

INTERRELATIONSHIP OF WOOD PROPERTIES OF LOBLOLLY PINE

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Within the short span of less than a decade, interest has burgeoned remarkably fast around genetic control of certain wood properties. In line with this manifestation research has been initiated to determine the degree of genetic influence on specific gravity, summer wood per cent, tracheid length, cell wall thickness, cell diameter, fibril angle, cellulose yields, per cent lignin, and other characteristics. In most instances each characteristic has been studied by itself, ignoring possible interrelationships among the variable properties; study of several characteristics jointly has been rare. Now it seems clear that if really meaningful results regarding genetic control of wood are to be achieved, it is necessary to determine whether characteristics are wholly independent, or whether several are so closely interrelated that if some are changed, the others will change also. Effective progress through the application of genetic principles is unquestionably dependent to a very large degree on the nature and extent of interrelationships existing between different characteristics. Failure or neglect to recognize such interrelationships where they exist could well render breeding programs ineffective or inconsequential.

Although the present paper does not deal in genetics per se, nor in actual inheritance patterns of various wood properties, it does represent an exploration of possible interrelationships in several important wood characteristics. Supporting data obtained from both genetic and non-genetic wood studies will center on characteristics largely of loblolly pine.

This paper will be divided into two parts, namely, (1) a report of interrelationships of four wood characteristics (both for core and outer wood) on 14 loblolly pine trees selected from lands of the Riegel Paper Corporation for use in their seed orchard, and (2) data from wood studies of the trees used in the Industry seed orchards. Wood property interrelationships both within individual trees and among large numbers of trees from a 10-state area will be emphasized.

¹ Most of the data obtained were from joint college-industry studies of trees used in the N. C. State-Industry Forest Tree Improvement Program.

What Is a Wood Property?

First, let us be sure we all understand what is meant by a wood property. Some "properties" are clean and easily defined; thus, tracheid length is unambiguous, and the only qualification needed is to designate "where" it is being measured. On the other hand, specific gravity, although commonly referred to as a wood property, must at least from a growth or genetic standpoint be considered as a complex of characters that may or may not closely interrelate to other specific characters, singly or in combination. Thus, even though specific gravity, per se, can be specifically defined and is relatively easy to measure, genetically it is essentially not an element but a compound. As stated by Schreiner (Zabel, 1956) "The genetics of specific gravity is a complicated problem--I have indicated earlier that it is an oversimplification to say that specific gravity of wood is inheritable. Specific gravity is obviously not controlled by a single hereditary factor. The length and diameter of the wood cells, thickness of the cell walls, proportion of springwood and summerwood, per cent of cellulose and lignin, and composition and amount of other chemical constituents of the wood, are some of the wood characteristics that--probably determine wood specific gravity. In respect to these wood characters, it is possible: (1) that they may be controlled by individual genetic factors; (2) that two or more may be under the control of a single factor; (3) that some, such as per cent of summerwood, may depend on more than one genetic factor; (4) that some may be linked, i.e., transmitted as a unit from parent to offspring--specific gravity is therefore the final expression of the effect of environmental factors on the inheritable potential of the tree to produce wood with a number of particular characters."

Schreiner has appropriately and succinctly emphasized the complex involvement of specific gravity in the genetics picture. Nevertheless, despite widespread recognition of this complexity, specific gravity is usually still regarded and handled as a unit wood characteristic. It will be so handled here, again, but not without the preceding preface to warn of these complexities. It is also well to keep in mind that numerous other characteristics of wood may be as complex as specific gravity.

RELATIONS OF FOUR WOOD CHARACTERISTICS OF LOBLOLLY PINE

For all trees used in the seed orchard of the Riegel Paper Corporation, determinations were made of the following wood characteristics in an effort to ascertain the worth of each selection: (1) specific gravity, (2) tracheid diameter, (3) tracheid length, (4) tracheid wall thickness, (5) cellulose, termed WRC¹, and (6) alphacellulose.

¹Stands for Water Resistant Carbohydrates, similar to holocellulose.

By means of the large (10 mm) increment borer, wood samples were extracted from the bole of the tree at the breast height position, i.e., 4.5 feet above the general level of the ground. These increment cores were then divided into two sections: (1) the first 7 rings from the pith (referred to as core wood, and (2) the remainder of the core from the 8th ring out to the cambium (referred to as outer wood). All trees sampled were excellent phenotypes and were the fastest growing, dominants in the stand. Six of the trees were from the North Carolina Coastal Plain, the remaining eight from the North Carolina Piedmont. All were young, vigorous trees averaging 34 years in age, 11.8" in diameter, and 70 feet in height.

Specific gravity, tracheid lengths, and cellulose were determined separately of each segment of each increment core; i.e., the core segment comprising the first 7 rings was handled and pulped as a unit, and similarly the outer wood from the 8th ring was treated as a unit. Maceration techniques and measurement methods were similar to those we normally use (Zobel, et al, 1960) with one major exception: all tracheids, whether whole or cut were measured so the average lengths will be less than for the whole tracheids only reported later in this paper. Length, width, and wall thickness data are based on 50 to 70 tracheids per core segment. Measurements of the tracheid characteristics were made for the Riegel Paper Corporation at the Institute of Paper Chemistry, Appleton, Wisconsin, while specific gravity and cellulose determinations were made at the School of Forestry, N. C. State College.

