respiration response to high temperature or recovery from effects of high temperature.

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The Inheritance of Compression Wood and its Genetic and Phenotypic Correlations with Six Other Traits in Five-Year-Old Loblolly Pine

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Introduction

The inheritance of compression wood has not previously been directly studied or for that matter, even seriously considered. It is the common belief that compression wood is formed as a direct response to inclination of the tree bole from the vertical. This explanation presupposes that trees within a species will not differ appreciably in their response to a given amount of inclination from the vertical. In fact, WESTING (1965, p. 434), in his comprehensive review of all aspects of compression wood, went so far as to say:

> "Little would be gained by such a study, because structure, pattern of occurrence, and extent of formation of compression wood are remarkably uniform from individual to individual and from species to species."

This statement appears to be too sweeping. Evidence is presented in this paper that direct as well as indirect genetic control of compression wood formation exists and considerable inter- and intra-specific variation in proportions of compression wood occurs.

There is good evidence that bole straightness is quite strongly inherited, at least in Southern pines. PERRY (1960) and GODDARD and STRICKLAND (1964) both showed that spiral crook in loblolly pine is heritable; MCWILLIAM and FLORENCE (1955) and NIKLES (1966) reported large gains in straightness for open and control pollinated progenies from select parents. In a study of six-year-old open pollinated progenies of select trees, WOESSNER (1965) found straightness to be one of the most strongly inherited characteristics. Evidence from a well designed heritability study of loblolly pine (SHELBOURNE, 1966) also supports these findings. On these grounds there is a strong probability of indirect inheritance of compression wood through genetic control of bole straightness.

Compression wood is also associated with branch development. It is found in the stem below the points of branch insertion (ZOBEL and HAUGHT, 1962). The amounts and intensity of such compression wood development are believed to be related to branch angle which itself has been shown to be moderately heritable (e.g. EHRENBERG, 1963; CAMPBELL, 1958).

Inter-generic differences in response to a given amount of inclination of the stem were demonstrated as early as 1888 by KONUNCHUK (WESTING, 1965), who found that Norway spruce formed compression wood more strongly than Scots pine. Similar differences in response to slight inclination were observed for white spruce and red pine by RENDLE (1956). Large intra-specific differences in compression wood percentage by volume (up to 50%) were reported by Low (1964). He found that differences between trees in compression wood percent were only very weakly correlated with size and number of stem deviations, indicating that compression wood percent was in fact behaving as a phenotypically variable, independent trait. It is not unreasonable to infer from this that, in direct contradiction to WESTING'S statement, study of compression wood might well yield evidence of inheritance of this characteristic.

The investigation[4]) reported here involved a study of compression wood percentage, specific gravity, and growth rate in a number of open pollinated (half sib) families of loblolly pine. This investigation is one of a series (SHELBOURNE loc. cit.) dealing with the inheritance of bole straightness, with the effect of differing intensities of compression wood on specific gravity, tracheid length and spiral checking of tracheids, and also the variation and relationships among compression wood, bole straightness and other traits. The latter study revealed that the widely-held assumption that amounts of compression wood formed

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are strongly correlated with straightness and perpendicularity of tree bole, was wrong. Although the relatively small amounts of intense forms of compression wood (3 to 5% by volume) were positively correlated with straightness (i.e. crooked trees produced most of this "severe" compression wood), the rather large amounts of "non-severe" compression wood (25% by volume) showed a weak negative relationship with straightness. Thus, even though straightness has quite a high heritability, indirect genetic control of the proportion of compression wood by volume via genetic control of straightness is unlikely to be strong. Compression wood formation in both its causative and genetic aspects is therefore a more complex phenomenon than previously supposed, and needs intensive study.

Materials and Methods

1. *Experimental Design and Material*

The experimental design and the material used in this study were described in detail by Cech *et al.* (1962), Stonecypher *et al.* (1964), and Stonecypher and Zobel (1965). Open-pollinated seed was collected from randomly located parent trees growing in wild unselected stands of loblolly pine on a Piedmont-type site on the International Paper Company's Southlands Experiment Forest near Bainbridge, Georgia. Sufficient progenies from randomly selected parents were available to sample 48 half-sib families. These were growing in a randomised complete block design with four replications originally planted at 1×1 foot spacing, but progressively thinned to 1×3 feet spacing by harvests made in 1961 and 1962. In this study two trees per plot (eight trees in all) were harvested from each family at age five years. Trees averaged 7.7 feet tall and 1.0 inch in diameter at 0.5 foot above ground level at time of harvest.

