Inheritance of Wood Properties in Conifers

By Bruce Zobel[1])

(Received for publication March 10, 1961)

Introduction

For many years the emphasis in forest genetics studie; and forest tree improvement research has been primarily on increasing yields, improving tree form, obtaining resistance to insects or diseases or to producing a tree able to withstand new or different conditions. Only during the past 5 to 10 years has much attention been paid to wood, and even then most of the emphasis has been on variation patterns within the tree, between trees, and between different sites and geographic areas rather than on inheritance per se.

Interest in genetics of wood has now become widespread. But to intelligently use genetics as a tool to improve wood, we need to know everything possible about inheritance patterns of specific wood characteristics. This article is written in response to a request to summarize present knowledge about inheritance of wood properties. The field of research in wood genetics is rapidly expanding with a large number of studies now underway, some of which are presently far enough advanced so that results are becoming available. Thus, by the time this article is published, there will undoubtedly be new and better information about inheritance of wood properties than was available when it was written in October, 1960.

In order to attain its objectives, the present article will be divided into: (1) Measurements of Inheritance. (2) Present Knowledge of Inheritance in Wood. (3) Studies Yielding Supplementary Information. Examples will be mainly drawn from coniferous species. No separate "Review of the Literature" will be included, but references to pertinent literature will be scattered throughout the text.

Measurement of Inheritance

To simply speak of inheritance as being strong or weak is rather meaningless, although this must be the first approach. Thus, lists of important wood characteristics and their possible influence by genetics and environment (Schreiner, 1958, Dadswell and Wardrop, 1960) have been very helpful when used as a guide. But to be of maximum value, inheritance must be expressed in some manner that has a definitive meaning for all. Unfortunately, this degree of precision has not always been attained in forest genetics, and scattered throughout the literature are many vague, and sometimes questionable, measures of inheritance. Such a situation can be misleading and often dangerous, with the result that published figures may be taken, re-cited subsequently many times, and often given significance which the original author never intended. This unhappy situation has developed especially in wood studies; thus, I feel compelled to caution about the potential dangers and to emphasize care in interpreting published results.

Especially in a new field such as wood genetics it is natural to be enthusiastic and excited about any results obtained. This tendency in no way implies intellectual dishonesty, for in this new field of work all of us are eager to publicize any inheritance patterns that might seem to have emerged. The result of all this can be exemplified by the typical query, "What should I do? I can obtain heritabilities from .21 to .45 from the same data, depending on the formula used and the interpretation of the answers obtained." Whichever of these figures becomes incorporated in the mainstream of literature could have a far-reaching influence on initiation of future genetic investigations in that area.

One way of expressing inheritance is through use of the long-accepted term "heritability," which is still being employed in crop and animal breeding. Expressing the genetic control by means of heritability is the most common method currently used in forestry; and if properly interpreted, it can be very valuable. One prominent plant breeder recently criticized the excessive emphasis on heritability by the forest geneticists and pointed out that what is needed is a knowledge of the genetic gain. Most of the published heritabilities are for seedlings or young stands, and it is important to remember this when interpreting results. Although our present state of knowledge is often not enough to accurately determine genetic gain, yet we must at all times remember that not heritability per *se*, but genetic gain is our ultimate interest.

Very simply stated, heritability is the relationship of the heritable portion of the variability of a specified characteristic compared to the total variability of that characteristic. For plants and animals it is used usually in reference to the portion of additive genetic variability, thus providing an indication of the genetic gain possible for the characteristic under consideration. Other concepts of heritability are referred to in the literature; especially in forestry literature, distinguishing between heritability in the narrow sense or heritability in the *broad* sense has been stressed. Toda (1957) makes a clear explanation of these differences. He states, "When the material is propagated by sexual means, the non-additive effects of individual genotypes cannot be passed on to their progenies, so the term heritability must be employed in the narrow sense — when vegetative propagation is used, the effects of dominance and epistasis are passed on the next generation because the genotypes of individuals are transferred unchanged. So the term heritability may be ernployed in its broad sense." His definitions are based on ideas of Lush (1949).

Both of these terms for heritability have been used to describe wood characteristics. Fielding and Brown (1960) calculated heritability of wood specific gravity in both the narrow and the broad sense, although they use the term "gross heritability" meaning essentially the same as heritability in the broad sense. For wood specific gravity, these authors obtained heritabilities in the broad sense (gross heritabilities) of 0.7, 0.5, and 0.7, while their narrow sense heritability of specific gravity was 0.2. Similar resulti were obtained by Toda et al. (1958) who obtained heritabilities in the broad sense of 68% (0.68), and in the narrow sense of 27% (0.27) for heigth growth of *Cryptomeria*. As can be seen, it is absolutely necessary for the writer to clearly state and for the reader to clearly understand whether the heritability figures quoted are in the *narrow* or in the *broad* sense.