Both core and outer wood values are shown in Table 1. We shall examine these data from three directions, namely, (1) variation from tree to tree for each characteristic; (2) strength of the correlations of core to outer wood values; and, (3) interrelationships of wood characteristics among trees.

1. Variation from tree to tree.

For all four characteristics shown in Table 1, individual tree variation is impressively large; it can be noted here that variation also is equally large for cellulose values. For convenience, the data showing means and range have been consolidated in Table 2. The variation in tracheid lengths is less than that usually reported, but this outcome is not surprising since both cut and uncut tracheid measurements are included in this data. Inclusion of cut tracheids results invariably in a reduction in the percentage of the long tracheids which suffer disproportionately in the maceration treatment. Published data on cut tracheid lengths always show less tree-to-tree variation than is found when only whole, uncut tracheids are used.

Table 1 . Wood properties of trees used in the Riegel seed orchard, The "core" portion consists of rings #1 through #7 counting from the pith; the "outer" portion is from ring #8 outwards All samples taken at breast height (4.5 feet above the base of tree).

Tree No.	Tracheid Length ¹ Millimeters		Tracheid Width Millimeters		Wall Thickness Microns		Specific Gravity	
	Core	Outer	Core	Outer	Core	Outer	Core	Outer
9-2	2.63	3.73	.050	.049	5.16	7.69	.42	.55
9-3	2.28	3.58	.049	.046	4.82	9.49	.49	.58
9-4	1.64	2.81	.042	.049	3.39	4.44	.42	.49
9-5	1.44	3.26	.045	.046	3.53	6.46	.39	.46
9-6	2.00	3.30	.044	.047	3.92	6.20	.51	.61
9-7	2.30	3.54	.045	.053	3.59	5.61	.39	.50
9-9	1.89	3.76	.047	.050	2.82	6.94	.46	.52
9-10	1.84	3.67	.046	.056	3.67	6.81	.42	.52
9-12	2.49	3.55	.055	.050	4.81	7.84	.47	.59
9-14	2.28	3.86	.046	.053	4.22	6.30	.46	.49
9-15	2.02	3.88	.047	.051	4.14	6.84	.44	.50
9-16	2.13	3.83	.049	.061	4.19	5.85	.42	.43
9-17	2.02	3.56	.048	.054	4.07	6.94	.46	.52
9-18	1.82	2.86	.047	.052	3.90	5.62	.43	.51
Averages	2.06	3.51	.047	.051	4.02	6.65	.44	.52

¹ Tracheid lengths consist of measurements of both cut and uncut tracheids. Each value represents average of measurements on 50 to 70 tracheids.

Table 2. Averages and range of values for wood characteristics in the core wood and in the outer wood of some loblolly pine trees used in the Riegel seed orchard.

<u>Characteristic</u>	<u>Core Ave.</u>	<u>Outer Ave.</u>	<u>Core Range</u>	<u>Outer Range</u>
Specific Gravity	.44	.52	.39 - .51	.43 - .61
Tracheid Length (mm)	2.06	3.51	1.4 - 2.7	2.8 - 3.9
Wall Thickness (microns)	4.02	6.65	2.8 - 5.2	4.4 - 9.5
Tracheid Width (mm)	.047	.051	.042 - .055	.046 - .061
WRC	--	79.3	---	77.5 - 80.5
Alpha Cellulose	--	57.0	---	54.1 - 59.6

The observed individual tree variation is very encouraging to the geneticist; here it is of sufficient magnitude to indicate considerable chances for improvement. Having found this variability, his main job is to unearth the causes of the individual tree variation and to determine whether, or how much of, it is genetically controlled.

2. Relationship of Characteristics of the Core Wood to Outer Wood.

The strength of relationship of a wood characteristic near the center of the tree (core wood) to the same characteristic further from the tree center, (i.e., in the outer wood) is of a great deal of interest and importance. Although a complete literature review will not be made here, attention is called to a number of studies such as the ones by Kramer (1957), Jackson (1959), and Zobel & Rhodes (1955), in which the magnitude of relationships that might be expected for specific gravity and tracheid length have been indicated; these items will be discussed in considerable detail in the next section. It should be noted here, however, that even though the present data are based only on 14 trees, significant correlation coefficients of .55 and .54 were obtained respectively for the core and outer specific gravities and core and outer tracheid lengths. These coefficients are quite in line with other published data

Of special interest here, however, is the relationship between values for tracheid width and tracheid wall thickness for the core and outer wood samples, since previously published data for these characters are not available. As illustrated in Fig. 1, there is a statistically significant relationship in wall thickness between the first (core) and later formed wood having an "r" value of +061. In contrast to this finding about wall thickness, no significant relationship was found for tracheid width between the core and outer wood (Fig. 2). Lack of significance here would indicate that the tendency for development of thicker-walled tracheids shows up early in the life of the tree, while tracheid width, which often has considerable variation between the radial and tangential dimensions, has shown no relationship in the present study. Certainly better-designed examinations, including more trees, must be made before definite conclusions about tracheid width correlations can be made. However, judged from the present, though rather inadequate, data, it would appear that the trees with larger diameter tracheids at maturity do not necessarily have very wide tracheids near the pith.

The tracheids of outer wood are about 1.5 mm longer than those in the core wood; walls of outer wood tracheids are 2.6 microns thicker than those of the core wood; specific gravity of the outer wood is substantially (.08) higher than core wood; tracheid width of outer wood averages only slightly greater than core wood indicating that at least on these 14 trees the change isn't great from pith to bark.

