Genetics in Wood Quality Improvement

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The incorporation of genetic principles into a forest management program can be, and has been, justified for one or a combination of several different reasons. The papers already presented on this panel have developed ideas which show that genetic principles applied to management of forest lands will produce tangible gains in the form of increased growth and yields. By the application of tree improvement principles, including use of properly adapted seed sources, additional benefits can be gained by increasing volume and improving form of trees. The speaker immediately following me will show how increased benefits can be derived through reduction of losses to diseases and insects.

In this paper I shall attempt to emphasize benefits derived from a genetically oriented forest management program through improving the quality of wood produced. Other speakers have stressed improvement of yields of wood per acre but have not been primarily concerned with the anatomical characteristics of the wood or the overall benefits that can be gained from the control of the wood quality.

Benefits gained through improvement of wood quality are not of a type that can be credited back to forest management in the same manner as can an increase in yield. Evaluation of benefits to be gained from wood quality improvement is based on higher value of the end product. Final evaluation of benefits must be made by mill technologists and chemists rather than by foresters; thus, the responsibility of determining the direction and kind of wood quality improvement must be shared both by those who grow the trees and by those who convert them into the final product.

Methods of Achieving Improvement

Tree improvement practices for use on commercial forests have varied from judicious marking rules on areas to be restocked naturally, through seed production areas to seed orchards. For significant improvement in wood quality, very little can be accomplished below the level of seed orchards; this method is the only one through which sufficient control of the wood quality of parents and progeny can be feasibly determined and maintained. Selective marking for natural regeneration or seed production areas does not afford the opportunity to find desired qualities in large enough percentages of stems to achieve significant improvement.

This shortcoming can perhaps best be illustrated by a hypothetical situation in which it is desired to improve one wood characteristic, specific gravity, through the use of seed production areas. For simplicity, assume that it is desired to increase specific gravity in the next generation of trees obtained from the seed production area. It has been found that specific gravity is distributed normally among the individuals of the stands from which the seed production area has been established; thus, about 50 percent of the trees in the stand would have less than average specific gravity. Experience has shown that few of the remainder will have suitable form and growth, leaving too few trees with both desired wood and desired form to make an adequate seed production area. The difficulties of achieving desired goals in improvement of wood characteristics through seed production areas are thus limited. This example concerns only one property; if a second criterion is added the rigor of selection is increased several fold, and significant improvement of wood quality through means less intensive than a seed orchard becomes much more difficult.

Seed orchards, the most commonly applied breeding method, contain only individuals having the desired wood properties; however, this is always within the framework of the features of fast growth and good form. Each additional wood characteristic included results in a manifold increase of the difficulties of locating seed orchard material. However, the benefits to be gained outweigh these difficulties if wood quality is of any importance to manufacturing operations and quality control of the final product.

Measurement of Improvement

Wood properties, as other characteristics, vary in their expression among individuals. This variation is the result of the genetic makeup of the individual and the action of the environment on the genotype.

The genotype is defined by Johannsen (1911) as the reaction norm and is the modification of expression set within the limits of the genotype. This simply means that most characteristics of the individual, including wood characteristics, are controlled to some degree by the genetic makeup of the individual. Additionally, all environmental modifications influencing expression of the characteristic operate within the framework of this genetic make-up.

The magnitude of the genetically determined limits can be expressed mathematically by use of the term *heritability,* which is a numerical expression falling between 0 and 1. The exact value for any characteristic indicates the degree to which variation is received from the parents; thus, a heritability of 1.0 means that the expression of the characteristic is determined entirely from the parents, the environment playing no part in the expression. A heritability of 0 connotes that the characteristic is governed entirely by the environment, inheritance having no influence.

Heritability is but one part of the "equation" necessary to determine genetic gain, the other being the selection differential. Genetic gain in the final analysis is the factor which expresses the amount of improvement possible. Care must be exercised in discussions involving heritabilities; some of the points to be considered have been pointed out by Zobel (1961) as:

1. What type of heritability is being referred to? Broad sense heritabilities are those which include all of the genetic variances (additive, dominant, and epistatic) normally present in biological material. It is impossible to take advantage of all three types of heritability in forest trees unless working with clonally propagated trees such as the hybrid poplars.

Narrow sense heritabilities are derived using only additive genetic variances. Most wood properties in which we are interested are inherited quantitatively (several genes are conditioning the inheritance of a particular characteristic). Trees having the type of wood in which we are interested demonstrate the possibility of having the capability of producing the wood quality sought. By allowing many such individuals having this capability to interbreed in the seed orchard, we enhance the opportunity to produce trees having the desired wood quality. The amount of improvement in wood quality is partially determined by the narrow sense heritability for the particular wood property.