[1]) Professor of Forest Genetics, North Carolina State College, Raleigh, North Carolina.

One further point regarding heritability needs to be clarified. It *is not* a constant factor for all conditions, and will change with tree environment and with tree age. Because the heritability estimate is based on total variation, anything (such as environmental differences) that causes greater variability will automatically change the heritability figure obtained. In general, the more restrictive and uniform the site under which a particular test is conducted, the greater will be the heritability value obtained. Thus, a heritability estimate of specific gravity for any given characteristic will undoubtedly be different if the test is made on trees growing on a well-drained, fertile site, or on an infertile, deep droughty sand site. Because of this influence of differences of environment, all published heritability figures should state under what conditions the tests were made. A similar change will be observed with age of the material tested; thus, for example, it is very possible that heritability of tracheid length will change with age of the tree when the wood was laid down. It might be very low in seedlings and very high in mature trees or vice versa. This potential change with age was aptly pointed out by Fielding and Brown (1960), and it necessitates all the more that each heritability figure be translated in terms of age and environment. This situation is particularly critical now since most of the published results for wood studies are based on seedlings or young trees. Thus, obtaining a high heritability now may not necessarily be of too much significance at the really important time, when the tree is to be harvested. Conversely, failure to obtain high heritability from young progeny tests should not be taken as a final indication that this characteristic will be of no importance at the specific or the desired age of maturity. Eventually, heritability as well as "repeatability" will be obtained for trees at age of harvest; in the interim our heritability information should be regarded merely as indicative.

In summary, then, in our appraisal of heritability figures on wood properties we must constantly ask ourselves: (1) What kind of heritability? (2) Under what environmental conditions was it determined? and (3) To what age trees does it apply? (4) How was heritability estimated? Failure to evaluate heritabilities in this scrutinizing manner will lead to trouble and error in using genetics to improve wood characteristics.

Present Knowledge[2]) of Inheritance in Wood

Much research is currently underway on genetic phases of wood properties, some of which has been completed while this manuscript is being written, and is now in press. In many reports the results are not too specific. In others heritabilities are reported, but practically none gives actual figures for gains that might be achieved through the use of genetics to improve wood. For simplicity in this paper, wood properties in general will be divided into several categories or groups of properties. Information of this kind was partly covered in a recent report to the World Forestry Congress (Zobel, 1960).

I. Tracheid Length

There are many general references to tracheid length inheritance in the literature. For example, Greene (1956), and Jackson and Greene (1957, 1958) reported that for slash pine (*P. elliottii*) and loblolly pine (*P. taeda*), the genetic factor has a controlling influence, and that tracheid length of the progeny was more influenced by the female than by the male parent. They did not express heritabilities quantitatively, but stated that progeny from parents with long tracheids had longer tracheids than progeny from trees with short tracheids. For hybrid larch, (*Larix eurolepis*) Chowdhury, (1931) reported that springwood tracheids favored the female parent while summerwood tracheids were intermediate between the two parents, his results being somewhat similar to those of Greene (1956). Wellwood (1960), found that for second-growth hemlock "there is an apparent genetic effect whereby trees having tracheids either initially shorter or longer than average will retain that feature as they continue to grow."

On a survey of tracheid lengths of 15 loblolly pines of the same age, and of the same crown class (growing together) Kramer (1957) determined the individual tree variation and tried to tie this to factors that might cause tracheid length to vary. He found no relationships, and cautiously concluded that "genetic control may well be involved in the determination of tracheid lengths in an individual tree." Many similar studies have inferred genetic control, or have attempted to give a basis for such inference. In his summary paper, Schreiner (1958) states without reservations that there is considerable evidence for the heritability of fiber length. Large tree-to-tree variability has been repeatedly demonstrated in a number of studies (Zobel, *et al.*, 1960), but care should be excercised not to construe unexplained variation *de facto* as genetic control. It is tempting to reason that large tree-to-tree variation, whose patterns are repeated over and over again under all environments in the species range, is caused by heritable factors. But such tacit jumping to conclusions is dangerous. Information on tree-to-tree variation *per se* can be of great value, but still tells little about the magnitude of genetic gains, if any, that might be achieved.

One of the few publications in which actual heritabilities were reported for tracheid length is by Dadswell *et al.* (1960). The authors made gross heritability (broad sense) estimates, based both on clonal and seedling progeny. They reported results for growth rings 2 to 8, and also for growth rings 6 to 8 (*Table 1*).

Table 1. — Broad Sense Heritabilities for Tracheids of *Pinus radiata* (from Dadawell *et al.*, 1960)

	Clonal	Seedling
Rings 2—8	.73	.83
Rings 6—8	.81	.86

The authors caution about possible weaknesses of their study including lack of sufficient replications and the young (8 years) age progenies which may reduce the reliability of the results. Despite these shortcomings and any questions that might be raised with respect to the meaningfulness of the exact figures, it is noteworthy that they found a relatively high gross heritability, which is concordant with the more generalized results to which previously cited authors have referred.