The trees were cut 0.5 foot above the ground line and a segment about 10 inches long was removed from above the basal cut for examination in the laboratory. Total tree height and diameter outside bark at half total height were measured in the field. Diameter inside bark was measured on the laboratory samples. Cubic volumes of the trees were computed using an equation developed for small trees by Perry and Roberts (1964).

2. *Laboratory Methods*

The green, 10-inch-long samples were cut into four sections. The basal 3 inches were removed and discarded as being likely to contain atypical wood near the root collar. Two 0.1 inch-thick cross-sections were removed, one from the base and one from the top end of the sample. Two knot-free samples were removed from the remaining piece, one for specific gravity determination and the other for cellulose analysis.

Specific gravity was determined by the usual water displacement method and the dry weight to green volume ratio. After extraction by alcohol-benzene, the wood was dried and the dry weight to green volume ratio recalculated to give extracted specific gravity and resin content.

Compression wood was assessed by examining the two thin, 0.1 inch sections from each stem, over a light-box. Areas of compression wood were delineated and were then measured by a dot grid and expressed as a percentage of the cross sectional area of the stem. Compression wood was clearly visible in variable forms of dark to light brown coloured bands and sickle-shaped areas, but it was not feasible to allocate different compression wood grades in this young material.

Alpha cellulose and holocellulose contents were estimated by the technique described by Zobel *et al.*, (1966). It is a rapid survey method which has limitations in quantifying the relatively small differences that existed in the young trees used in this study. Because of this and because no inheritance pattern was found, cellulose will not be further dealt with in this paper.

Statistical Analysis

The methods of estimating heritability and genetic correlations and the assumptions and quantitative genetic theory involved for this experiment are described fully by Stonecypher (1967) and also more briefly by Stonecypher *et al.*, (1964).

The use of analysis of variance and covariance techniques enables mean squares and mean products for replications, families, interaction of replication $\times$ families (plot error), and within plot error to be computed. The expected mean squares, expected covariances, and degrees of freedom for this analysis are shown in *Table 1.*

Table 1. — Form of analysis of variance and covariance used for all traits.

Source	Degrees of Freedom	Expected Mean Squares a)	Expected Covariances e. g., Traits 1 and 2 b)
Replications	3		
Families	47	$\sigma^2_w + 2\sigma^2_{rf} + 8\sigma^2_f$	$\sigma_{w_{12}} + 2\sigma_{rf_{12}} + 8\sigma_{f_{12}}$
Replications $\times$ families	141	$\sigma^2_w + 2\sigma^2_{rf}$	$\sigma_{w_{12}} + 2\sigma_{rf_{12}}$
Within plot	192	σ^2_w	$\sigma_{w_{12}}$

a) σ^2_w = within plot variance.

σ^2_{rf} = variance due to replication $\times$ family interaction, i. e., plot to plot variance.

σ^2_f = variance due to differences among families.

b) $\sigma_{w_{12}}$ = within plot covariance between traits 1 and 2 (as an example).

$\sigma_{rf_{12}}$ = plot to plot covariance for traits 1 and 2.

$\sigma_{f_{12}}$ = covariance due to families for traits 1 and 2.

The following genetic interpretations of components of variance and covariance were used in this study:

$\sigma^2_f = 1/4\, \sigma^2_A$

$\sigma_{f12} = 1/4\, \sigma_{A_1A_2}$

where: σ^2_A = additive genetic variance

$\sigma_{A_1A_2}$ = additive genetic covariance between traits 1 and 2.

σ^2_f and $\sigma_{f_{12}}$ — see *Table 1.*

Narrow sense heritability was computed on an individual tree basis by:

$$h^2 = \frac{\sigma 4^2_f}{\sigma^2_w + \sigma^2_{rf} + \sigma^2_f}$$

where σ^2_f, σ^2_w, and σ^2_{rf} are defined as in *Table 1.*
The genetic correlation was computed by:

$$r_g = \frac{\sigma_{f_{12}}}{\sqrt{\sigma^2_{f_1} \times \sigma^2_{f_2}}}$$

The phenotypic correlation was computed by:

$$r_p = \frac{Cov_{12}}{\sqrt{V_1 - V_2}}$$

where Cov_{12} = mean cross product for between families between traits 1 and 2

V_1 = between family mean square for trait 1

V_2 = between family mean square for trait 2.

The standard errors of variance components were computed using the following equation from ANDERSON and BANCROFT (1952):

$$V(\sigma^2) = \frac{2}{C^2}\left[\sum_i \frac{V_i^2}{f_i + 2}\right]$$

where $V(\sigma^2)$ = the variance of the component

C = coefficient of component

$\sum_i V_i^2$ = the sum of the squared mean squares involved in the computation of σ^2

f_i = the degrees of freedom for each mean square.