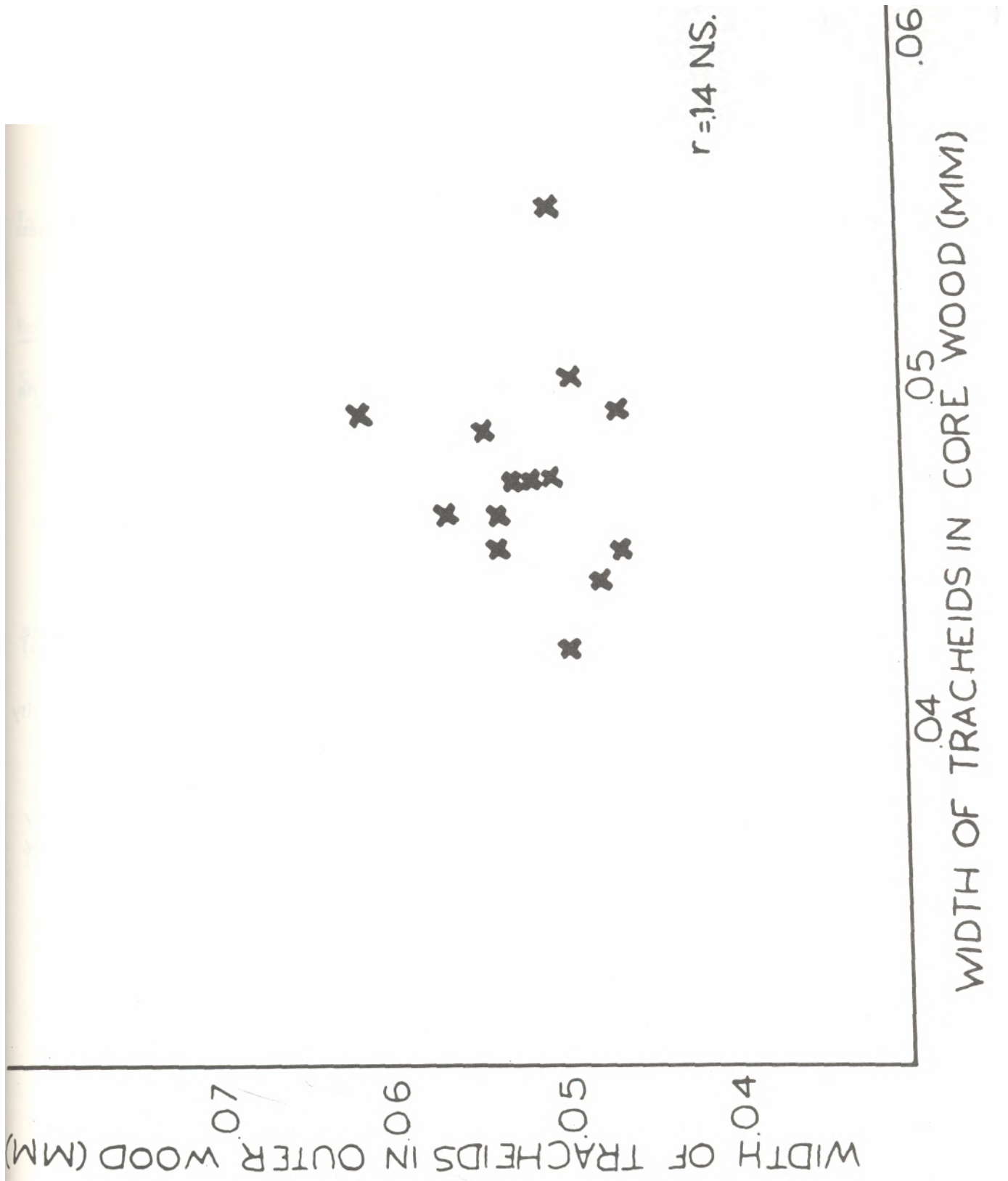


Figure 2. Graph Showing the lack of statistical significance found for tracheid width between core wood and outer wood.

In summary, then, it was found that specific gravity, tracheid length, and wall thickness of the wood formed in the first 7 rings from the pith are indicative of these characteristics during later years. Tracheid width did not show this relationship.

3. Interrelationships of Wood Characteristics.

To make the desired progress in breeding for wood properties, it is necessary to determine whether various properties in which interest is centered are interdependent, i.e., they are inherited as a unit, or does each one change without affecting the other.

A number of correlations were calculated among the six wood properties for the Riegel Paper Corporation seed orchard trees. Relationships shown in Table 3 include simple correlations for WRC and alpha cellulose

Partly because of the small sample number, (only 14 trees) none of the correlation coefficients in Table 3 were highly statistically significant. However, the coefficients indicate some *very* interesting trends, as will be briefly discussed below.