A number of studies have indicated variation in tracheid length with geographic location of the species. Such studies on variation of tracheid length in natural stands with geographic source were started a number of years ago (Lee and Smith, 1916). Many reports are available for differences among geographic areas (Bissett *et al.*, 1951). For example, a recently completed study on loblolly pine in the southeastern United States (Zobel *et al.*, 1960), showed a defi-

[2]) As of October, 1960, based on published reports and personal communications.

nite increasing trend in tracheid lengths from S. to N. from trees in natural stands *(Fig. 1)*.

II. Specific Gravity

Wood specific gravity is often spoken of as being a single characteristic, and may be so considered from the use standpoint. As pointed out by SCHREINER (ZOBEL, 1956), genetically it consists of a complex of characteristics, each of which contributes to the overall specific gravity. For example, per cent summerwood is one factor influencing specific gravity; another is the actual cell dimensions, including wall thickness and cell diameter. Undoubtedly, each factor contributing to specific gravity is genetically complex in itself. Despite this complexity, all present published studies deal with specific gravity as a unit, and thus the heritabilities are, therefore, based on a complex of characteristics. It is important to keep this complex nature of the characteristic clearly in mind.

At the present time, specific gravity is the most intensively studied wood characteristic because of its economic importance and because of its relative ease of measurement. Currently, many studies are underway, and results of a number will soon be published; thus, data on heritabilities in wood specific gravity are now becoming available. For example, FIELDING and BROWN (1960), and DADSWELL *et al.* (1960), found the heritabilities of specific gravity for Monterey pine as indicated in *Table 2*.

Table 2. — Heritabilities for Wood Specific Gravity of *Pinus radiata* (from DADSWELL *et al.*, 1960, and FIELDING, 1960)

Description of Progeny	Broad Sense Heritability		Narrow Sense Heritability
	Clonal	Seedling	
19 year	0.7	—	—
20 year	0.5	—	—
13 year	0.7	—	—
6 year	—	—	0.2
8 year (rings 2 to 8)			
Whole ring	0.74	0.57	—
Latewood	0.45	—	—
8 year (rings 7 & 8)			
Whole ring	0.75	0.53	—
Latewood	0·54	—	—

The one determination of heritability in the narrow sense is based on 14 open pollinated progenies and, as the authors point out, cannot be considered as very definitive. However, it does indicate the degree of inheritance; although 0.2 is not high, it is considered to represent a useful increase for a quantitative characteristic so complex as specific gravity and suggests that real gains through selection should be possible.

A large number of authors report "inheritance" of specific gravity in general terms. For example, progeny from wind-pollinated seed from parent trees with the highest specific gravities produced progeny with higher specific gravities at 4 to 12 years of age than those from parent trees with lower specific gravities (ZOBEL and RHODES, 1957). Some recent findings by BROWN and KLEIN (1960), from control-pollinated progeny involving loblolly pine crosses of partial factorial combinations of high and low specific gravities, as well as open-pollinated progeny led them to summarize as follows — ". . . leaves little doubt that the wood specific gravity of two-year-old seedlings reflects, to a high degree, the specific gravity of the parent tree wood." They found that all crosses were significantly different at the 1% level with the following results: high × high = .389, high × wind = .385, and low × wind = .356. Rather strong inheritance is certainly indicated.

In an even more recent paper KLEIN and BROWN (1961) determined heritability of wood specific gravity on loblolly pine seedlings by using the regression of progeny values on the mean of the parent. Seventeen crosses among 8 trees of high and low specific gravities were made. The regression was significant at the one per cent level and "indicates that there is a real association between parent tree wood specific gravity and progeny wood specific gravity in the crosses tested. Presumably, this association is the result of inheritance." They found that about one-fifth of the variability has been genetically transmitted.

For Scots pine and Norway spruce ERICSON (1960) reported good correlations between the basic density of the original tree and that of the graft tree. He states, of his study, "The use of the relative basic density as an indicator when selecting genotypical plus varieties is the most important result for the purpose of practical tree breeding."

Numerous studies have been made regarding the variation in specific gravity with geographic location of stand. Results of many papers were recently summarized (ZOBEL *et al.*, 1960), and will not be treated in detail here; only a few will be cited. Large differences in specific gravity among provenances were reported for slash pine (PERRY and WANG, 1958), LARSON (1957), (WHEELER and MITCHELL, 1959), and for loblolly pine in the U. S. (ZOBEL and RHODES, 1955, WHEELER and MITCHELL, 1959), and in South Africa (SCOTT and DU PLESSIS, 1951). Considerable attention has been paid to such geographic variation in Douglas-fir *(Pseudotsuga menziesii)* — for example, by DROW (1957), and KNIGGE (1960), and for other species such as Hinoki *(Chamoecyparis obtusa)* (MIYOSHI, 1951). In as early paper (MYER, 1930) pointed out regional differences in four North American species. All such studies have indicated some degree of variation in specific gravity with geographic location of stand. Just as for tracheid length, it cannot be definitely ascertained whether these regional differences are controlled by genetic or environmental influence.

