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Genetic and Environmental Factors Affecting Growth and Wood Properties of Loblolly Pine Seed Sources in Louisiana.

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ABSTRACT

This study was initiated to determine the geographical variation in wood properties and growth traits of loblolly pine trees from local Louisiana seed sources, to investigate seed source-plantation interaction, and to test for correlation between wood properties and growth characteristics.

Data were collected from 13-year-old trees derived from five geographic seed sources (East Feliciana, St. Tammany, Vernon (N), Vernon (S), and Washington parishes) growing in plantations located in Vernon Parish, East Feliciana Parish, and Washington Parish, Louisiana. Growth rate (diameter and height) was measured and wood core samples were taken for determination of specific gravity, tracheid length, percentage latewood, annual ring width, and cell dimensions.

Analyses of variance revealed no significant differences among seed sources in diameter, height, percentage latewood, and tracheid length. Significant seed source variation was found for specific gravity, annual ring width, and cell dimensions. There appeared to be an east-west pattern associated with annual ring width, but no definite geographic pattern could be associated with the other characteristics. It was apparent that the St. Tammany seed source had the highest growth rate and together with the Vernon (S) seed source, had the highest specific gravity among the five seed sources tested.

Significant plantation differences were found for specific gravity, tracheid length, and cell dimensions, suggesting strong environmental control over these traits.

Linear regression and correlation analyses of percentage "normal" seasonal precipitation (spring, summer, and autumn) and growth and wood properties revealed that autumn precipitation was critical for height growth rate and production of high density wood, while spring and summer precipitation were critical for diameter growth rate, production of wider annual rings, and large lumened cells in the xylem of loblolly pines in this Louisiana study.

Simple correlation analyses between the wood properties and growth traits showed that specific gravity was highly positively correlated with cell wall thickness, percentage latewood, tracheid length (in the bark section), diameter, and height, and was significantly negatively correlated with cell lumen width. No correlation was found with annual ring width. Latewood and earlywood tracheid lengths were highly correlated within a growth ring but not between core sections (pith and bark). Annual ring width, diameter, and height were strongly positively correlated.

It was concluded that very little geographic variation in growth and wood properties existed among the five Louisiana seed sources. Also, the differences in performance of seed

sources among the three planting sites were attributed to a great degree to differences in rainfall distribution among the three plantations.

INTRODUCTION

The ultimate goal of provenance testing is tree improvement. According to Zobel (1971) this means improvement in growth, form, adaptability, resistance to insects and diseases, and wood quality.

Moving plants from their native location to another affects their growth and form because growth is a function of the genetic make-up of the plant and the environment where it grows. Generally, some forest tree selections perform better in certain localities than individuals of the same species from other places. The best adapted geographic strain of trees is of paramount importance to foresters in the selection of planting stock that can grow at minimum cost in the shortest possible time. Use of stock of the wrong geographic source can eliminate any chance of profit from a plantation.

It is therefore imperative to have a practical guide for the choice of the best seed source for reforestation. Conventional provenance tests, in which trees of several different geographic origins are planted together in one place and observed for a number of years under field conditions, are designed to provide this information. The major objectives of these tests are to determine genetic differences related to geographic origin and to choose the best regions from which to collect seed for commercial purposes. Additional information on underlying

physiological and genetic differences, on the inheritance of a number of traits other than growth rate and form, and on the response of genotypes to different environments may also be obtained through provenance testing.

Growth rate and wood qualities are measures of the potential commercial value of a particular geographic seed source. Specific gravity was once considered as the main indicator of wood quality. It is an index of the amount of wood substance in a given piece of wood, and is related to certain other physical properties of wood. Also, it is very simple to determine. However, a specific gravity determination does not provide information about the actual constitution of the wood substance, i.e., amount of cellulose, lignin, extractives, etc., or the distribution of these. Specific gravity is not only affected by the cell wall material, but also by the packing (apparent) density of this material and the amount of the other cell constituents such as extractives.

As it relates to tree growth, an increase in specific gravity is attained principally by an increase in percent latewood in the annual ring and an increase in the cell wall thickness of the individual tracheids. Wood properties, as other characteristics, vary their expressions among individuals. This variation is the result of the genetic constitution of the individual tree and the action of the environment on this genotype. According to Zobel (1971), wood specific gravity is

really a complex of several characteristics and has responded well to selection because it is highly genetically controlled.

Tracheid length is another wood characteristic that affects wood quality. Like specific gravity, it is genetically as well as environmentally controlled (Greene 1966, Smith 1967, Rone 1970).

Height growth rate has a moderate genetic component (Van Buijtenen 1963, 1969) but diameter is more affected by environment (Van Buijtenen 1963, Steinhoff and Hoff 1971). Since growth *per se* is genetically controlled, wood will be affected by genetic manipulation of growth rate to the extent that the two are related. The growth rate-specific gravity relationship is controversial and varies with species and geographic location.

Knowledge of the amount of geographic variation in a species is of paramount importance before any further genetic improvement method, such as selection and breeding, is attempted because it helps determine the limits for genetic improvement. Several studies have been made involving different geographic seed sources of loblolly pine (*Pinus taeda* L.) (Lantz and Hofman 1969, Wells 1969, Saucier and Taras 1967, Thor and Brown 1962) but the seed sources studied were usually widely distributed. The present study was designed to determine the amount of variation in growth and wood properties of loblolly pine populations within a small portion of the species range

in southern Louisiana. The specific objectives of this investigation of loblolly pine seed sources were:

1. To determine the extent of variation in growth rate, specific gravity, percentage of latewood, average annual ring width, tracheid length, and cell dimensions among five southern Louisiana populations of loblolly pine replicated at three planting sites.

2. To test for correlations between these characteristics.

3. To investigate seed source-environment interactions through evaluation of the data from the three planting site replications.

REVIEW OF LITERATURE

Heritability and variation studies of measurable tree characters usually use materials from progeny tests, seed source studies, and plus or elite trees in natural stands. Specific gravity and tracheid length dimension have been the most intensively studied wood properties. Literature on the subject of wood variation, correlation, and inheritance is voluminous. Therefore, the literature cited in this review is only that which is most relevant to this study. Goggans (1962) presented quite an intensive review of research on the genetics of wood properties through 1961. The literature reviewed for this investigation is summarized and presented under the broad categories of variation, inheritance, and correlation in each wood property or trait.

Variation

Specific gravity

There is a wide range of variation in specific gravity within an individual tree (Spurr and Hsuing 1954). Within the stem of many conifers, specific gravity generally increases from the pith outward to the cambium and decreases from the base of the tree toward the crown. While exceptions can be found, this general pattern has been reported by numerous authors (Paul 1957, Wellwood 1960, Zobel and Mc Elwee 1958, Panshin *et al*. 1964).

Geographic variation in wood specific gravity has been well documented. In general, for the commercial southern pines (*Pinus taeda* L., *P. elliottii* Engelm., etc.), wood specific gravity is higher in the southern and coastal parts of the species range and decreases northward and inland (Zobel *et al.* 1972). The pattern for individual species is more complex, however. For loblolly pine, wood density decreases from south to north in the Coastal Plain while in the western part of the range, density decreases from north to south (Zobel *et al.* 1960, Jackson and Strickland 1962). In the southern part of its range it increases from east to west. In contrast, Lantz and Hofman (1969) found that variation in specific gravity of young loblolly pine in North Carolina was associated with plantation location, with all geographic sources exhibiting their highest specific gravities in coastal plantations.