Specific Gravity, There appears to be a slight trend indicating that the higher specific gravity trees have slightly shorter tracheids. This trend is quite weak in the present study with $r = -.30$ as it was found in another recent study (Zobel et al., 1960), where "r" was $-.162$. However, because of the large number of trees involved in the latter, the "r" was significant at the 1% level, but though specific gravity accounted for only about 2.5% of the variability in tracheid length.. Trees with higher specific gravity might be expected to have more narrow cells, as was found here. Also, the higher specific gravity trees have thicker cell walls. For several previous studies we reported that the higher specific gravity trees yielded less WRC per unit dry weight of wood than the lower specific gravity trees, while in other studies the reverse was found. Thus, the picture on WRC is confusing and not susceptible to a satisfactory interpretation at this time; however, alpha-cellulose yields seem to be slightly to strongly related to specific gravity of the wood (Zobel & McElwee, 1958) unless these earlier results simply reflect some peculiarity in the method of analysis used.

Tracheid Length. There appears to be a trend for the trees that have longer tracheid to also have thicker walls and also to have higher cellulose yields, although again the correlation coefficients failed to reach an acceptable level of significance with the small number of trees involved, It might be expected that the larger diameter tracheids would have thicker walls, but it is difficult to reason why they should have higher cellulose yields, unless again it is a reflection of the method of cellulose determination.

Table 3. Correlation coefficients of several wood and growth characteristics for 14 loblolly pines, outer wood only for trees used in the Riegel seed orchard.

<u>Relationship of Wood Characteristics</u>	<u>Correlation Coefficient</u>
Specific gravity x tracheid length	-.30 NS
" " x tracheid width	-.58*
" " x wall thickness	.56*
" " x WRC ¹	-.35 NS
" " x alpha-cellulose	.24 NS
Tracheid length x tracheid width	.44NS
" " x wall thickness	.49 NS
" " x WRC	.12 NS
" " x alpha-cellulose	.04 NS
Tracheid width x wall thickness	.32 NS
" " x WRC	.48 NS
" " x alpha-cellulose	.39 NS
Wall thickness x WRC	.56*
" " x alpha-cellulose	-.15 NS
WRC x alpha-cellulose	.56*

¹Water resistant carbohydrates, similar to holocellulose.

* Significant at the 5% level.

NS Not statistically significant.

Correlation of Several Characteristics: No multiple correlations were calculated for this study, but a rough ranking was made to show the relative position of each of the 4 tracheid characteristics for each tree. When making this ranking, one fact immediately becomes evident; i .e., that most of these characteristics seem to be present in any one tree in a rather random manner without particular relationship to the other. This indication, of course, is reflected in the magnitude of the correlation coefficients. For example, we have high specific gravity trees with long tracheids and narrow cells, as well as with short tracheids and wide cells. Nearly all such combinations were found in the 14 trees studied. For purposes of illustration, eight of the trees so ranked are shown in Table 4, below. Four of these are shown graphically in Figure 3.

Table 4. Ranking of selected trees by four characteristics. The numbers indicate relative positions in the order of the 14 trees studied, the higher numbers indicating high specific gravity, long tracheids, wide tracheids, and thick-walled tracheids; the low numbers indicating low, short, narrow, and thin-walled, respectively.

Relative Rankings - From 1 to 14								
Tree #	Total Points	Specific Gravity	Tracheid Length	Tracheid Width	Wall Thickness	Classification		
						Sp. Gr.	Length	Width
3	35	12	8	1	14 high	inter.	narrow	thick
4	9	3	1	4	1 low	short	narrow	thin
6	28	14	4	3	7 high	short	narrow	inter.
9	36	9	11	6	10 inter	long	inter.	inter.
10	40	10	9	13	8 high	inter	wide	inter.
12	38	13	6	6	13 high	inter	inter	thick
15	36	5	14	8	9 low	long	inter	inter.
16	31	1	12	14	4 low	long	wide	thin

From Table 4 it is obvious that we have trees with many combinations of wood characteristics such as high specific gravity with short, narrow, intermediate-walled cells, or of high specific gravity, intermediate tracheid length with narrow, thick-walled cells. These results are encouraging to the geneticist because they indicate that intensive selection for specific gravity, for example, will not result in also having all short tracheid trees, or all wide tracheids. Although there is some indication that thick walls and short tracheids tend to be carried along with high specific gravity, individual trees are found with nearly

Ranking of four selected trees by four characteristics indicating the lack of interdependence of the characteristics. The vertical position of each point indicates the relative value for that characteristic.