There is considerable evidence of genetic control of specific gravity expressed when trees from different geographic sources are grown under uniform environmental conditions. ECHOLS (1958) found highly significant differences among a number of races of Scotch pine when grown in New Hampshire. In the same study as reported for tracheid length in loblolly pine, THORBJORNSEN (1960) found significant differences among several provenances of this species. However, rankings changed so that seed collected from the natural stand with highest specific gravity wood did not produce trees with highest specific gravities when grown in Tennessee, outside the natural range of the species. In addition to Scotch pine and loblolly pine, varying degrees of difference with differing seed source were found for red pine *(P. resinosa* — REES and BROWN, 1954), for *Pinus pinaster* in South Africa (WICHT, 1947), and for white spruce *(Picea glauca* — HOLST, 1958). For Norway spruce KLEM (1957) found higher specific gravity in German spruce than in that of Norwegian origin. In New Zealand, the ponderosa pine provenance *(P. ponderosa)* from California produced consistently lower specific gravity wood than the provenance from British Columbia, (HARRIS and KRIPAS, 1959). Occasionally reports are made in which geographic origin of seed source was found to have no effect on specific gravity of the plantation (KNUDSEN, 1956).

There are a host of papers, many of them contradictory, that indicate relationship (or lack of such) of specific gravity to site differences. Almost all authors agree, however, that there is a very large amount of individual tree variation under all sites and conditions. This tree variation has been especially emphasized by GÖHRE (1958) and several other authors.

The weight of evidence indicates that regardless of site, growth rate, or geography, definite genetic control of specific gravity among individual trees is present, and moreover, that it is large enough to have a significant effect on yields. Initially, to be sure, genetic gains through sexual means may not be large, but they should be real and significant, and become increasingly important as more generations of trees are manipulated. Gains could be large at once where vegetative propagation is feasible.

III. Spiral Grain

There are perhaps more papers dealing with genetic control of spiral grain than of any other wood property. In many of these we can find large, general claims about genetic influence. For example, JENNINGS (1957) states that spiral grain certainly is under genetic control. CHAMPION (1930), NOHL (1933), SCHMUCKER (1956), and NORTHCOTT (1957) are only a few of the many who have published and indicated possible genetic control of spiral grain. DADSWELL *et al.* (1960) actually worked out heritabilities for this character in Monterey pine. From clones for rings 2 to 8 he obtained heritability in the broad sense of 0.66, but for the 7th and 8th rings his value dropped to 0.28, a figure lacking statistical significance, indicating little or no genetic influence. Spiral grain has caused a lot of defect in plantations. This situaton has become manifest especially in the earlier plantings of South Africa and of Australia. The possible inheritance of spiral grain has been emphasized by CHAMPION (1945) and coworkers. Much of the literature dealing with spiral grain has been based on studies of chir pine *(P. longifolia* or *P. roxburghii)*; KADANIO and DABRAL (1955) review and summarize the previous work on this species and report more recent studies. They show that, for seedlings, the tendency to develop twist is inherited, and can be recognized already in the cotyledons of germinating seeds! When they found seed from self-pollinated twisted chir pines producing 68 to 82% twisted seedlings, they concluded that twist would seem to be a dominant character.

Despite all the positive statements regarding the genetic control of spiral grain, much additional study needs to be done. Like specific gravity, spiral grain is not a simple characteristic, but a composite, and as NOSKOWIAK (1960) and others have shown, the spirality changes with age of wood laid down. Actual heritabilities in the narrow sense are not available for this important characteristic, but very definitely they need to be determined. To date, the mass of evidence suggests that spiral grain should be taken into account when dealing with genetics of wood properties.

IV. Tracheid Characteristics Other Than Length

A number of tracheid characteristics have been studied, but essentially nothing is known about their inheritance, except by inference.