Results and Discussion

1. Genetic variance and heritability estimates

Narrow sense heritabilities of the seven traits measured ranged from .95 to .23, compression wood percent having the highest value, followed by specific gravity. Heritabilities and genetic correlations were reported for specific gravity (extracted and unextracted), diameter (inside and outside bark), height and volume by STONECYPHER and ZOBEL (1965). Heritabilities for compression wood percent and these traits are shown in *Table 2* for purposes of comparison.

An index of reliability of these estimates is given in *Table 2* by the standard error of the family component of variance, σ^2_f, which is shown as a ratio of the component itself. F ratios with their probability levels are also shown for each family mean square. If the standard error ratio is more than 0.5 then the heritability estimate should be regarded as being only an indication of a trend.

Compression wood shows a remarkably high heritability, highest in fact of any characteristic assessed in both open pollinated and control pollinated phases of the heritability study. As reported previously, (STONECYPHER *et al.*, 1964, STONECYPHER and ZOBEL, 1965) heritability of specific gravity, extracted and unextracted, has remained high and fairly constant from age two through age five years, while heritabilities of growth characteristics such as height, diameter, and volume show lower values.

The frequency distribution of family mean compression wood percentages is shown in *Figure 1*. It is highly skewed with no families in the zero to 5% class. The majority of families contained 5 to 25% compression wood with very few with larger amounts. Arcsin square root transformation effectively normalised this distribution.

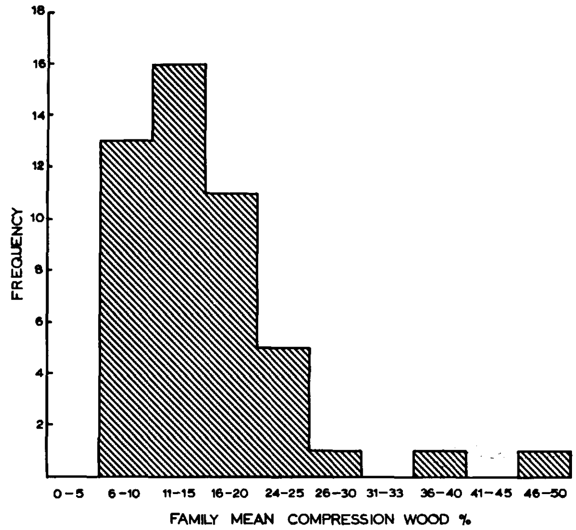

Fig. 1. — Frequency distribution of family mean compression wood percent for 5 years old loblolly pine.

An additional analysis was made of within-tree variation in compression wood. Two samples were taken from each tree; they revealed considerable within-tree sampling error. The within-tree component of variance for untransformed compression wood percent (σ^2_{wt}) was about three times larger than the within-plot component (σ^2_{wp}). This indicated that within-tree variation in compression wood was an important source of variation and this could be reduced by taking several samples per tree. However, heritability (of untransformed compression wood percent) dropped only from 1.14 to .91 if it was recomputed on a within-tree basis (including both σ^2_{wt} and σ^2_{wp} in the denominator), indicating this characteristic is still strongly inherited, in spite of considerable within-tree sampling error.

Table 2. — Estimates of narrow sense heritability (h^2) for eight traits of loblolly pine, aged 5 years.

Traits	h^2	S. E. (σ^2_f) / σ^2_f	F Ratio (Families)	Ratios of Variance Component to Sum of All Components			
				σ^2_r	σ^2_f	σ^2_{rf}	σ^2_w
Arcsin Compression Wood Per cent	.95	.29	3.30**	.02	.23	.07	.68
Compression wood Per cent	1.14a)	.28	3.84**	.02	.28	.08	.62
Extracted Specific Gravity	.64	.34	2.53**	.02	.15	0	.83
Unextracted Specific Gravity	.73	.32	2.80**	.02	.17	0	.81
Diameter Inside Bark	.28	.66	1.49*	.01	.07	.22	.69
Height	.34	.59	1.57*	.02	.08	.26	.64
Diameter Over Bark	.32	.55	1.81*	.01	.08	.08	.83
Volume	.23	.73	1.42	0	.06	.17	.78

a) Compression wood per cent data was not normally distributed (hence h^2 value $>$ 1.0) but arcsin square root transformation normalized its distribution and resulted in a lower heritability.

* Significant at the 5 per cent level.

