedling and clonal material. At 15 years they had clones varying in height from 20 to 50 feet and with foliage color differences; each clone was characterized by its own vigor state and set of systems. These sharp differences in site adaptability certainly reflect important selection criteria and point the way to greater gains where site extremes are encountered.

Working with 7- and 8-year-old slash pine data (Barber 1961) and using an approximation of cubic-foot-volume [cubic foot volume = (d. b.h.)' (ht.) (0.002315)1, I have found that the faster growing progenies average about 2 times the volume (0.41 to 1.21 cubic feet; 0.87 to 1.59 cubic feet) of the slower growing ones. If calculated on total plot volume, the range would have been greater because the faster growing progenies had the better survival, resulting in more trees per plot.

Toda (1958) has been very optimistic about the values to be achieved with selections of Cryptomeria. He calculated that selection of the top 5 percent of seedling trees, when propagated vegetatively, would increase volume by 43 percent. This was based on increases of 8 percent in height and 15 percent in diameter.

I will mention specific gravity only briefly. There are numerous references on variation and inheritance of specific gravity (Dadswell et al. 1961, Goggans 1961, Van Buijtenen 1962, Thorbjornsen 1961, Zobel 1961). Heritabilities are quoted from about 20 to 70 percent, depending upon material examined and methods used. Squillace et al. (1962) calculated values of 21 to 42 percent among open-pollinated material and 56 percent for controlled crosses. Let us assume a heritability of 30 percent—this means that we can expect yield increases of 4 to 6 percent simply by confining selection to the top 20 percent of our stands.'

Now let us add to this the increase in yield and quality associated with the reduction in compression wood. By appropriate selection, we might improve the straightness of our trees to achieve a reduction in average compression wood of as much as 25 percent. I am sure we would be hard-pressed to place a value on this, but if compression wood is important, then such a reduction should be meaningful.

Oleoresin yield is another factor I've not previously mentioned. This is the trait about which we have the best data arrived at from breeding. Squillace and Dorman (1961) summarized this work recently and reported heritabilities of 45 to 90 percent for the trait. They used an average heritability of 55 percent to calculate estimated gains with various methods and levels of selection. If a selection level of 200 percent average yield was taken, then their open-pollinated progenies would be expected to yield a gain of 27 percent. In a clonal seed orchard, proven 200-percent yielders should give progenies with a yield 100 percent above average. In the case of a seedling seed orchard based on 9 F_1 clones from crosses among 200 percent proven high yielders, the expected increase would be 152 percent or 2 1/2 times present yields. They also projected yields for a seed production area using the top 10 percent from a stand

[3] Ibid
[4] Data of the Southeast. Forest Expt. Sta. on file at Macon, Ga.

of 300 trees per acre. These seedlings should reflect an increase of about 30 percent for this one trait.

Toda (1956) has introduced the possibility of increasing total yields by increasing the number of trees per acre. He calculated that a 17-percent decrease in crown diameter would permit 50 percent more trees per acre, and though they may grow slower as individuals, the gross yield would be higher.

Discussion

Now how can you use this information? There are several ways, depending on the management programs for your forest holdings and whether you have or contemplate having an active tree improvement program as such. No matter what your situation, you can put certain principles of forest genetics into action.

Let's consider the situation of the landowner who uses natural regeneration. He can begin by paying particular attention to the trees that will produce the seed for his new stand. He should remember that his new stand may be established several years before he makes his final cut and adjust his marking rules to insure the elimination of all undesirable parents before regeneration becomes established. This landowner can expect to make appreciable improvement in only those traits that can be readily evaluated by ocular estimate. He can select for straightness, growth rate, form, and possibly disease resistance. In some situations he may be able to make a crude selection for oleoresin yield. It is not now practical to make quick screenings for the various wood quality traits. If he uses the shelterwood method, he may be selecting at a level equivalent to the top 5 to 10 percent of the stand. Of course, he is limited to the particular stand on the site, but gains can be appreciable.

The first step for those land managers who use some form of artificial regeneration is the establishment of seed production areas in the best stands they have. This will provide seed requirements for the immediate future and will serve on a continuing basis or until seed orchards have been placed into production.

The availability of stands for conversion to seed production areas determines how effective the program may be. Those of you who have tried to find suitable stands with sufficient trees meeting requirements such as those of the Georgia or South Carolina Certification Standards know that these stands are rare and difficult to locate. Where these top quality stands are not available we must still take the best we have and work with them. We would probably all agree that our "best" stands are much above those from which the majority of State and commercial seed are usually obtained when purchasing cones from unrestricted collectors. We have here a real opportunity to upgrade the genetic quality of our seed by converting our best stands to seed production areas and realizing the gains from limiting the parentage to the top 5 to 10 percent of the stand. Easley (1963) in a first report on growth of trees from loblolly seed production areas, has found a height superiority of 17 percent above controls at 5 years on a sandy site and 27 percent on a clay site.