To determine whether specific gravity is affected by site factors, Zobel and Rhodes (1955) took wood samples from some 7000 trees from vigorous second-growth stands in East Texas. They concluded that the interaction of the site and genetic factors plays a large role in producing differences in specific gravity. Mitchell and Wheeler (1959) studied specific gravity variation in the major southern pines, and concluded that the variation pattern for loblolly pine showed a good relationship with warm-season rainfall. They found that this resulted in a broadly diagonal effect of increasing specific gravity from

northwestern to the southeastern part of Mississippi. Another seed source study of loblolly pine (Thor and Brown 1962) showed that in Tennessee the specific gravity of the six sources was significantly different.

Variation in specific gravity for other southern pines (e.g., slash, shortleaf, longleaf, and Virginia pine) has also been reported by numerous authors. Specific gravity of selected slash pine from throughout the species range was determined from breast-height wood samples by Goddard and Strickland (1962). Grouping the trees into relatively discrete geographic areas, they found that highly significant differences in wood density exist between areas, increasing from west to east and from north to south in a definite pattern. For shortleaf pine, (Pinus echinata Mill.), the variation pattern for specific gravity was more pronounced in a north-south direction than east-west (Posey and Bridgwater 1970). In their study, specific gravity was determined from both unextracted and extractive-free wood. The variance associated with seed source was greater for specific gravity of extractive-free wood than for unextracted wood, indicating that extractives may tend to mask actual specific gravity differences between sources.

In a study conducted in Virginia, specific gravity among seed sources of longleaf pine (Pinus palustris Mill.) was found to be significantly different (Saucier and Taras 1966). One Florida source had significantly lower specific gravity than all other

sources tested and was less frost resistant. Although data indicated a racial difference in specific gravity, a valid conclusion cannot be made because of confounding by the incompatible environment of the plantation site which is far north of the natural range of longleaf pine. It is possible that differences among sources in susceptability to frost damage may have caused or were associated with specific gravity differences observed in the study. When the Florida seed source was omitted from the analysis of variance, there were no significant differences in specific gravity among the other five sources (Virginia, Louisiana, Mississippi, Georgia, and South Carolina). Specific gravity of Virginia pine (*Pinus virginiana* Mill.), however, showed significant differences among 13 natural stands in Kentucky and Tennessee (Thor 1964). Differences in specific gravity among both trees and stands proved to be largely due to differences in the amount of extractives in this case, illustrating that extractive content may serve to create differences in specific gravity as well as to mask these differences in other instances.

Geographic variation in specific gravity for some other commercially important pines has also been studied. Rees and Brown (1954) in correlating wood density and seed source in a young plantation of red pine (*Pinus resinosa* Ait.) tried to hold constant or statistically uniform all variables that might introduce systematic variation in the average specific gravity

by localities. Using trees from 18 sources grown in the same plantation for 17 years, they found that there were significant differences in specific gravity among seed sources. However, when one source was omitted, no significant differences were detected among the remaining 17 sources. It was therefore concluded that the wood produced in trees from all other sources did not differ in density. This finding was similar to that of Peterson (1967) whose provenance study revealed a slight but statistically significant difference in specific gravity among provenances of red pine.

Geographically, specific gravity of white pine (Pinus strobus L.) and red pine generally tends to increase from north to south and from west to east (Gilmore 1968). While the directional effect is not as pronounced in these northern species, these results conform to the patterns found for the southern pines.

Provenance studies in Scots pine (Pinus sylvestris L.) also showed wood specific gravity to be significantly different among seed sources (Echols 1958 and Dorn 1969).

When geographic variation in specific gravity of five-year-old jack pine (Pinus banksiana Lamb.) was analyzed by King (1968),he found that even though real differences existed among seed sources, the selection of seed sources for higher specific gravity is apparently not feasible in trees of this age because: (1) the over-all variation in specific gravity in juvenile wood is too low to allow any meaningful selection; (2) there is a strong negative correlation between specific gravity and growth

rate in juvenile wood and (3) growth rate has only a minor effect on specific gravity in mature trees. It is apparent that as trees mature, factors other than growth rate assume an increasing importance in determining specific gravity.

Tracheid length

The within-tree variation pattern for tracheid length in conifers is remarkably similar to that of specific gravity. Coniferous tracheids, at any given height, increase in length from the pith outward (Echols 1955, Kramer 1957, Dadswell and Wardrop 1960, Choong *et al*. 1970). In loblolly pine, tracheid length increased to a maximum with increasing height in the tree, and then varied irregularly (Greene 1966). Jackson and Greene (1957) reported that there was no difference in length of earlywood or latewood tracheids in slash and loblolly pines. However, Dadswell and Wardrop (1960) found that tracheids of latewood were slightly longer than those of earlywood in *Pinus radiata* D.

Variation in tracheid length among trees within a stand and among geographic areas does exist. Kramer (1957) found that there were large differences in tracheid length in a loblolly stand. This was confirmed by Zobel *et al*. (1960) who also discovered large and statistically significant differences in tracheid length between trees from different physiographic areas. In their study, a gradual increase in tracheid length in a north-to-south direction was apparent. This north-to-south increase in tracheid length was also found for shortleaf pine (Posey *et al*.

1970) and for Scots pine (Dorn 1968), but Virginia pine tracheid length increased from south to north (Thor 1964).

In other provenance studies of coniferous species, tracheid length was found to vary among seed sources but no clinal patterns were evident. Echols (1958) found that Scots pine trees from different provenances had significantly different tracheid length. Henderson and Petty (1972) reported that in lodgepole pine (Pinus contorta Dougl.) tracheid length was significantly different between provenances. For several Mexican species, Zobel (1965) presented evidence to show that tracheid length varied among geographic areas.

King (1968) determined the tracheid lengths of jack pine from 100 seed sources and found significant differences. He concluded that tracheid length as estimated from three-year-old wood may give a fair indication of mature-tree tracheid length when a wide range of genetic diversity is under investigation. Posey et al. (1970) found highly significant differences in tracheid length among seed sources in 10-year-old shortleaf pine (Pinus echinata Mill.) grown in one of two plantations in Oklahoma. In the other plantation, differences were not statistically significant indicating a very high degree of genetic-environmental interaction in this trait. In an earlier study, Thor and Brown (1962) found that tracheid length of loblolly pine did not show significant differences among six seed sources tested in Tennessee. Similar results were found for Norway spruce (Picea abies) (Stairs and Adapa 1969).

Tracheid cross-sectional dimension

The variation pattern for tracheid cross-sectional dimension is not as well investigated as that for specific gravity or tracheid length, but published data (Hata 1949, Miller 1959) seem to indicate that the variation follows a pattern similar to that of tracheid length. The diameter and wall thickness of the earlywood tracheids increase from the pith to the cambium while diameter of the latewood tracheids is variable in Pinus and Larix (Schultze-Dewitze 1958). They also found that wall thickness of latewood tracheids tended to increase from the pith outward.

There are indications that tracheid cross-sectional dimension varies not only within a tree but also between trees and among provenances. In a provenance study in Pinus contorta Dougl., Henderson and Petty (1972) found that the width of tracheids differed significantly between two provenances.

Proportion of latewood

Proportion of latewood, like specific gravity, usually increases from the pith toward the cambium as ring width decreases. This change from pith to cambium in conifers is generally recognized and has been reported by Rendle (1958b). Paul (1939) and Young (1952) stated that, in a ring, the percentage of latewood decreased from the ground level to the top of the tree.

Kennedy (1961) found considerable between-tree variations

during earlywood cessation in Douglas-fir, with large proportions of latewood when formation of earlywood ceased early. However, Van Buijtenen (1955) observed that mature loblolly pine in Texas occasionally developed a second earlywood ring if a wet period followed a prolonged summer drought.

Very little has been reported concerning the geographical variation of percentage latewood. Larson (1957) found that percentage latewood in slash pine increased from north to south and west to east within the species range. In a provenance study, Klem (1957) discovered that Norway spruce of German origin had a higher specific gravity than native spruce because it grew for a longer period during each year and thus produced more latewood. A comparison of wood properties of coastal and interior provenances of lodgepole pine revealed that percentage of latewood differed significantly between the two provenances (Henderson and Petty 1972).