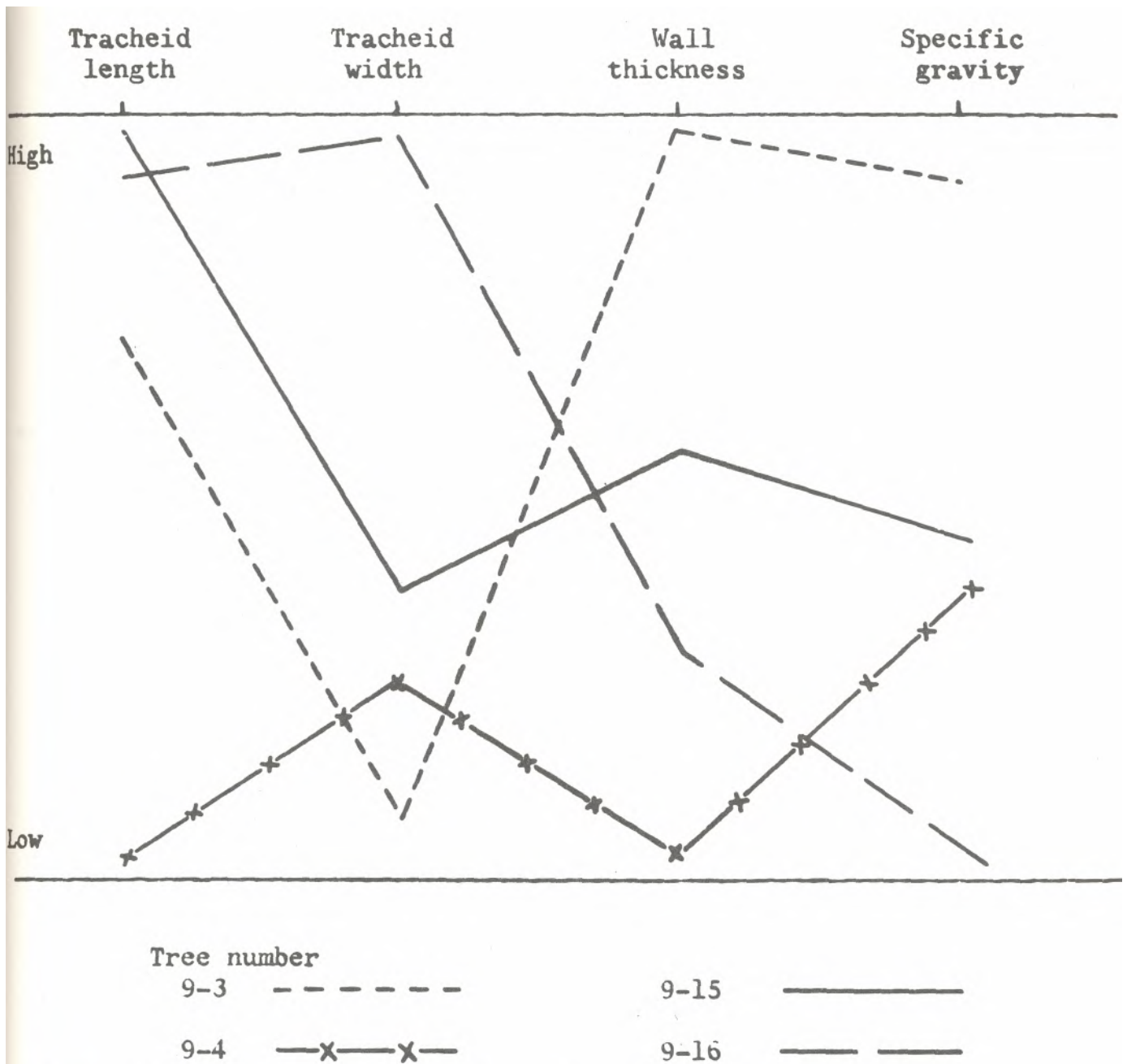


Figure 3. Graph showing lack of interdependence of four characters.

all possible combinations of factors. Since specific gravity itself is not a unit character, but the resultant of several characteristics, such as wall thickness and cell width, each of which appear to be fairly independent, indications would then be that gains in specific gravity would be modest. Heritabilities already in the literature (Zabel, 1961) indicate that very useful improvement can be made in specific gravity despite this complexity. With care, these gains can be achieved without sacrificing desired tracheid lengths or cell widths.

SOME MISCELLANEOUS WOOD PROPERTY RELATIONSHIPS

During the course of years, a mass of data has been obtained involving wood property relationships, both within trees and between trees. These data were not obtained as the result of studies specifically designed to determine such relationships, but were accumulated during analysis and assessment of the wood properties of the trees selected for use in the seed orchard program. This large amount of data gives a good opportunity to assess wood character variations within trees as well as relationships of certain characteristics among trees. The bulk of the data was obtained for loblolly pine trees selected for seed orchards of companies in the N. C. State--Industry Cooperative Tree Improvement Program. Trees were analyzed from a number of different sites and geographic regions within a 10-state area in the southeast. Although the trees analyzed are from numerous different environmental situations, they all have two things in common; i.e., all are the dominant, fastest growing, best formed trees in their respective areas, and all are somewhere near rotation age (30 to 50 years depending on the company involved).

Relationships of a Single Wood Characteristic Within a Tree

Specific gravity relationships of core wood to outer wood (i.e., wood near the tree center to that near the bark) have been reported several times. Correlations were from fairly high to quite high, and all reported figures are significant at the 1% level, showing that the specific gravity of the core wood is indicative of the specific gravity of the outer wood. In the present study, the correlation coefficient obtained was +.476 for trees from the Piedmont, +.506 for trees from the Coastal Plain, and +.517 for both physiographic provinces combined, representing measurements from a total of 313 trees. It is quite surprising that the core to outer wood specific gravity relationship turns out to be as strong and consistent as the data reported here indicated. The large amount of pitch and compression wood usually found near the center of the tree render accurate determination difficult.

In some preliminary studies, Kramer (1957), Zobel et al. (1960), and others have determined that there are within-tree relationships in tracheid length. Kramer found good correlation between tracheid lengths of wood formed in the 10th ring from the pith and that formed nearer the bark. From our studies, as well as from some made by Albemarle Paper Company, it would appear that the 15th ring is the earliest one that can be used for acceptable classification of a tree as to tracheid length. In our industrial work, we have made it a standard procedure to measure tracheid lengths (uncut tracheids) for the 15th and 30th ring from the pith, in order to determine an indicative tracheid length for the tree.