Fibril angle has been reported to be highly correlated to ring width (PILLOW *et al.*, 1953). This relationship has been demonstrated to hold especially within a tree, but among trees of the same species the picture is not clear. It is definitely known that the fastest growing trees are not always the trees with the flattest fibril angle. HILLER (1954), for example, found slash pine of the same age and same vigor class as expressed by diameter, size of crown and yearly increment, differ in size of fibril angles in comparative rings from the pith. SMITH (1959) studied hoop pine *(Araucaria cunninghamii)* and found only a very weak relationship between initial micellar angle and that formed at a later age in the tree. In an unpublished study involving clones of F_2 *Pinus* × *attenuradiata* (the cross between knobcone pine *P. attenuata* and Monterey pine *P. radiata)* CALLAHAM[3]) (personal communication) stated that there was a highly significant difference among six clones, but did not calculate the exact heritability. Much more work needs to be done on this character, at the same time avoiding the blanket assumption that fibril angle is closely tied to growth rate differences *between trees.* It has been stated by several foresters that since diameter growth shows considerable heritability (as shown by TODA *et al.*, 1953), fibril angle should exhibit equal heritability. However, this assumption is unwarranted until more data are available on variation and inheritance of fibril angle.

Actual cell dimensions, i. e., wall thickness, tracheid width, and lumen size are under study, but as yet little seems to be known about them, either as to their variation patterns among trees or their inheritance patterns. MERGEN (1960) reported that on the average tracheid characteristics from a cross between *P. thunbergii* and *P. densiflora* showed greater values for the hybrid than for the parents with the exception of cell wall thickness and fibril angle, which were intermediate. Such information on tracheid characteristics is vital since it is these tracheid characteristics that are the basic "units" which determine the magnitude of the grosser characteristics such as specific gravity.

V. Chemical Characteristics

Chemical constituents of the wood are in some ways the most important, but least studied, of wood characteristics. Variations in chemical constituents have been noted but, with the exception of cellulose and lignin, tree to tree variations within the tree are not well known. Within the wood itself practically nothing is known about the variations and inheritance of resins, although a considerable body of knowledge, including heritabilities, has been obtained for tapping or "bleeding" trees for gum production. In recent years considerable attention has been directed toward variation and inheritance patterns of cellulose, and to a lesser extent lignin for several species. Most emphasis has been on variation patterns (KLEM, 1945, ZOBEL *et al.*, 1960a, 1960b, and KENNEDY, 1960) in spruce, loblolly pine, and Douglas-fir. All authors reported considerable variation from tree to tree. In a study of strains of lodgepole pine *(P. contorta)* SCHÜTT (1958), in addition to encountering large individual tree differences, found differences among progeny grown from different seed sources. An actual heritability study has been reported by DADSWELL *et al.* (1960) for the 7th and 8th ring of Monterey pine. Heritability in the broad sense was low (0.29) and was not significant, indicating that inheritance played a very small part in the differences in cellulose yields obtained. The authors state that this most interesting result needs further investigation. Thus, it seems to be the concensus of men working on cellulose yields that there is much variation which follows no definite pattern that might reveal whether these observed variations are either under strong genetic control

[3]) CALLAHAM, R. Z., Western Institute of Forest Genetics, Placerville, California. U. S. Forest Service.

or influenced by specific environmental effects. Up to now, of all the inheritance studies on wood to determine strength of genetic control, the evidence seems unimpressive for cellulose yields.

VI. Other Characteristics Affecting Wood Properties

Bole straightness, limb angle, limb size, and related characteristics affecting wood properties have been studied and deserve mention. However, allotted space here precludes even a general discussion of these items, though a few examples will be cited to illustrate the significance of some interrelationships.

Consider the single characteristic, bole straightness. It affects wood properties to a very important degree, and is considered especially significant for loblolly pine which has an "inherent" twist to the stem. Straightness affects compressionwood, which in turn affects the properties of both pulp and lumber. In a preliminary study HAUGHT (1958) found that the total merchantable volume of moderately straight trees contained less than 10% compressionwood, while more crooked trees commonly had over 15% of the total volume as compressionwood. In excessively crooked trees compressionwood exceeded 50% of the total bole volume!

Several studies on inheritance of bole straightness have been reported, one of the most recent being that by PERRY (1960). For young trees of loblolly pine, PERRY found that bole straightness has a fairly strong inheritance pattern. Progeny from crooked parents were significantly more crooked than those from straighter parents. Heritability figures as such were not reported in this study, but they would appear to be rather high. For slash pine McWILLIAM and FLORENCE (1955) found that use of seed from better phenotypes (straighter trees) resulted in twice the number of "acceptable" stems per acre. Even more impressive, progeny from controlled cross pollination between individual selections for straightness resulted in a four-fold increase in the number of acceptable stems per acre.

It is obvious from the literature that a real improvement in wood quality can be achieved through breeding for tree characteristics that have a direct effect on wood properties. Improvement of this nature will be automatically achieved in most genetic programs as an end result of breeding for better form.