Width of annual ring

Within-tree variation in the width of annual rings is well established. Width of annual ring decreases from pith to bark. Many investigators also recognize the existence of corewood and maturewood in a tree; however, these two types of wood must be differentiated in studies of ring width. Compared to maturewood, the corewood, which occurs in the center portion of the bole, has wide growth rings, very little latewood, short tracheids, and low density. No definite line of demarcation can be established

between corewood and maturewood within an individual tree, for the transition from one type of wood to the other takes place gradually over several years. The duration of corewood formation varies with species. In a group of loblolly pine studied by Zobel and Mc Elwee (1958), corewood extended outward from the pith for approximately seven annual rings at any height in the merchantable portion of the bole. In a later study, Zobel et al. (1959) reported that corewood formation is extremely variable, ranging from five to eight years for slash pine and from seven to 11 years for loblolly pine. In Monterey pine (Pinus radiata D.), corewood is formed for nine to 15 years (Entrican 1957). For slash pine and hoop pine (Araucaria cunninghamii), Jennings (1957) reported that in Queensland the corewood was approximately five inches in diameter at the one-foot level and included all wood formed in the first rings from the pith.

Variation in width of annual rings has been found among trees and geographic locations. Henderson and Petty (1972) compared the wood properties of coastal and interior provenances of lodgepole pine and they found that ring width significantly differed between the two provenances. In loblolly pine, Thor and Brown (1962) reported that the variation in rate of growth among seed sources resulted in significant differences in ring width, and this effect may have accounted for the variation pattern in specific gravity. However, Dorn (1968) did not find

any differences in growth rate among Scots pine provenances, even though there were differences in annual ring width.

Growth rate

In the Southern Pine Seed Source Study, Wells (1969) reported that for height growth of loblolly pine there was a high degree of interaction between planting location and seed source with a definite geographic pattern. In most of the plantings, trees from seed collected in areas with high summer rainfall and mild winters were tallest, but in the two coldest planting locations, Maryland and Tennessee, trees from such areas were outperformed by those from areas with low summer rainfall and cold winters. It is also quite apparent that loblolly pine coastal sources have faster growth rates than inland sources, as confirmed by Kraus (1968) in a study on the geographic variation of loblolly pine in Georgia. In his study, there were only minor exceptions to this pattern which were apparently due to local site conditions in the Georgia flatwoods. In the Southwide Pine Seed Source Study in Alabama, Saucier and Taras (1967) reported that in a 13-year-old loblolly pine plantation, coastal sources exhibited greater volume and dry weight than inland sources. In another study in North Carolina, the growth of loblolly pine from coastal seed sources was superior to that of Piedmont, sandhills,and fall line seed sources (Lantz and Hofman 1969). They reported that the coastal sources produced up to 13 percent greater volumes and dry

weights than other sources. Loblolly pine from local seed sources in Louisiana, however, did not show any significant variation in height and volume (Crow 1964). In slash pine grown in South Florida, Saucier and Dorman (1969) found that there was great variation in volume growth among seed sources.

Inheritance

Most results of heritability studies are based on data from young trees and only a few on data from older trees. It can be predicted that the genetic variation and heritability values will change as the trees grow older because the corewood is more sensitive to environmental influences than the maturewood. Also, tracheid characteristics change more rapidly during the first seven to ten years. The genetic variance and heritability values obtained from young trees should then be used only as guidelines for tree improvement until data from mature trees are available. There are some authors (Stonecypher and Zobel 1966), however, who contend that early age genetic values can be used to predict values of later ages.

From these studies, it is apparent that some wood properties are heritable as shown below.

Specific gravity

Considerable evidence has been accumulated to show that the specific gravity of wood is strongly inherited. In trials

of six-year-old progenies of loblolly pine (Van Buijtenen 1963) and in a later study of micropulping loblolly pine grafts for extreme wood specific gravity (Van Buijtenen *et al*. 1968), a strong inheritance of wood specific gravity was found. In a study of inheritance of open-pollinated *Pinus taeda* L. progenies, Stonecypher and Zobel (1966) reported that there is a close agreement between heritability estimates of specific gravity for three- and five-year old material. Their results indicated that mean progeny values of specific gravity at early ages can be used to predict specific gravity at later ages. For unextracted specific gravity in the three-year-old plantation, narrow-sense heritability was 0.72, while for the five-year-old plantation the narrow-sense heritability was 0.73. Jackson and Warren (1962) studied the variation and inheritance in slash pine and loblolly pine progeny and found a highly significant correlation between specific gravity of two-year-old branches and that of stem wood. The specific gravity of the progeny in both species was significantly correlated with that of the parents. They concluded that specific gravity of the first two rings of branchwood can therefore be used for evaluating variations in young progeny.

Goggans (1964), in his correlation and inheritance study of certain wood properties in loblolly pine, interpreted heritabilities by relatively ranking the 19 characteristics

according to the ease with which progress may be made in a selection program. From this ranking, it was concluded that latewood tracheid length, percentage of latewood in the core, and specific gravity of the core are the three characteristics for which progress through selection could be obtained. Brown and Klein (1961) studied the wood density of two-year-old progeny from controlled pollinations of loblolly pine. Crosses were made between parents both having high specific gravity, both with low specific gravity, and also between low and high specific gravity parents. Significant differences between progeny of the different crosses were found, and the ranking of the progeny groups suggested that wood density was under strong genetic control. These authors concluded that the progeny groups inherited density differences approximate to the specific gravity differences between the parent trees and that selection of trees for high or low density appeared to be feasible. Zobel and Rhodes (1957) analyzed the progeny of three apparently self-pollinated loblolly pines and found that the higher density parent had higher density progeny than the low density parent.

The inheritance of compression wood, and its genetic correlations with six other traits in five-year-old loblolly pine, was studied by Shelbourne et al. (1969). They reported that narrow-sense heritabilities of the seven traits ranged from 0.95 to 0.23, percentage of compression wood having the highest value, followed by specific gravity. The high heritabilities of

0.73 for specific gravity and 0.95 for compression wood indicate a large amount of additive genetic variance for these characters in the natural, unselected population they sampled.

In slash pine, the inheritance of specific gravity has been studied by numerous researchers (Squillace et al. 1962, Einspahr et al. 1964, Goddard and Cole 1966). In a progeny test of slash pine, Goddard and Cole (1966) reported a significant correlation between parent and progeny specific gravity which accounted for 24 percent of progeny variances. Based on the half-sib progenies, heritability of specific gravity was 0.43. Using 12-to 14-year-old clones of Pinus elliottii Engelm., Squillace et al. (1962) found a narrow-sense heritability of 0.73 for specific gravity. Einspahr et al. (1964), made a heritability study of various properties of micro-pulped wood from 20 five-year-old grafted trees. Eleven of these were 24 feet. high and 2.7 to 5.8 inches in d.b.h. Lignin and extractive contents were also determined and, of the properties measured, fiber length, fiber strength, and lignin percentage had, at 0.84, 0.74, and 0.72, respectively, the highest broad-sense heritability values. Heritabilities for specific gravity, percentage of latewood and pulp yield were about 0.5.

Fielding and Brown (1960) reported that in six-year-old open-pollinated progeny from 14 parents of Monterey pine, the narrow-sense heritability of specific gravity was 0.2. Using both clonal and seedling material to determine heritabilities

of eight-year-old Monterey pine, Dadswell et al. (1960) reported that for growth rings 2 through 8, gross heritability of whole ring density was 0.74 when based on clonal material and 0.57 when based on seedling material. Under the same conditions, gross heritability of latewood density was 0.45 in clonal material.