In a previous report (Zobel et al. 1960) the lengths of tracheids from the 15th and 30th rings were reported to be very highly correlated. Upon analyzing the data for 340 of our select trees, we have found correlation coefficients as shown in Table 5.

Table 5. Relationship of core to outer wood specific gravities and of 15-year and 30-year tracheids within the same tree. These measurements were made on the same group of trees.

Geographic Location	Specific Gravity		Tracheid Length	
	Number of Trees	"r" Value (core to outer)	Number of Trees	"r" Value (15 to 30)
Piedmont (Ala., Ga., S.C., N.C., and Va.)	114	.48**	134	.56**
Coastal Plain (same states)	199	.51**	206	.55**
All Trees Combined	313	.52**	340	.59**

The above indicates, then, that the length of the 15-year tracheids are a fairly good indication of the 30-year length, though certainly not precise enough for prediction purposes for any one individual tree. Use of tracheids from rings less than the 15th year would be desirable and probably will be feasible in later progeny tests. However, for an estimate of tracheid length characterizing the parent, we plan to continue to use 15 and 30-year tracheids. Near the center of the tree there is so much compression wood (about 50% of total volume of first 7 rings) and the tracheid length increase is so rapid from one year to the next, that working too near the pith can introduce chances for errors of very great magnitude.

Relationship Among Specific Gravity,
Tracheid Length, and Growth Rate

It is our objective in this section to report interrelationships (by simple correlations) among the three variables of specific gravity, tracheid length, and growth rate. Data for these variables were obtained from the same group of trees for which within-tree variations were shown in the previous section (Table 5). As shown in Table 6, the data were calculated for Piedmont and Coastal Plain trees separately, and for the trees from both provinces combined.

Table 6. Interrelationships of the three variables of specific gravity, tracheid length, and growth rate for trees used in industrial seed orchards.

<u>Relationship</u>	<u>Geographic Location</u>	<u># of Trees</u>	<u>Correlation Coefficient</u>
Specific gravity x tracheid length	Piedmont	149	-.152 NS
	Coastal Plain	213	-.070 NS
	All trees	362	-.160*
Specific gravity x rings per inch	Piedmont	153	.199**
	Coastal Plain	216	.026 NS
	All Trees	369	.117*
Tracheid length x rings per inch	Piedmont	130	-.017 NS
	Coastal Plain	206	.181**
	All trees	336	.105 NS

* Significant at 5% level

** Significant at 1% level

NS Not statistically significant

Caution must be exercised in interpreting these data. As was pointed out previously, the correlation coefficient must be viewed from two angles: (1) is it statistically significant, and (2) is it large enough, numerically, to be of practical importance? The number of samples on which correlations are based is important; for example, the correlation coefficient of tracheid length to tracheid width (Table 3) for the 14 trees in the first section of this paper was .49 but not significant. However, specific gravity to tracheid length had $r = -.160$ (Table 6) which proved to be significant at the 5% level, because 361 trees were involved. The analysis that follows will take into consideration both interpretations of the correlation coefficient.

There is a consistent, though very small negative relationship between specific gravity and tracheid length. Although this relationship would suggest that higher specific gravity trees have shorter tracheids, the correlation coefficients are so small as to be of no practical importance (Table 6).

As has been found for other studies, when outer wood is compared, the relationship between specific gravity and growth rate is very low. In the present case, for all trees, the relationship was significant at the 5% level, but the correlation coefficient was so low that less than 2% of the variation in specific gravity is accounted for by growth rate; the coefficient indicates that slower growing trees have slightly higher specific gravities.

The difference in significance of correlation coefficients between Coastal Plain and Piedmont is of interest (Table 6); if it developed to be real, it would be of interest to attempt to explain. It is commonly assumed that in much of the Piedmont, soil moisture during the warm part of the year may be limiting. It is also assumed that plentiful soil moisture during summer would keep the tree growing for a longer period into the fall and thus would result in the trees having a higher specific gravity. However, a tree that would continue to grow longer in the fall probably would have faster growth if measured by rings per inch as was done in this study. Thus, the result would be higher specific gravity with less rings per inch (faster growth), just opposite to the relationship reported in Table 6. Because of changes that occur within the tree, one might expect the rings-per-inch: specific-gravity relationship to be greatest for stands where age variation is the greatest. In the present study, however, the greatest age variation was in the Coastal plain, but the best relationship of growth rate to specific gravity was obtained in the Piedmont.

¹Although rings per inch is not a good measure of growth per se, it is satisfactory when the trees compared are of similar ages and when the time of growth involved in the measured period does not comprise greatly different weather "cycles".

It has commonly been considered that the faster growing trees usually have shorter tracheids than the slower growing trees. The data in Table 6 show this only for trees growing in the Piedmont. Although the correlation coefficient here is significant at the 1% level, only about 3% of the variation in tracheid length is accounted for by growth rate. Additional concepts regarding this relationship are given in the Discussion section that follows.

Discussion and Summary

From the two groups of data analyzed in this paper, and from the data in papers cited, it appears that (I) Within a tree at the breast height position on the bole:

(a) Specific gravity of the wood of the first formed rings (from 7 to 10) is highly correlated to that formed nearer the bark. Although highly statistically significant, the correlation values themselves are not numerically high. Actually, when one considers the potential experimental errors, the magnitude of errors that can be caused by pitch and compression wood near the tree center, the natural variation within a tree around the circumference of its trunk, it seems surprising to find correlation coefficients of the order of .5 to .6. Results of the relationship of wood near the pith to that near the bark have been reported a number of times by a number of different authors for a very large number of trees, and all show some degree of relationship.