We must realize that the amount of gain for any single trait is going to depend upon its heritability and the selection differential used. As we add additional traits to our selection criteria, the selection level at which we work for each trait must be reduced sharply if we are to retain sufficient trees for seed production. As an example, if we wish to retain only trees that are within the top 10 percent of the population for one trait, we could keep an average of 1 out of 10. When we go to the second trait and select at the same intensity, we could keep 1 out of 100, assuming traits are independent. The third trait drops it to 1:1,000 and the fourth to 1:10,000. This means that where more than two traits are involved we must reduce our standards or have too few trees remaining for practical use. If we lower our standards of selection to maintain sufficient trees for efficient seed production, then we sacrifice some of the gain we might have achieved from a single trait. To many people, the standards for individual trees on seed production areas seem rather liberal, but when you consider height, diameter, straightness, branching, natural pruning, and pest resistance, you find a reason to remove most trees.

For single traits we might expect appreciable gains from seed production areas, such as the 30-percent increase in oleoresin yield calculated by Squillace and Dorman (1961) for selection of the top 10 percent. Other individual traits, such as height and diameter, might produce gains of 5 to 10 percent, but when several traits are considered we must sacrifice part of the gains possible for each because of the limited population and area concerned.

With immediate seed needs stop-gapped by seed production areas, and recognizing their limitations, the next step for a land manager is the seed orchard. He must project his needs to determine what characteristics are important to his goals and then draw up selection criteria to evaluate plus-tree selections. The same rules of probability apply here where many traits are rated, but the individual tree may be found anywhere without regard for frequency per unit area. Clonal establishment of an orchard means that a broad spectrum of selections may be assembled to interbreed freely—each parent possibly representing the best among many thousands of trees. Each parent must be tested to insure that it will transmit the desirable traits for which it was selected and that it does not transmit any undesirable trait.

When these clones have been tested and the poor ones rogued, we will be producing seed that should eventually yield appreciable gains in several traits simultaneously. I believe we can conservatively think in terms of increased volumes of 10 to 15 percent, gains in specific gravity of 4 to 6 percent, and reduction in compression wood of several percent. Add to this increased quality value for straightness, form, and pruning, further increased yield achieved by disease resistance and improvement of other wood quality traits, and you can recognize the worth of an aggressive tree improvement program.

I expect someone to raise the question of which type of orchard to use—clonal or seedling? Both have merits—I do not believe there is any single answer. We have recommended both. Quickly, I might say that seedling orchards are somewhat cheaper to establish, but remember that parent selection costs the same and control pollinations on widely scattered trees are expensive and time consuming; at least 3 years are needed after selection to get seedlings in the field and by then you could have 2- or 3-year-old grafts. My observations are that clonal orchards will "flower" earlier and more abundantly than seedlings of slash and loblolly pines. Seedling slash pine orchards planted in 1955 by the Callaway Foundation have produced no "flowers." Clonal orchards established by the Georgia Forestry Commission since then have been "flowering" well for several years.

Possible inbreeding (selfing) in clonal orchards has been raised in objection, but the effects may be low. In seedling orchards, we have the risk of mating the full-sibs and half-sibs, but less risk of selfing. The effect of this is unknown. Where the usual 6 to 10 traits are rated, we have the problem of probabilities in seedling orchards. How many trees per acre will we have left if we keep only the top 10 percent for each of six or more traits—hardly enough to recognize the area as a seed orchard. In clonal orchards we select the parents at whatever level we wish without particular concern, for the probabilities or frequency of occurrence per unit area or per unit of population.

Theoretically, the idea of seedling orchards is good when considering a limited number of traits and when juvenile-mature correlations are high. Practically, the idea is sound under similar restrictions and it has a place—but when time is of essence, I personally prefer to place the added investment in clonal orchards. However, until we have seedling orchards established on at least a pilot-plant scale, we will not be able to make a sound comparison with the extensive clonal orchards now beginning to produce seed.

In closing, let us look at the values Perry and Wang (1958) placed on seed of varying yield potentials. A meager 2-percent increase in yield over a 25-year pulpwood rotation is equivalent to $18.93 per pound of seed when used in the nursery for seedling production. A 10-percent yield increase would amount to $90.63 in value per pound of seed; a per acre per year yield increase of $1.05. These values are what we can afford to spend to improve our seed. We cannot afford to lag any longer. We should be aggressively pursuing our tree improvement programs now.