** Significant at the 1 per cent level.

The very high heritability found for compression wood was quite unexpected. Although it is known that bole straightness shows moderately high heritability with values as high as .42 for 5-year-old loblolly pine (Shelbourne, loc. cit.) the relatively weak relationship between severe compression wood and straightness parameters and ist very weak inverse relationship with non-severe compression wood (Shelbourne, loc. cit.), indicate that the high heritability of compression wood can only be explained to a certain extent by association with bole straightness. It is possible that the compression wood observed in the young trees sampled in this study is not closely related to any particular environmental stimulus. If so, the amount of compression wood is a trait whose variable expression is largely under direct genetic control and not governed mainly by stem inclination, as previously thought. However the intensity of compression wood development appears to be largely dependent on bole inclination. This hypothesis is being tested by further studies.

2. Phenotypic and Genetic Correlations

All genetic and phenotypic correlations between the traits studied are shown in *Table 3*. Stonecypher and Zobel (1965) previously reported genetic correlations for specific gravity (unextracted), specific gravity (extracted), diameter inside bark, height, diameter outside bark, and volume, and emphasized the relatively low degree of reliability of genetic correlations which are even less reliable than the components of variance and covariance from which they are computed. The phenotypic correlations were also computed, particularly to examine relationships between traits whose family components of variance and covariance had very high standard errors, and whose genetic correlations were, therefore, highly unreliable.

Traits with low heritability and a high standard error of the family component of variance σ_f^2, showed a large decrease from genetic to phenotypic correlation. However in all cases the algebraic signs of the correlations and the relative ranking of correlations for the different traits were the same for both genetic and phenotypic values.

Relationships between compression wood and other traits demonstrated by genetic and phenotypic correlations are in general agreement with those found in other studies by the author (Shelbourne, loc. cit.) and those described in the literature, e. g. Low (1964). Compression wood percent shows low positive genetic and phenotypic correlations with height (.37 and .21), diameter (.38 and .26) and volume (.74 and .40). Wider rings than normal are known to be associated with compression wood development within the stem and an association has been demonstrated in older trees between amount of compression wood and growth rate. Fairly low negative phenotypic correlations are evident between compression wood and specific gravity (—.22) in this study. This agrees with the low negative correlation (—.19) between specific gravity and both severe and slight compression wood found in a study of 12-year-old and older material (Shelbourne, loc. cit.). Results from another study (Shelbourne and Ritchie, 1967) indicated that overall specific gravity was unaffected by compression wood, but that specific gravity of compression wood in the summerwood portion of the annual ring was lower than normal wood. Depending on the relative amounts of summer- and springwood, this could produce a negative relationship. These relationships between specific gravity and compression wood shown here are in direct contradiction to reports in the literature. (See Shelbourne and Ritchie, 1967, for discussion of this problem.)

The high heritabilities of .73 for specific gravity and .95 for compresssion wood indicate there is a large amount of additive genetic variance for these characters present in the natural, unselected population sampled. It is necessary however to be cautious about predicting heritability of compression wood in older trees from the results obtained with five-year-old trees grown in a nursery under severe competition.

Genetic and phenotypic correlations are reported for all traits. The proportion of variation accounted for by most of these correlations is not large except between such obviously correlated growth traits as diameter and volume. The relationships demonstrated between specific gravity, compression wood, and growth rate, are all in general agreement with those reported in the literature. The one exception is the lack of a strong positive relationship between specific gravity and total compression wood. This weak negative correlation is confirmed by the other studies on Southern pines which will be published soon.

Although straightness of the saplings whose characteristics were examined was not assessed, straightness of other members of these same half-sib families was examined. A weak negative relationship (r = —.17) existed between amounts of compression wood and straightness.

Table 3. — Genetic correlations and phenotypic correlations between compression wood, specific gravity, and growth rate.

Traits		Specific Gravity		D. I. B.	Ht.	D. O. B.	Vol.	Compression Wood %	Arcsin Compression Wood %
		Unextracted	Extracted						
Unextracted	G*)		1.03	—.75	—.32	—.75	—.82	—.30	—.29
Specific Gravity	P**)		0.94	—.47	—.16	—.51	—.45	—.24	—.22
Extracted Specific	G			—.82	—.36	—.79	—.86	—.26	—.23
Gravity	P			—.48	—.18	—.49	—.45	—.18	—.17
Diameter Under	G				.90	1.01	.98	.40	.42
Bark	P				.82	.92	.90	.26	.28
Height	G					.81	.88	.37	.48
	P					.78	.81	.21	.27
Diameter Outside	G						.96	.38	.41
Bark	P						.93	.26	.28
Volume	G							.74	.77
	P							.40	.40

*) G indicates genetic correlation.
**) P indicates phenotypic correlation.