(b) Although most studies have emphasized specific gravity, several, have looked into the relationship of uncut tracheids formed near the tree center compared to those formed nearer the bark. Some authors have reported that the tracheid length near the pith can be used as predictive value for those formed farther out. Others indicate this predictive function not to be reliable unless the comparison is made with tracheids taken some distance from the pith, for example, from the 10th ring. Although we have not set up tests to specifically show this, some of our preliminary results have indicated that the tracheid length for the 15th and 30th ring best characterizes a tree. Therefore, correlations between the tracheid length at year 15 and at year 30 have been made and are always found to be highly correlated with statistically significant "r" values from .5 to .7. However, in the first section of this paper, comparisons were made between tracheid lengths, including cut ones, between the core segments comprising the first 7 rings from the pith and that formed later, and the correlations were highly significant statistically with "r" = .54. Just as for specific gravity, it is believed that the prevalence of compression wood especially affects the tracheid lengths from the rings nearest the pith. However, results reported here are for a large number of trees, and they suggest that a strong relationship between tracheid lengths formed at different distances from the pith may be expected.

(c) There is a highly statistically significant correlation ($r = .61$) between the thickness of tracheid walls at the center of the tree and of those formed farther out. Conversely, there was no correlation between the width of tracheids formed near the center and width of those formed farther out. These results must be considered only as preliminary indications, since they were for only 14 trees and the methodology for studying cell dimensions has not been as yet perfected.

(2) Between trees at the breast height location:

(a) For all characteristics studied, between-tree variation was very large, a phenomenon now becoming widely recognized. Often the difference between trees can be in the order of 100%; for example, the tree with the shortest tracheids at 30 years was 2.6 mm, while the tree with longest tracheids was 6.1 mm. The magnitude of this tree-to-tree variation cannot be overemphasized, and must be recognized when any wood property studies are made. This magnitude of variation makes it appear that the possibilities of improvement may be large.

(3) Relationships between different characteristics in trees sampled at breast height:

(a) Specific gravity x tracheid length. There is a very weak negative relationship between specific gravity and tracheid length. This means that trees with higher specific gravities will have slightly shorter tracheids. In a previous study (Zobel et al., 1960) obtained an "r" of $-.16$ for over 300 trees. In the present study, "r" of $-.16$ was also obtained for 362 trees, while "r" of $-.3$ was obtained for the 14 selected trees (but here with cut tracheids included in the sample rather than whole tracheids only). In a similar study, van Buijtenen et al. (1961) obtained an "r" of $+.22$ for 23 trees. These results make it obvious that the effect of specific gravity on tracheid length is very small. The possibility, or danger, of changing tracheid length by intense selection for specific gravity does not appear to be great.

(b) Specific gravity x tracheid width. Data for this relationship were obtained only for 14 trees, but seems reasonably strong with "r" equal to $-.58$. Thus, judged from this limited sample of 14 trees, it would appear that trees with higher specific gravities have distinctly narrower tracheids. This is not an unexpected relationship since it is entirely feasible that higher specific gravity may not be only the resultant of thicker cell walls, but also the resultant of having narrower cells, even though the walls are of the same thickness.

(c) Specific gravity x wall thickness. Again we have data only for 14 trees, but as would be expected, the trees having thicker cell walls also had higher specific gravities ($r = .56$). The correlation coefficient was not so high as might have been predicted, but it

is quite evident that part of the specific gravity variation is due to the cell width as well as the wall thickness. (This outcome in turn, is all confounded with the percentage summer wood). This relationship is illustrated in Figure 4.

(d) Tracheid length x tracheid width. For the 14 trees studied, a correlation coefficient of .44 was obtained for tracheid length to width, This "r" is not statistically significant, due to the small number of trees involved, but it would indicate a possibility that trees having longer tracheids also have wider tracheids. Such a relationship could logically be expected.

(e) Tracheid length x wall thickness. Results are nearly identical to those for length x width, with a correlation coefficient of .49, Thus, it appears for the 14 trees involved in this study that the trees with longer tracheids will also have thicker-walled tracheids.

(f) Tracheid width x wall thickness . The "r" value here was .32, which was nonsignificant. Any trend present would suggest that the wider tracheids have thicker walls, but this relationship is weak for the 14 trees used in the present study.

(g) Cellulose characteristics. Cellulose characteristics seem to be independent of tracheid characteristics with the exception of wall thickness. Because of the gross method employed in these cellulose determinations, a cellulose wall-thickness relationship should be viewed with caution, and may simply reflect ease of penetration of the chlorite; however, the "r" value of .56 is of a magnitude that points toward the necessity for a better and more precise study of this relationship.

(h) Growth rate x specific gravity. In the present study, for 370 trees, it was found that the slower growing trees had slightly higher specific gravities, but growth rate accounted for less than 2% of the specific gravity difference. These results are similar to those in a recent report by Zobel et al . (1960), in which it was indicated that for over 300 trees also less than 2% of the variation in specific gravity could be accounted for by growth rate. Growth rate x specific gravity relationships are also in turn confounded with compression wood. It would seem to be a fair summary from our data to say, then, that on the basis of analyses of over 670 trees, all of which were either dominants or strong co-dominants in their respective stands, growth rate plays a very minor part in influencing specific gravity values.