Kennedy (1966), determined the heritability of some wood properties of *Picea abies* clones. He found that specific gravity of the whole ring (0.279 - 0.375) was highly correlated with percentage latewood and specific gravity of early wood. The estimated broad-sense heritability for specific gravity was 0.84 for the whole ring (range within ring 0.86 - 0.56). The same species was studied by Rone (1970) using two- and three-year-old seedling progeny of six open-pollinated trees. Analysis of his study showed that it was difficult to select simultaneously for high wood density and rapid growth rate. Mean density in the population did not vary and heritability of wood density was low. In *Pinus pinaster*, Polge and Illy (1968) found that the heritability value for mean density was 0.75 for four-year-old seedlings from nine families. Heritability estimation by progeny-parent regressions in seven families showed a high inheritance of specific gravity.

Tracheid length

In conifers, tracheid length is moderately to highly heritable in at least the first nine-years increment (Smith 1967).

Interspecific differences in the degree of genetic control of latewood tracheid length were found, and the latewood tracheid length seems to be rather more highly heritable than earlywood tracheid length. Although no heritability values were given by Greene (1966) for a progeny test from open and controlled pollinated loblolly pine, it is implied that tracheid length is heritable. He concluded that tracheid length may be altered by selection, controlled crossing, and selfing, and that breeding for long or short tracheid length is feasible.

A number of progeny studies give evidence of hereditary influence on tracheid length. According to Greene (1956), different strains of loblolly pine and slash pine exhibit initial tracheid lengths that are significantly different. Sixty-seven percent of the slash pine parents with significantly longer tracheids produced open-pollinated progeny with longer tracheids. In reporting on tracheid length variation in slash and loblolly pines, Jackson and Greene (1957, 1958) stated that the tracheid length in the progeny controlled crosses was intermediate to that of the parents. For Monterey pine, Dadswell et al. (1961) reported broad-sense heritability for tracheid length to be 0.73 based on growth rings two through eight in clonal material. When growth rings six, seven, and eight, were used, heritability of tracheid length increased to 0.81. Echols (1956) reported tracheid lengths in the F_1 progenies of known crosses of slash pine to be intermediate between their parents. He concluded that

tracheid length appeared to be under rigid genetic control and stated further that the pattern suggested tracheid length inheritance was governed by a multiple gene series.

Tracheid cross-sectional dimension

There are few reports on the heritability of tracheid cross-sectional dimension. Chowdhury (1931) examined the wood of hybrid larch and found the tangential diameter and wall thickness of the tracheids to be intermediate between the same properties of the parents. Smith (1967) reported that, in yellow poplar (*Liriodendron tulipera* L.), heritability of certain tracheid cross-sectional dimensions is apparently quite high within individual early-formed rings. The pattern of variation in transverse tracheid dimension is also apparently genetically controlled.

Perhaps the strongest evidence of the inheritance of cross-sectional dimensions of coniferous tracheids is that the variation pattern seems to be similar to those wood density and tracheid length which are under strong genetic control (Goggans 1962).

Proportion of latewood

For loblolly pine, Van Buijtenen *et al*. (1968) suggested that there is considerable evidence that percent latewood and specific gravity are strongly inherited. This was further confirmed by Gladstone *et al*. (1970) in their investigation

of kraft pulping in earlywood and latewood of loblolly pine. They reported that the differential yields from earlywood and latewood indicate an indirect inheritance of cellulose. The heritability of latewood percentage is relatively strong, and since latewood yielded two to seven percent more pulp (ovendry, unextracted basis) a tree with higher specific gravity would be expected to yield greater amount of cellulose. Einspahr et al. (1964) found some broad-sense heritability values in their study on slash pine. They reported that percent latewood has a broad-sense heritability of about 0.5. Likewise, Dadswell et al. (1961) found indications of heritability at percentage of latewood in Monterey pine. He reported that broad-sense heritability for growth rings two through eight (from the pith) in clonal material was 0.54 and in seedling progeny the narrow-sense heritability was 0.47.

Width of annual ring

The author was not able to find a study that dealt solely with heritability of annual ring width. There are reports, however, which show specific gravity and width of annual rings are correlated, which in effect indicates that width of annual rings could be inherited. Polge and Illy (1968) studied the heritability of wood density and correlations with growth in four-year-old *Pinus pinaster*. They found that in wood from the western side of the tree, annual ring width and specific gravity are positively correlated, both between families and within

families. In Norway spruce, Mergen et al. (1964) reported that percentage of latewood and ring width are highly correlated.

Height and diameter

Variation and heritability of wood and growth characteristics of five-year-old quaking aspen (Populus tremuloides Michx.) were studied by Einspahr et al. (1967), who found that the narrow-sense heritability estimates based on interclass correlations and progeny/mid-parent regression data indicate moderate possibilities for genetic improvement of height and diameter growth. These two characteristics are slightly heritable. The result was similar for loblolly pine when Van Buijtenen (1963) found a moderate inheritance of height and diameter growth. Steinhoff and Hoff (1971) made an estimate of heritability of height growth in western white pine (Pinus strobus L.) based on parent-progeny relationships and found that the average for the various estimates increased by one and a half times as the growth rate of the progenies approximately doubled. In a study in Populus deltoides, Mohn and Randall (1971) found that height and diameter were strongly correlated genetically and phenotypically. Phenotypic and genotypic correlations between measurements made in the first three years and those in the sixth year were high.

Correlation

Specific gravity as related to growth, percent latewood, tracheid length, and tracheid cross-sectional dimension

Literature on the relationship between growth and specific gravity is both abundant and controversial. It is generally, believed that correlation of the two is not very strong in conifers (Zobel and Rhodes 1955, Larson 1957, Miller 1959, Zobel *et al*. 1960, Gilmore *et al*. 1961, Thor 1964, 1965, Zobel *et al*. 1969) primarily because half of the variation in specific gravity is attributed to variation in percentage of latewood. According to the TAPPI Forest Biology Committee (1960), an appreciable part of the density variation that has been attributed to width of growth ring is in reality associated with age; ring width of trees of the same age has relatively little independent influence upon either specific gravity or the percentage of latewood. Zobel *et al*. (1958) had earlier concluded that there is little relationship between growth and specific gravity in wood of loblolly pine of the same age. In direct contrast, weak to strong negative correlations have been reported for young southern pine that have not encountered intraspecific or interspecific competition (Stonecypher and Zobel 1960, Squillace *et al*. 1962, Van Buijtenen 1963, Polge and Illy 1968, Saucier and Dorman 1969).

On the other hand, Wheeler and Mitchell (1962) reported that diameter, when tested independently of other variables,

was significantly related to the increment core specific gravity of the four major southern pines. With the exception of slash pine, they found that diameter-age and specific gravity were significantly related. In red pine (*Pinus resinosa* Ait.), Jayne (1958) and Peterson (1967) found significant correlation between growth and specific gravity.

Studying the relationship of specific gravity to growth rate, Dorn (1968) reported that in some Scots pine provenances there exists a positive correlation between specific gravity and growth rate. Stairs and Adapa (1969), however, found a negative correlation between growth rate and specific gravity in *Picea abies*.

Latewood is made up of tracheids having narrow lumens and thick walls, consequently it has a much higher density than earlywood. Because of this higher density, numerous investigators have found a strong relationship between specific gravity and percentage of latewood in conifers (Schafer 1949, Smith 1956, Larson 1957, Miller 1959, Van Buijtenen *et al*. 1961, Squillace *et al*. 1962, Mergen *et al*. 1964).

The tracheid cross-sectional dimensions *per se* are related to many properties of wood and wood products (Pew and Knechtges 1939, Wellwood 1961) and these dimensions have a significant effect on specific gravity. Echols (1958) and Zobel *et al*. (1961b) reported that tracheid diameter and wall thickness in

the southern pines have a major effect on wood density.