Summary

Not too much is currently known of the actual inheritance patterns for wood properties in coniferous species, but a great many studies to determine this are currently underway. The most convincing evidence is available for tracheid length which appears rather strongly inherited, enabling considerable improvement through selection programs. Specific gravity, which must be regarded not as a single characteristic, but as a complex of characteristics, has been found to have a high heritability (in the broad sense) and to be large enough (in the narrow sense) to give significant gains from selection. Lumen size, wall thickness, and other tracheid characteristics have scarcely been investigated at all; early though meager results would indicate that improvement, even for these, in possible. From an inheritance standpoint of chemical characteristics of the wood itself, very little study has been done to date, although one study on cellulose yields indicated that inheritance played a very small part in the variations found.

In any consideration or evaluation of inheritance it is very important to be fully cognizant of how it is measured and expressed. The most common way is to express it as the ratio termed "heritability". Since two types of heritabilities are employed, namely that in the *broad sense* and that in the *narrow sense,* it is essential to keep the distinction between them clear and unconfused.

Zusammenfassung

Titel der Arbeit: *Die Vererbung der Holzeigenschaften.*

Der tatsächliche Vererbungsmodus der Holzeigenschaften der Coniferen ist bisher noch weitgehend unbekannt, es wurden aber eine große Anzahl Untersuchungen zu seiner Aufklärung durchgeführt. Das überzeugendste Ergebnis wurde für die Länge der Tracheiden erhalten, die ziemlich stark erblich zu sein scheint. Dies ermöglicht, durch ein geeignetes Selektionsprogramm eine bedeutende Verbesserung zu erzielen. Das spezifische Gewicht, welches nicht als eine einzelne Eigenschaft sondern als ein ganzer Komplex anzusehen ist, besitzt eine hohe Heritabilität (im weiteren Sinne), und ist (im engeren Sinne) signifikant genug, um sich für eine Selektion zu eignen. Größe des Zelllumens, Wandstärke u. a. Eigenschaften der Tracheiden sind noch kaum untersucht, aber frühere, obgleich dürftige Resultate legen die Möglichkeit nahe, daß eine Verbesserung auch hier möglich ist. Über den Wert der Vererbung chemischer Eigenschaften des Holzes liegen bisher nur wenige Untersuchungen vor, jedoch zeigen die des Zellulosegehalts, daß der Anteil der Vererbung an der vorhandenen Variation nur gering ist.

Für jede Berücksichtigung oder Bewertung der Erblichkeit ist es von Bedeutung, genau zu wissen, wie sie zu messen oder auszudrücken ist. Der allgemeinste Weg ist der, sie in dem Begriff „Heritabilität" zu fassen. Seit man zwei Typen der Heritabilität entwickelt hat, nämlich den im weitesten Sinne und den im engeren Sinne, ist es unbedingt erforderlich, klar und eindeutig den Unterschied zwischen ihnen zu bewahren.

Résumé

Titre de l'article: *Hérédité des qualités du bois chez les conifères.*

On connait peu de choses avec certitude en ce qui concerne les modèles d'hérédité des caractéristiques du bois chez les conifères mais de nombreuses études sont actuellement en cours. Les résultats les plus nets ont été obtenus pour la longueur des trachéïdes, caractère qui semble avoir une héritabilité assez forte ce qui doit permettre un gain considérable par la sélection. La densité du bois qui doit être considéré plutôt comme un complexe de caractère que comme un caractère unique présente une héritabilité forte (au sens large), et assez forte (au sens strict) pour donner des gains appréciables par sélection. La dimension des lumens, l'épaisseur des membranes et les autres caractères des trachéïdes ont été que étudiés jusqu'ici; mais les premiers résultats semblent indiquer que, même ici, une amélioration parait possible. L'hérédité des caractéristiques chimiques du bois a été également très peu étudiée; cependant, un travail sur la teneur en cellulose indique que l'hérédité joue un faible rôle dans les variations observées.

Pour toute évaluation de l'hérédité, il est très important de définir parfaitement la méthode et l'expression de la mesure. On l'exprime le plus couramment sous forme du rapport qui définit »l'héritabilité«. Il est essentiel de distinguer parfaitement, sans risque de confusion, s'il s'agit de l'hérédité au sens large ou de l'hérédité au sens strict.