(i) Growth rate x tracheid length . In the present study no significant relationship was found between growth rate and tracheid length with $r = .105$. This study has limited validity, however, since it is relating growth rate of the tree from the 10th year on to the length of tracheids at the 30th year The objective of the present study was to determine, in a

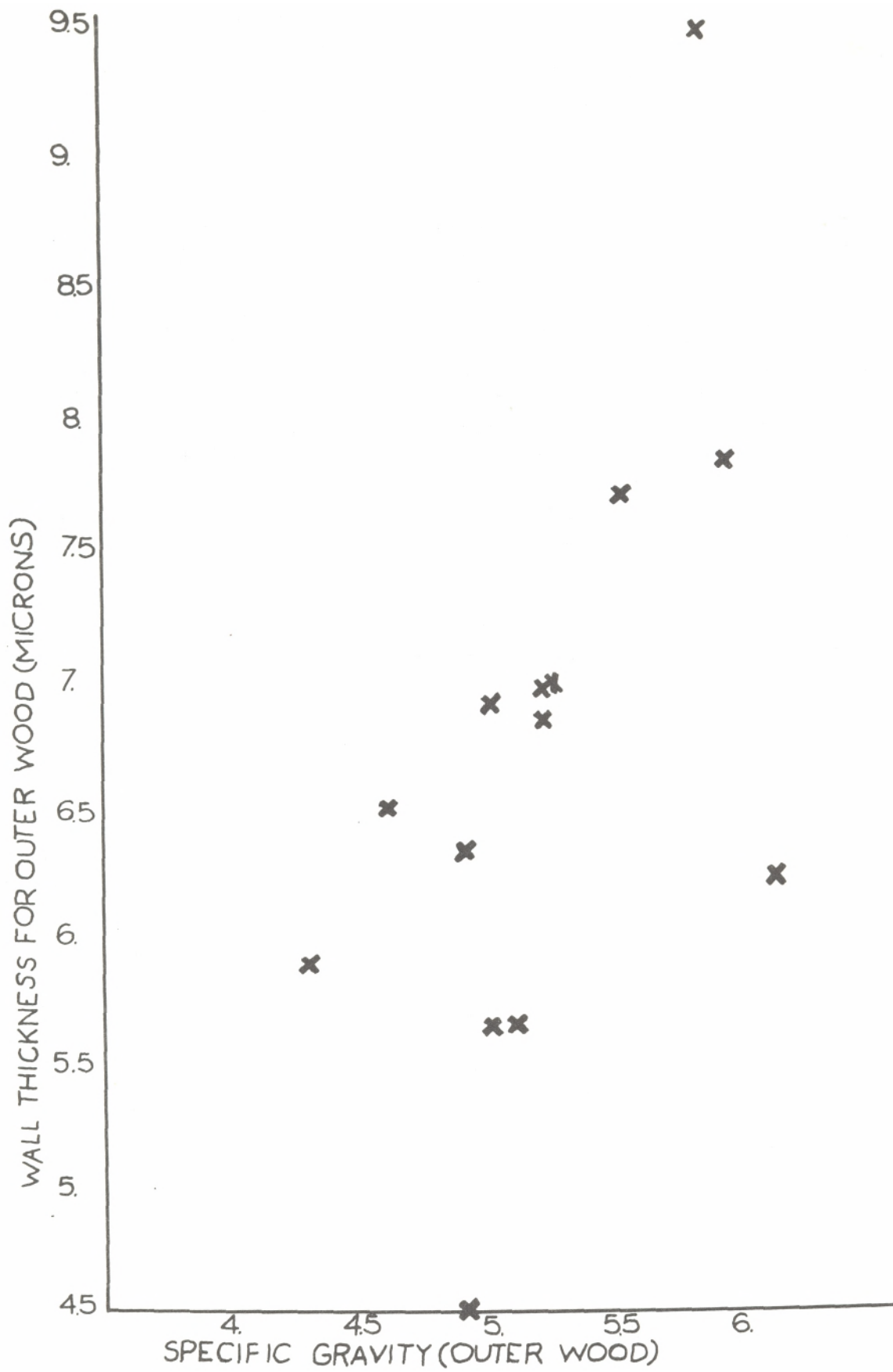


Figure 4 . Graph showing relationship between wall thickness and specific gravity for 14 trees, $r = .56$.

broad way, if the fastest growing trees had different tracheid lengths than the slower growing ones, using length of tracheids at 30 years to characterize the tracheid length of the whole tree. Such a comparison would have general implications only. In a previous study, however, the controls were made on a more limited time period with growth of the 24th to 30th year compared to tracheid length at the 30th year. Under these conditions 10% of the variation of tracheid length could be accounted for by differences in growth rate. If individual years had been used, the relationship might have been even higher. From the data presented here, then, we can deduce that the fastest growing dominants and codominants do not have tracheids much different in length than the slower growing dominants and codominants.

It has been shown that a change in growth rate within a single tree (Bissett et al., 1951) is accompanied by a change in tracheid length.

(4) No multiple correlations were calculated, but it was found that trees with almost all possible tracheid characteristic combinations were found. This outcome indicates that there is considerable basis for hopes of developing strains of trees with varied wood characteristics.

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