Correlation between specific gravity and tracheid length is not clear and reports on this relationship have been conflicting. Smith (1959) in his studies with plantation-grown hoop pine, could find no relationship between tracheid length and wood density. Kramer (1957) obtained no significant correlation between these characterisitics in his work with loblolly pine. However, in their study of variation patterns of wood properties in loblolly pine, Zobel et al.(1960) found a significant, though small, negative correlation between specific gravity and tracheid length when comparing trees on any one site. On the other hand, Craig et al. (1966) found a negative but significant relationship in loblolly pine grown in Maryland and Delaware. In Scots pine, an increase in average tracheid length was found to be accompanied by a decrease in average wood density (Echols 1958). It is interesting to note, however, that Dadswell et al. (1961) found a positive correlation between fiber length and density of the entire annual ring in Pinus radiata when they used the 6th, 7th, and 8th annual rings. But in Abies lasiocarpa, Kennedy and Wilson (1954) found that the cork-barked trees had wood with higher density and shorter fibers than the smooth-barked trees.

Tracheid length as related to growth, percent latewood, and tracheid cross-sectional dimension

Reports on the relationship of tracheid length to diameter

growth rate are also contradictory. Many researchers (Hata 1949, Bisset *et al.* 1951, Echols 1958, Zobel *et al.* 1960, Thor 1964) have reported that the relationship is negative; others have either found a positive correlation (Kennedy 1957, Cech *et al.* 1960, Kennedy and Smith 1960, Wellwood 1960, Thor 1965, Posey *et al.* 1970) or no relationship (Echols 1955, Mergen *et al.* 1964, Stairs *et al.* 1966, Zobel *et al.* 1969). When height growth rate was investigated, Echols (1958) and Dorn (1968) reported a strong correlation with tracheid length in Scots pine.

The relationship between proportion of latewood and tracheid length has not been investigated but the variation of tracheid length in earlywood and latewood has. There seem to be some differences of opinion with respect to whether tracheid length of latewood differs from that of earlywood. Gerry (1961) reported that the latewood tracheid length of Douglas-fir and southern pines is shorter than the earlywood, whereas Jackson and Greene (1957) did not find any differences between latewood and earlywood tracheids in southern pines. Most investigators (Bisset and Dadswell 1950, Anderson 1951, Dadswell and Wardrop 1960) indicated slightly longer tracheid in latewood.

Proportion of latewood and tracheid cross-sectional dimension as related to growth

In conifers, Scott and Mc Gregor (1952) found that Sitka spruce (*Picea sitchensis* (Bong.) Carr.) develops latewood

independently of growth rate, but Schafer (1949) and Zobel and Rhodes (1955) found no correlation between growth rate and percentage latewood in southern pines. Larson (1957) also reported that growth rate had a negligible influence on percentage of latewood in slash pine. In contrast, Pillow (1954), indicated a definite correlation between growth rate and percentage of latewood in loblolly pine.

There is also some evidence that the change in tracheid cross-sectional dimension is related to growth rate (Pew and Knetchges 1939).

Site effect on growth, specific gravity, and tracheid length

The early literature on the effect of site on specific gravity has been summarized (Spurr and Hsuing 1954, Larson 1957) and it contains many conflicting reports. Part of the confusion is probably caused by confounding the age of the tree (i.e., wood type) with other factors. Paul (1952) expressed the view that soil type, principally through its capacity to retain moisture, has an important influence on the growth and structure of wood. Specific gravity has been reported to be affected by soil moisture. Results obtained by numerous investigators (Wellwood 1952, 1960, Larson 1957, Jayne 1958) indicated that coniferous trees growing on good sites generally have a tendency to produce lower density wood than those growing on poor sites. However, others (Zobel and Rhodes

1955, Knigge 1958, Schniewind 1961) reported no relationship between site index and specific gravity. Smith and Wilsie (1961) presented data which showed that summer soil-water deficits reduced the width of latewood in loblolly pine, with the greatest effect occurring in wood near the base of the tree.

Tracheid length seems to be the wood characteristics least affected by site. Wellwood (1960) reported that site had little effect on tracheid length in western hemlock (Tsuga heterophylla (Raf.) Sarg.), but that crown class had an apparent effect.

Altitude has been found to affect specific gravity. Echols and Conkle (1971) observed that specific gravity of Ponderosa pine (Pinus ponderosa Laws.) decreased as the altitude of origin of the seed parents increased. All genotypes produced wood of significantly lower specific gravity in the plantations at high altitude (5650 feet).

METHODS AND PROCEDURE

Species description

Loblolly pine (*Pinus taeda* L.) is one of the most important commercial species in the southeastern United States. It has a wide range and is the dominant pine species in each of the Atlantic and Gulf Coastal States south of New Jersey. It does not occur in the Mississippi River bottoms, and is scarce on the deep, coarse sands of the lower Gulf Coastal Plain and the sandhills of North and South Carolina. It grows at sea level and reaches elevations above 2,000 feet in northern Alabama and Georgia. Rainfall in the loblolly pine range averages 40 to 60 inches. Temperature extremes range from -10° to over 100° F.

The trees grow best on soil with poor surface drainage, a deep surface layer, and a firm subsoil. Height growth begins about March 1 in the Gulf States and about 6 weeks later near the North Carolina - Virginia border.

Individual trees may attain diameters of 50 to 60 inches and heights of 150 feet at advanced ages.

Geographic seed sources

The geographic seed sources used in this study were selected by Professor A. B. Crow of the Louisiana State University, School of Forestry and Wildlife Management in 1956. Seeds were collected from East Feliciana, St. Tammany, Vernon (North), Vernon (South),