2. To what age material does the heritability apply? Heritabilities change as plants get older. A characteristic may have high heritability at a young age and be lower nearer maturity of the tree, or the converse.

3. Under what environmental conditions were the heritabilities estimated? Heritabilities will differ for the same plant material under different environmental situations in which it might be planted.

4. How was the heritability estimated? Several methods of estimating heritability are available, which may give considerably different estimates.

Statistical procedures for determining heritabilities are complicated and beyond the scope of this paper, but results (i.e., the heritability figures) will be cited as indication of genetic control. In general, the characteristics considered to be of importance to wood quality improvement have heritabilities within the range of 0.2 to 0.7.

Heritabilities are not the same for each wood property in which we are interested, and improvement possible in one character will be different from another character using the same breeding procedure in a given period of time. In an improvement program for wood quality, it behooves the forester to work with production technologists to decide which characters are most important to the finished product, as well as develop a system of priorities allowing most rapid progress toward achieving improvement.

Amounts of Improvement Possible

The following discussion will emphasize heritability estimates in pines, principally the southern pines; these estimates will be used as indicative of possible genetic gain.

Specific gravity.—Much interest has centered on improvement of wood qualities by varying specific gravity. Such improvement has been approached in three ways: (1) increase in average specific gravity, (2) decrease in average specific gravity, and (3) no change in the average out elimination of the extremely high and extremely low gravities. Such manipulation of specific gravity is needed to increase quality of pulp, such as tearing strength, bonding strength, or burst, or to provide a more uniform raw material for production of a more uniform end product. Table 1, based upon the

TABLE 1.—*Heritabilities of specific gravity of certain species of pines*

Species and progeny	Broad sense heritability	Narrow sense heritability	Source
Slash pine:			
14-year open-pollinated seedlings		0.2	Squillace et al. (1962)
14-year control-pollinated seedlings		.5	Do.
12- to 14-year grafts	0.7		Do.
Monterey pine:			
20-year grafts	.5		Fielding and Brown (1960)
6-year open-pollinated seedlings		.2	Do.
8-year grafts	.7		Dadswell and Wardrop (1960)
Grafts (rings 7 and 8)	.7		Do.
Loblolly pine:			
1-year grafts	.2-.6		van Buijtenen (1962)
5-year grafts	.6-.8		Do.
2-year control-pollinated seedlings		.4- .5	Do.
6-year open-pollinated seedlings		.6-1.0	Do.
Core wood—open-pollinated seedlings 5 years old		.8	Goggans (1962)
Core wood—open-pollinated seedlings 2 and 3 years old		.7	Stonecypher [1]

[1] R. W. Stonecypher, personal communication.

results of several different workers, emphasizes the high degree of heritability of this complex character.

The average for all of the above heritabilities is around 0.7 for broad sense and 0.5 for narrow sense. The heritabilities are for young trees, and indications are that they may increase in older material so that narrow sense heritabilities are approaching the broad sense values. Assuming a differential in paper yield of 25 pounds per cord for each increase of 0.01 in specific gravity, 90 pounds green weight (Taras 1956), selection for higher specific gravity can increase paper yields from 25 to 80 pounds per cord of wood cut, the amount of the increase depending upon the selection differential employed in the selection. Assuming the moderate increase of 40 pounds of paper per cord for all the wood used, a 400-ton-per-day paper mill would realize an annual increase of 4,200 tons of paper using no greater volume of wood.

Increase in specific gravity is attained principally by an increase in the percent summerwood growth of the annual ring and an increase in the cell wall thickness of the individual tracheids. Such properties are not consistent with an increase in certain qualities; for example, increasing specific gravity will increase tearing strength but reduce bursting, tensile, and folding strength (Watson and Dadswell 1962).

It is unfortunate that certain factors of cell and tree anatomy which contribute to higher weight yields may also contribute to a reduction in quality of the paper produced. It is in this realm of determining where the balance will be made between gross fiber yield per cord and quality of product that mill technologists must aid in decisions influencing tree improvement programs.

Tracheid length.—A second important wood property for products which is under strong genetic control is that of tracheid of fiber length. This characteristic is important in the areas of strength properties of both pulp and paper.

Many authors have reported tracheid length of progenies to be intermediate between those of the parents; these include Chowdhury (1931), Jackson and Greene (1958), and Echols (1955). However, there are few reports of actual heritabilities for this characteristic. Dadswell et al. (1961) found gross heritabilities for tracheid length to be about 0.75 in *Pinus* radiata and Goggans (1962) obtained an even greater value in the narrow sense for *Pinus* taeda. High heritability for tracheids will produce rapid progress from selection resulting in an increase of the mean fiber length. By including only long-fibered parents in the seed orchards, it is possible to obtain an increase up to one-half millimeter in the first generation of selection.