Literature Cited

(1) BISSET, I. J. W., DADSWELL, H. E., and WARDROP, A. B.: Factors influencing tracheid length in conifer stems. Aus. For. 15 (1): 17—30 (1951). Div. For. Prod Repr. 145. — (2) BROWN, C. L., and KLEIN, J.: Observations on inheritance of wood specific gravity in seedling progeny of loblolly pine. Jour. For. 1960 (In press). — (3) CHAMPION, H. G.: Genetics of forestry. Quarterly Jour. For. 39 (2): 74—81 (1945). — (4) CHOWDHURY, K. A.: Anatomical studies of the wood of a hybrid larch. Jour. For. 29 (5): 797—805 (1931). — (5) DADSWELL, H. E., and WARDROP, A. B.: Some aspects of wood anatomy in relation to pulping qualitiy and to tree breeding. Jour. Aust. Pulp and Paper Ind. 13 (5): 161—173 (1960). — (6) DROW, J. T.: Relationship of locality and rate of growth to density and strength of Douglas-fir. FPL Rept. 2078, 56 pp. (1957). — (7) ECHOLS, R. M.: Variation in tracheid length and wood density in geographic races of Scotch pine. Bull. No. 64, 1958. Yale University School of Forestry, New Haven, Connecticut. — (8) ERICSON, B.: Studies of the genetical wood density variation in Scots pine and Norway spruce. Statens Skogsforskningsinstitut. Nr. 4 (4): pp 52. (1960). — (9) FIELDING, J. M., and BROWN, A. G.: Variations in the density of the wood of Monterey pine from tree to tree. Leaflet No. 77, pp. 1—28 (1960). Commonwealth of Australia, Forestry and Timber Bureau. — (10) GÖHRE, K.: Über die Verteilung der Rohwichte im Stamm und ihre Beeinflussung durch Wuchsgebiet und Standort. (The distribution of density through the stem, and the effect on it of growth region and site.) Holz Roh- u. Werkstoff 16 (3): 77—90 (1958). — (11) GREENE, JAMES T.: Variation in tracheid length of slash pine parents and progeny. Master's thesis, University of Georgia 1956 (Unpublished). — (12) HARRIS, J. M., and KRIPAS, S.: The physical properties of two provenances of ponderosa pine grown in Kaingaroa State Forest. New Zealand For. Res. Notes No. 16, pp. 3—16 (1959). — (13) HAUGHT, A. E.: An exploratory study of compression wood in loblolly pine *(P. taeda)*. Master's thesis, School of Forestry, North Carolina State College, 1958 (Unpublished). — (14) HILLER, C. H.: Variations in fibril angles in slash pine. Rep. U. S. For. Prod. Lab., Madison, No. 2003, 6 pp. (1954). — (15) HOLST, M. J.: Thoughts on wood density. Proc. 6th Meeting of the Comm. on For. Tree Breeding in Canada, Part II, pp. S—31 and S—32 (1958). — (16) JACKSON, L. W., and GREENE, J. T.: Hereditary variations in slash pine tracheids. 4th South. Conf. on For. Tree Improvement, Athens, Ga. pp. 23—26 (1957). — (17) JACKSON, L. W. R., and GREENE, J. T.: Tracheid length variation and inheritance in slash and loblolly pine. For. Sci. 4 (4): 316—318 (1958). — (18) JENNINGS, S. G. Dip. For., 1957: Forest Products Research, "An apprecation of future policy," Seventh Brit. Commonwealth For. Conference, pp. 11—16. — (19) KADAMBI, K., and DABRAL, S. N.: On twist in Chir *(Pinus longifolia* ROXB.) Indian For. 81 (1): 58—64 (1955). — (20) KLEIN, J., and BROWN, C.: Preliminary observations on the inheritance of wood specific gravity in loblolly pine seedlings, 1961 (In press). — (21) KLEM, G. G.: Undersøkelser av granvirke i forbindelse med slipe og sulfitkokeforsøk. (Investigations of spruce wood in connection with mechanical wood pulp and sulphite pulp experiments.) Meddelser fra Det Norske Skogforsøksvesen NR 31, IX (1): 127 pp. (1945). — (22) KLEM, G. G.: Kvalitetsundersøkelser av norsk og tysk gran. (The quality of Norway spruce [*Picea abies*] of Norwegian and German origin). Det Norske Skogforsøksvesen (Reports of the Norwegian Forest Research Institute), Vollebekk, Bind XIV, Hefte 48, 1957. — (23) KNIGGE, W.: The natural variability of wood as it affects structural application of wood and selection of test material. Fifth World For. Cong. Seattle, Washington, 1960. — (24) KNUDSEN, M. V.: A comparative study of some technological properties of Norway spruce in a provenance test (Docum.) 