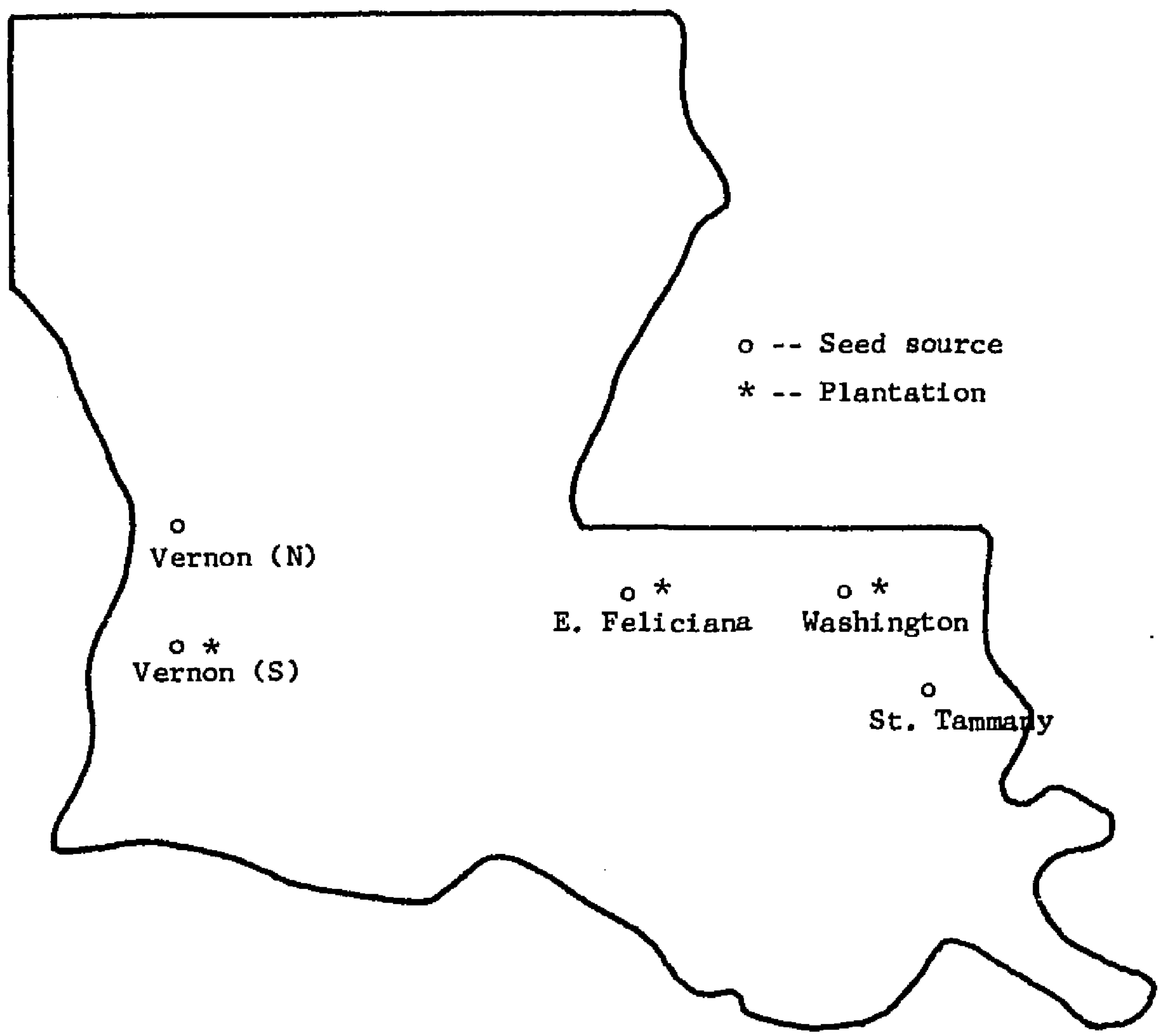

Figure 1. Location of seed sources and plantations in the State of Louisiana.

and Washington parishes (Figure 1). These seed sources were planted in 1958-59 as 1-0 seedlings in plantations located in Vernon Parish (West Louisiana Experiment Station, De Ridder), East Feliciana Parish (Idlewild Plantation, Clinton), and Washington Parish (Lee Memorial Forest, Bogalusa) (Figure 1). Previous publications (Crow 1964, 1969) have reported survival and growth of the seed source tests. Each plantation site is described generally below. Descriptions were excerpted from the soil survey reports prepared by the USDA Soil Conservation Service in cooperation with the Louisiana Agricultural Experiment Station (Anonymous 1970).

Plantations

Vernon Parish (West Louisiana Experiment Station, De Ridder): The topography of the plantation area is generally flat to gently rolling. Soils are of the Bienville, Bowie, and Ruston series. The soils of the Bienville series have sandy surface horizon and a brown loamy fine sand subsoil. They are somewhat excessively drained and runoff is slow. Permeability is moderately rapid. This soil is medium acid to very strongly acid and is low in natural fertility. The available water holding capacity is low. Root and moisture penetration are deep in this soil.

The soils of the Bowie series have dark grayish brown fine sandy loam A horizon, yellowish brown sandy clay loam

upper subsoil horizon and mottled yellowish brown, red, and gray lower subsoil horizons. They are moderately well-drained and moderately slowly permeable. This soil is medium acid to very strongly acid and is low in natural fertility. The available water-holding capacity is medium. Roots and moisture penetrate deep in the soil.

The soils of the Ruston series have dark gray fine sandy loam surface horizon and red sandy loam subsoils. They are well-drained and moderately permeable. Available water capacity is high. Roots, and moisture, penetrate deep into the subsoil. This soil is highly acid to very strongly acid and is low in natural fertility.

East Feliciana Parish(Idlewild Plantation, Clinton). The topography of the plantation is generally flat to gently sloping. Soils are of the Providence series. This soil is moderately drained. The surface layer is absent over 20 percent of the area. The subsoil is a strong brown silty clay loam overlying a brown and gray fragipan with a higher sand content. Depth of the pan is about 20 inches.

Permeability is slow and runoff is medium. Available water capacity is high. When cultivated, good tilth is difficult to maintain. The reaction is medium to strongly acid in the surface layer unless limed, and ranges to very strongly acid in the subsoil.

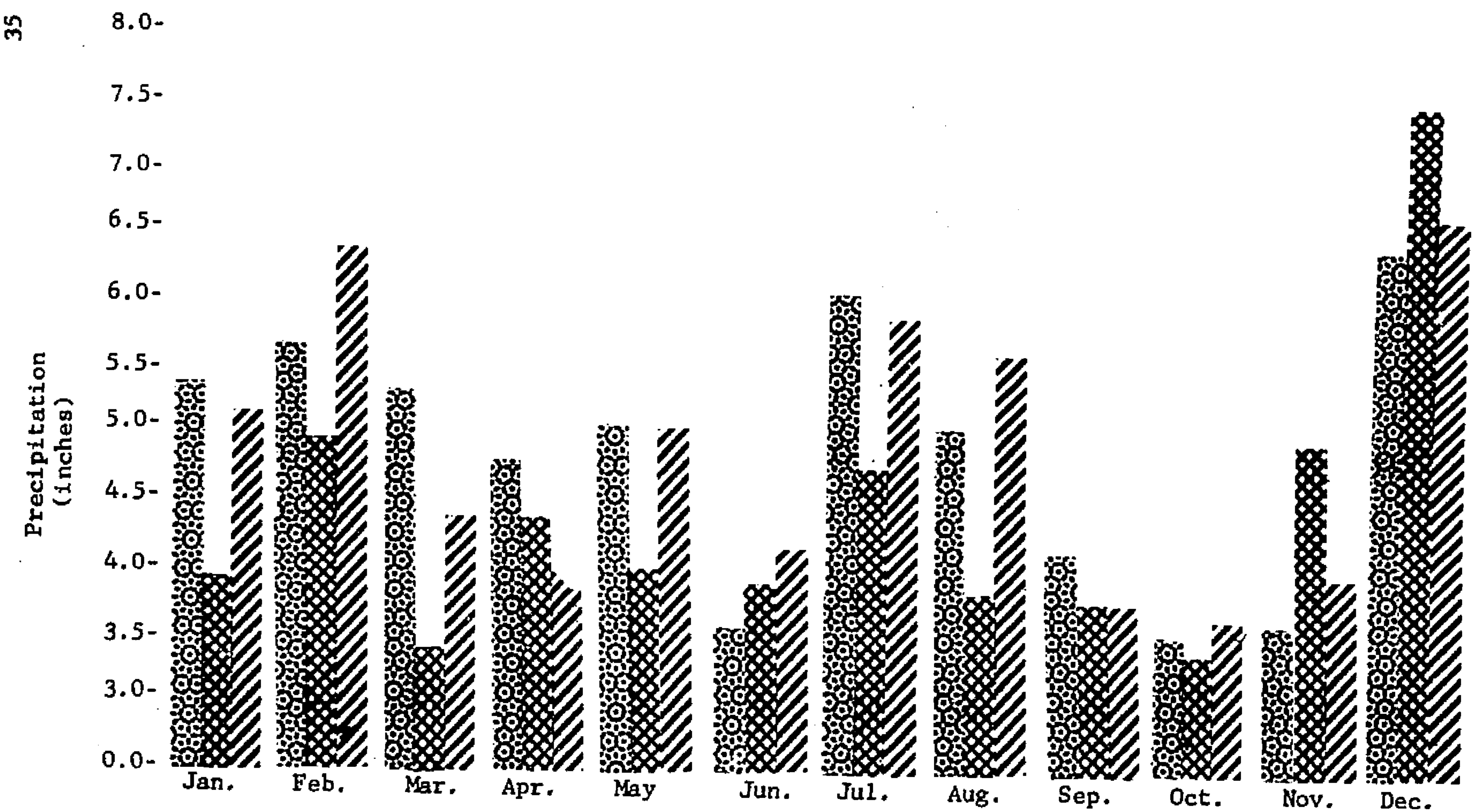

Figure 2. Mean monthly precipitation for the period 1958 - 1971 in the three plantation locations.