There is little reason to believe that short fibers per se will ever be desirable, since bonding strength is an asset to any product. It is possible to produce short tracheids in the mill—thus, it would appear that in the future longer fibers and tracheids will be sought. For fiber length, as well as for specific gravity, the objective is to improve the average for the characteristics. Inherent within tree variations in wood properties and between-tree variation will always dictate variability in the wood coming into the mill.

Cell wall thickness.—This characteristic of fibers and tracheids affects specific gravity as well as being important in influencing bonding properties. Thin-walled cells collapse, become ribbon-like, and provide a strong bond with adjacent fibers. Thick-walled fibers, on the other hand, tend to retain a round shape, do not collapse, and provide a poorer bonding surface, reducing the bonding strengths of pulp.

Inheritance of wall thickness was found by Goggans (1962) to be 0.84 in summerwood and only 0.13 in springwood. Improvement in wall thickness will go hand-in-hand with improvement in specific gravity.

Percent summerwood.—Percent summerwood, like cell wall thickness, influences pulp properties much as does specific gravity. According to Dadswell and Wardrop (1959), tearing strength and bulk density increase with higher percentage late wood; but bursting strength, tensile strength, and fold endurance decrease with increase in late wood percent.

Narrow sense heritability of summerwood in the entire core in young stems was found to be around 0.8 by Goggans (1962). This value is somewhat higher than the broad sense value of 0.5 found by Dadswell et al. (1961). Progress toward improvement of percent summerwood is tied very closely with progress in specific gravity, just as is cell wall thickness.

Percent reaction wood.—Reaction wood such as compression wood in conifers reduces quality in all types of products. Poor yields and strength properties result in paper produced from such wood while lumber cut through zones of compression wood is subject to a high degree of shrinkage, warp, and crook.

The type of material produced in reaction wood is inferior in both softwoods and hardwoods. Quality of compression wood is such that low yielding, short-fibered wood, unsatisfactory for high-grade products, is produced.

Reaction wood is produced whenever a tree stem grows out of the vertical plane. Auxin balances are upset, the result being the "abnormal" type wood. Extent of such wood, therefore, is closely tied to straightness of stem. Amount of compression wood in 50-year-old loblolly pine has been found by Zobel and Haught (1962) to vary from 6 percent in essentially straight trees to 16 percent in a crooked tree, with one exceptionally crooked tree having 67 percent of its bole volume in compression wood.

The actual heritabilities of straightness are unknown; however, Perry (1960) believes straightness to be under the control of several genes. Evidence that straightness is strongly inherited has also been shown by Mergen (1955) and McWilliam and Florence (1955). Even though straightness of stem and consequently percentage of reaction wood is subject to many environmental influences, it is apparent that heriditary influences are also important, offering the opportunity to reduce amount of this inferior material through producing more straight trees. It is because of the phenomena of compression wood production that straightness of stem is given so much weight in selecting material to be used in tree improvement programs.

Other characters.—Several other wood characteristics have been studied by Goggans (1962) to determine heritabilities in loblolly pine. Several of the characteristics Goggans worked with are of practical importance to wood users; economic importance of others is not recognized at present, principally because their influence on end products is not known. Table 2 is a modified ranking, taken from Goggans' paper, listing the ease with which improvement can be made in wood characteristics in an improvement program.

Table 2.—*Relative* ranking of wood *characteristics according* to *the ease with which progress may be made in a selection program*.

Numerical rank	Characteristic
1	Summerwood tracheid length
2	Percent summerwood
3	Specific gravity
4	Springwood tracheid width
5	Springwood tracheid length
6	Summerwood tracheid width
7	Summerwood tracheid wall thickness
8	Springwood tracheid wall thickness

Several of the characteristics listed above are interrelated, and any work toward changing one will result in change of another, i.e., increasing or decreasing the percent Eummerwood will have a, similar effect on specific gravity.

Summary

Most tree improvement programs, in addition to bettering form, growth rate, insect and disease resistance, etc., have as one of their major objectives the improvement of wood quality. These wood quality objectives are directed toward the production of trees containing types of wood most beneficial to maintenance of yield and quality of the final product.

That such objectives are possible is shown by the results of several workers on the variation, inheritance, and heritabilities of wood properties. Studies on heritabilities are not numerous but enough have been reported to indicate that progress toward improvement of wood quality is possible. Many other studies are now under way and more concrete evidence of the amount of improvement that can be achieved will be available soon.

Information to date indicates that in seed orchards of loblolly pine it is possible to produce "strains" having one or more of the following characteristics, except where two characteristics are diametrically opposed:

Increased pulp yields of 40 or more pounds per cord.

Increased average fiber or tracheid length up to 0.5 mm.

Improved tearing strength.

Improved bonding strength.

Increased bulk density.

Improved bursting strength.

Improved folding ability.

Improved tensile strength.