This provides further evidence that compression wood and bole straightness are not closely, directly and quantitatively related, and that amounts of non-severe compression wood appear to be under direct, and quite strong genetic control.

Summary

Heritability of compression wood percent and its phenotypic and genetic correlations with specific gravity, diameter, height and volume were estimated from a study of 48 open pollinated families from randomly selected parent trees of loblolly pine. The offspring were grown in a nursery and sampled at age five years and average height 7.7 ft.

Compression wood was delineated on two cross sections from the lower part of the stem of each tree and expressed as a weighted average percentage by volume. Compression wood was found to have the highest narrow sense heritability of any of the traits measured (.95) followed by specific gravity (.73), while volume was least heritable (.23).

In its relationships with other traits, compression wood percent showed low positive genetic and phenotypic correlations with height (.37 and .21), diameter (.38 and .26) and volume (.74 and .40). Fairly low negative correlations were found with specific gravity (—.29 and —.22). This relationship is in direct contradiction to reports in the literature though is supported by the author's studies on Southern pines.

Though no direct measurement of bole straightness was made on the trees examined for compression wood etc., straightness assessed on other members of the same families showed a very weak negative relationship with their family mean compression wood percentages (r = —.17) indicating that although compression wood percent is strongly inherited this is not due to indirect inheritance and high genetic correlation with bole straightness, itself a highly heritable trait.

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Buchbesprechungen

Modern Genetics. Vol. 3. By J. A. Serra. 1968. 792 pp. (Author Index, Subject Index). Academic Press London and New York. 168 sh.

Die beiden 1965 und 1966 erschienenen ersten Bände dieses Werks behandelten die Übertragung der genetischen Information und die Theorien des Mendelismus, die Rekombination und die Chromosomenstrukturen, Genwirkung und Phänogenetik, Allelie und Interaktionen, biometrische Methoden und quantitative Genetik. Im vorliegenden 3. Band werden plasmatische Vererbung, die genetischen Einheiten einschließlich Mutationen, sowie die Geschlechtsbestimmung und die genetische Steuerung der Lebensabläufe behandelt. Wie schon bei den beiden ersten Bänden des Werkes ist auch hier die Beschränkung auf die wichtigsten Probleme und die geglückte Illustration des Textes durch Beispiele, Graphika und Fotografien hervorzuheben. Das Gesamtwerk erfüllt alle Anforderungen an ein Handbuch der Genetik und ist gleichzeitig ein ausgezeichnetes Lehrbuch für das gesamte Gebiet der Vererbungswissenschaften. Stern

Arbeiten von Freunden, Kollegen, Mitarbeitern und Schülern für Hans Stubbe zum 65. Geburtstag am 7. März 1967. Bearbeitet von R. Rieger und H. Böhme. 1967. 552 Seiten, mit vielen Abb. und Tab. Biologisches Zentralblatt, 86. Band, Supplement. Edition Leipzig, Verlag für Kunst und Wissenschaft. Ganzleinen DM 90,50.

An der Geburtstagsfestschrift für Herrn Stubbe haben sich wahrhaft viele Wissenschaftler aus aller Welt als Autoren beteiligt. Man zählt auf den 552 Seiten des Bandes 37 Originalpublikationen genetischen oder verwandten Inhalts und zuvor einen Geburtstagsbrief von Anton Lang aus East Lansing, Michigan, U. S. A., der für die Schmunzelecke gedacht ist. Der Anlaß hat, wie der vorliegende Band bestätigt, einen stattlichen Jahresband der bekannten Zeitschrift „Biologisches Zentralblatt" sowohl im Umfang wie aber besonders im Inhalt zusätzlich zum 86. normalen Jahresband ins Leben gerufen. Anton Lang hat schon ganz recht, wenn er schreibt, daß solche Zusatzbände mit eigener Paginierung bibliographisch oft Ärger bereiten können. Nun, wir werden also in Zukunft beim Zitieren nicht vergessen, hinter Band 86 den Zusatz „Supplement" zu setzen. Den guten Wünschen für das Institut für Kulturpflanzenforschung in Gatersleben und für seinen Leiter, die Anton Lang zum Ausdruck bringt, schließen sich Ref. und Schriftleitung dieser Zeitschrift auch jetzt noch nachträglich voll an. Es ist uns eine ganz besondere Freude, auf das Erscheinen dieses Supplement-Bandes an dieser Stelle hinweisen zu können. Es sei aber dem Ref. erlassen, eine Aufzählung aller abgehandelten Themen folgen zu lassen, zumal es sich ohnehin sehr empfiehlt, das Buch für die Bibliothek einschlägiger Institute der allgemeinen