Bogalusa De Ridder Idlewild

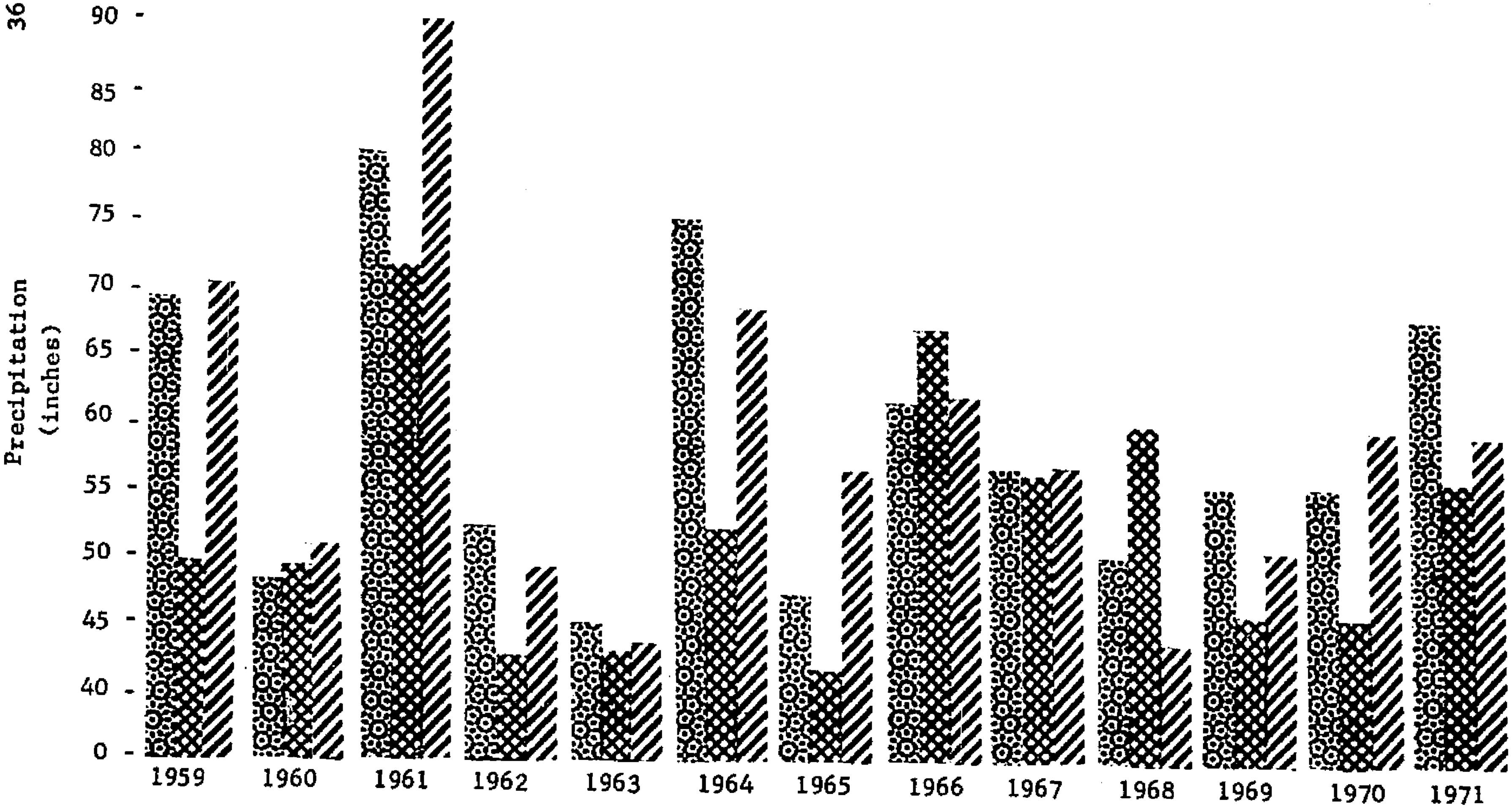

Figure 3. Total yearly precipitation for the period 1959 - 1971 in the three plantation locations.

Washington Parish (Lee Memorial Forest, Bogalusa). Topography of the plantation area is generally flat to moderately sloping. The soil of the area is of the Ruston series. This soil is well drained. The surface layer is dark grayish brown fine sandy loam about eight inches thick. The subsoil is yellowish red sandy clay loam and clay loam.

Permeability is moderate and surface runoff is medium to rapid. Available water capacity is moderate. It is medium acid in the surface layer and very strongly acid in the subsoil.

The amount of rainfall in each plantation was taken from records of weather stations nearest each plantation. The mean monthly precipitation and total yearly precipitation for the period 1959 to 1971 in the plantation areas are summarized in graphical form in Figures 2 and 3, respectively.

Field Procedure

The plantations were designed in randomized blocks with four replications per seed source at a 6' x 6' spacing. Each plot is a tenth of an acre in size.

In the winter of 1971 when the plantations had completed the 13th growing season, increment core samples from 10 trees per source in each block were taken at breast height in the first and most valuable log of the tree. Trees sampled were randomly chosen. However, when trees initially chosen were found to be damaged or infected with fusiform rust (*Cronartium fusiforme* Hedgc. & Hunt ex Cumm.), sample substitution was made in the field.

Only sound trees were sampled to avoid any effect of defect on wood properties. An oversize increment borer, about 10 millimeters in diameter, was used to extract the sample from the tree. This method of obtaining test samples has been found to be satisfactory for determining some properties of wood especially specific gravity (Zobel _et al_. 1960) because it does not crush or damage cells. For each tree, an increment core sample representing the North compass quadrant was taken from bark to pith.

The diameter and height of each sampled tree were measured. Diameter was measured at about four and one-half feet from the ground using a diameter tape. Total height of the tree was measured by the use of a Sunto hypsometer.

Laboratory Procedure

From each core sample the following wood properties were determined: percentage of latewood, width of annual ring, specific gravity (unextracted and extracted with hot water/ benzene-alcohol), tracheid length, and tracheid cross-sectional dimensions (cell wall thickness and width of lumen).

The following is a sequence of the laboratory operations and measurements to which each core sample was subjected: After extraction from the tree each core was numbered (coded) indicating plantation, seed source, and sample number. It was allowed to air dry for 24 hours. The amount of latewood in the entire core was measured simultaneously with the width of

annual ring. Each increment core was divided into two sections, namely, corewood(0 to 5 rings from the pith) and outer sapwood, i.e., from the 6th ring from the pith to the bark. The specific gravity of each core section was determined. The third ring from the pith and the 7th ring from the pith segments for corewood (pith) section and outer wood (bark) section, respectively, were split for tracheid length measurement. Tracheid cross-sectional dimensions of each core section were measured from the latewood segment only.

Following are more detailed descriptions of the procedures used in making the measurements summarized above.

Proportion of latewood and width of annual ring determination

The pith end of each core was trimmed. Using a vernier caliper, the latewood and width of annual ring were measured to the nearest 0.01 inch. To make the growth rings more visible before measurement the core was dipped in water. For all measurements, Mork's (1928) definition of latewood was used as a guide to distinguish the boundary between earlywood and latewood. At this time the annual ring width was also measured.

The proportion of latewood was obtained by totalling the width of latewood per ring, dividing by the total length of the whole core sample, and multiplying by 100.