12th Cong. Int. Union for Res. Organ. Oxford No. IUFRO 56/41/2, pp. 7 (1956). — (25) KOHL, E. J.: An explanation of the cause of spiral grain in trees. Sci. 78 (2012): 58—59 (1933). — (26) KRAMER, P. R.: Tracheid length variation in loblolly pine. Tex. For. Ser. Tech. Report No. 10, 1957. — (27) LARSON, P. R.: Effect of environment on the percentage of summerwood and specific gravity of slash pine. Yale University, School of For. Bull. No. 63: 87 pp. (1957). — (28) LEE, H. N., and SMITH, E. M.: Douglas-fir fiber, with special reference to length. Forestry Quarterly 14 (4): 671—695 (1916). — (29) LUSH, J. L.: Heritability of quantitative characters in farm animals. Proc. 8th Inter. Cong. Hereditas, Suppl. Vol., 356—375 (1949). — (30) MCWILLIAM, J., and FLORENCE, R.: The improvement in quality of slash pine plantations by means of selection and cross breeding. Jour. Inst. of For. of Australia 19 (1): 8—12 (1955). — (31) MERGEN, F., and FURNIVAL, G.: Discriminant analysis of *Pinus thunbergii* × *P. densiflora* hybrids. Ann. Meet., Soc. Amer. For., Washington, D. C., 1960. — (32) MIYOSHI, T.: Ecological studies on the qualities of the timber of Hinoki, *(Chamaecyparis obtusa)*: chemical and physical properties. Bull. Tokyo Univ. For. 40 (1—217), 1951. — (33) MYER, J. E.: The structure and strength of four N. A. woods as influenced by range, habitat, and position in the tree. N. Y. State Coll. For. Tech. Publ. 31: 39 pp. (1930). — (34) NORTHCOTT, P. L.: Is spiral grain the normal growth pattern? For. Chron. 33 (4): 335—52 (1957). — (35) NOSKOWIAK, A. F.: Spiral grain patterns in red pine and relationship of age and radial growth rate to change of grain angle. Ph. D. thesis, State Univ. Coll. of For. Syracuse University, N. Y. 1959 (Unpublished). — (36) PILLOW, M. Y., TERRELL, B. Z., and HILLER, C. H.: Patterns of variation in fibril angles in loblolly pine. For. Pro. Lab., For. Serv. U. S. D. A. No. D 1935: 11 pp. (1953). — (37) PERRY, T. O.: The inheritance of crooked stem form in loblolly pine *(Pinus taeda* L.). Jour. For. 58 (12): 943—947 (1960). — (38) PERRY, T. O., and WANG, CHI WU: Variation in the specific gravity of slash pine wood and its genetic and silvicultural implications. TAPPI 41 *(4)*: 178—180 (1958). — (39) SCHMUCKER, T.: Forstgenetic: einige Befunde am Rande. (Forest genetics: some marginal discoveries.) Forstwiss. Cbl. 75 (1/2), 1956. — (40) SCHREINER, E. J.: Possibilities for genetic improvement in the utilization potentials of forest trees. Silvae Genetica 7 (4): 122—128 (1958). — (41) SCHÜTT, P.: Variations in the cellulose and lignin content of some *Pinus contorta* strains grown in West Germany. Silvae Genetica 7 (2): 65—69 (1958). — (42) SCOTT, M. H., and DUPLESSIS, C. P.: The qualities of the wood of *Pinus taeda* grown in South Africa. J. S. AFR. For. Assoc. 20: 19—30 (1951). — (43) SMITH, W. J.: Tracheid length and micellar angle in Hoop pine *(Araucaria cunninghamii* AIT.) Res. Note 8, Queensland Forest Service, pp. 61, 1959. — (44) THORBJORNSEN, E.: Variation in loblolly pine *(Pinus taeda* L.). Ph. D. thesis, N. C State College, Raleigh, N. C., 1960 (Unpublished). — (45) TODA, R.: Variation and heritability of some quantitative characters in *Cryptomeria*. Silvae Genetica 7 (3): 87—93 (1958). — (46) TODA, R., NAKAMURA, K., and SATOO, T.: The heritability of tree height and stem girth in *Cryptomeria* through sexual reproduction. Silvae Genetica 8 (2): 43—48 (1958). — (47) WHEELER, P. R., and MITCHELL, H. L.: Specific gravity variation in Mississippi pines. Proc. 5th South. Conf. on For. Tree Imp. 1959, pp. 87—96. — (48) WELLWOOD, R. W.: Specific gravity and tracheid lenght variations in second-growth western hemlock. Jour. For. 58 (5): 361—368 (1960). — (49) ZOBEL, B. J., and RHODES, R. R.: Relationship of wood specific gravity in loblolly pine to growth and environmental factors. Tech Rept. 11, Texas For. Ser., 32 pp., 1955. — (50) ZOBEL, B. J.: Genetic, growth, and environmental factors affecting specific gravity of loblolly pine. (Comments by E. J. Schreiner.) For. Prod. Jour. 6 (10): 442—447 (1956). — (51) ZOBEL, B. J., and RHODES, R. R.: Specific gravity indices for use in breeding loblolly pine. For. Sci. 3 (3): 281—285 (957). — (52) ZOBEL, B. J., and MCELWEE, R. L.: Variation of cellulose in loblolly pine. TAPPI 41 (4): 167—170 (1958). — (53) ZOBEL, B. J.: Selection and breeding of coniferous trees with superior wood characteristics. Fifth World For. Cong., Seattle, Washington, 1960. — (54) ZOBEL, B. J., HENSON, F., and WEBB, C.: Estimation of certain wood properties of loblolly and slash pine trees from breast height sampling. For. Sci. 6 (2): 155—162 (1960).