Determination of specific gravity of the core samples

The maximum moisture method, described by Smith (1954) and Fogg (1967) was used to obtain both unextracted and extracted

specific gravity of increment core samples. A high vacuum pump was used to saturate the samples at periodic intervals until constant weights were obtained. This method has been found to be effective and accurate with large numbers of small samples (Smith 1954, Choong et al. 1970). After the unextracted specific gravity was determined, the cores were extracted to determine the extracted specific gravity. Extraction of the organic solubles from the whole core was made in a Soxhlet extractor using consecutive extractions of boiling water for 24 hours, 95 percent ethanol for 24 hours, and 2:1 benzene-ethanol solution for 24 hours, respectively. The following is the detailed procedure used:

a. Unextracted specific gravity - The oven-dry weight (Wo) of the core samples was determined as follows: Core samples were placed in a drying oven for 24 hours at 105 degrees Centigrade. Each core was then weighed in a Mettler top-loading balance, accurate to 0.001 gram. Following the oven-dry weight determination, the maximum weight (Wmax) was determined by impregnation and saturation of the core samples with distilled water. The core samples were placed in a medium-sized desiccator and a vacuum was applied for three hours. Distilled water was introduced into the desiccator from a separatory funnel while the vacuum pump was still running to avoid atmospheric air introduced to the samples. After the required amount of water was poured into the desiccator, the vacuum pump

and valve were shut off, and air was allowed to enter the desiccator. To saturate the samples, the vacuum pump was run for 30 minutes daily, and atmospheric air was introduced (the pressure difference within the sample will force water into the sample by mass flow and diffusion). When the samples were fully saturated, individual core samples were weighed on a Mettler balance. Before each measurement, excess surface water was removed by rolling the sample on paper towelling. Specific gravity was determined by taking the ratio of the saturated weight and the oven-dry weight of each wood sample (Wmax/Wo) and corrected values were obtained from a table prepared by Fogg (1967).

b. Extracted specific gravity - Saturated samples were placed in a Soxhlet unit and extracted with boiling water for 24 hours, and with 2:1 benzene-ethanol solution for 24 hours. Following this sequence of extractions, the samples were air-dried in a room for about a week, oven-dried at 105° C for 24 hours, and weighed. The extracted specific gravity was determined by taking the ratio of the maximum weight (Wmax) and the extracted oven-dry weight (W'o) and obtaining corrected values from a table (Fogg 1967).

Tracheid length measurements

The 3rd ring from the pith of the pith section and the 7th ring from the pith of the outer wood (bark) section, were

sampled for tracheid length measurements. The sample ring segments were split in half parallel to the grain. The ring segments were cut into small slivers about one-half of the size of a match stick and were macerated in a 25-cc test tube using a modified Franklin (1946) method, with 2:1 glacial acetic acid and hydrogen peroxide as delignification agents, at a temperature of 100° C for 24 hours.

Following maceration, the tracheids were washed several times with water to remove all traces of the macerating fluid and then stained with Safranin. The test tube was thoroughly shaken to separate the individual tracheids, and several tracheids were mounted on a glass slide for measurements. The lengths of twenty (20) tracheids per sample (segment) were measured with a fiberscope calibrated to 65 X magnification.

Cross-sectional dimension measurement

The 4th ring from the pith of the pith section and the 8th ring from the pith of the outer wood (bark) section were used for this measurement. Each ring was saturated with water under vacuum to soften it before cutting. A microtome with a very sharp blade was used to cut a cross-sectional sample, 25 microns in thickness. Extreme care was excercised to get the cut even and smooth over the entire ring and to assure a cut at right angles to the vertical tracheid axis. The freshly cut surface was stained with a few drops of aqueous Safranin. The width

of the cell lumen and cell wall thickness of the radial and tangential sections of the latewood segment were measured with a micrometer at 450X magnification.

Statistical Procedures

Analyses of data conformed to the randomized block design of the original study. There were three plantations, four blocks per plantation, five treatments (seed sources) per block, and 10 core samples (trees) per plot.

In measuring percentage of latewood and average width of annual ring, the sampling unit was the entire increment core. Here a split plot analysis was employed to evaluate the effects of the plantation, seed sources, and plantation x seed sources interaction. The same analysis was used for diameter and height with the tree being the sampling unit. However, in analyzing specific gravity, tracheid length, and cell dimensions, a split-split plot analysis of variance was conducted.

The extracted and unextracted specific gravity were determined in both the pith section and bark section of an increment core (sub-subplot factor). The average length of 20 tracheids of the earlywood and latewood segments in both the pith section and bark section of an increment core were also measured. In this case, the split-split plot was a 2^2 factorial. Also, in analyzing cell dimensions, the split-split plot was a 2^2 factorial because the cell wall thickness and width of

cell lumen were measured at the radial and tangential sections of the latewood segment in both the pith section and bark section of an increment core.

In addition to analyses of variance, correlation analyses of the various variables were also conducted.

Linear regression and correlation analyses were made to determine the possible effects of moisture on the different characteristics. Precipitation in all plantations was expressed as percent of the "normal" precipitation of the seed sources and the attributes of the different characteristics were expressed as percent of the seed source means.

Computations were conducted at the Louisiana State University Computer Reseach Center.

RESULTS AND DISCUSSION

Results

Variation

A major objective of this study was to determine if any variation in growth and wood properties could be discerned among the five Louisiana seed sources of loblolly pine grown in the three plantations. Such variation can be attributed to genetic and environmental (climatic and physiographic) influences and the interaction of the two. In this study, the location of seed sources and plantations was rather uniquely suited to an analysis of variation patterns within a very limited portion of the range of loblolly pine.

There were no great latitudinal differences among either the five seed sources used in this study or the three plantations in which they grew. In fact, the plantations were laid out in almost straight line from East to West as were the seed sources (Figure 1). Therefore, the major environmental influences associated with latitude such as temperature and photoperiod, which have been found to be of major importance in many previous studies of range-wide variation of loblolly pine, have been almost entirely eliminated in the design of the study. It is possible that there are soil differences at the plantation sites which could contribute to variation and interactions. However, the soil series do not differ very much in texture, acidity, and natural fertility among the three sites and small differences

would be extremely difficult to detect.

Given this high degree of uniformity among planting sites and geographic seed sources in variables such as mean temperature, length of growing season, photoperiod, and soils, it was not too surprising that few significant differences were found in the analysis of the growth and wood characteristics under study. However, upon close inspection, certain trends and patterns could be discerned which seem to be associated with the one major environmental factor that can be readily identified as a possible contributor to the variation encountered in some characteristics. This factor is the annual rainfall pattern, which differs among seed sources and plantation sites.

Monthly precipitation records for the 13-year period of the study were available for each planting site as were data on the "normal" monthly precipitation for each of the five seed sources. In the following discussion, these data will be used to develop a possible explanation in terms of moisture excess or deficit throughout the growing season for the pattern of variation found in some traits.

Variation in growth

Growth characteristics studied were diameter and height. In general, the differences among seed sources and among plantations were relatively small (Tables 1 and 2) but the results for the two characteristics were negatively correlated. This relationship will be discussed after the results for both

Table 1. Plantation means of the different characteristics measured +

Characteristics	Plantation			
	Bogalusa	De Ridder	Idlewild	Average
Diameter ..... inches	6.01	5.86	6.23	6.05
Height .... feet	45.50	48.00	44.50	46.00
Latewood...... percent	26.80	31.40	29.80	29.33
Annual ring width..in.	0.202	0.198	0.212	0.204
Specific gravity:				
a. Pith section				
1. Unextracted	0.38	0.39	0.38	0.38
2. Extracted.......	0.34	0.37	0.35	0.35
b. Bark section				
1. Unextracted.....	0.51	0.53	0.49	0.51
2. Extracted.......	0.48	0.51	0.47	0.49
Unextracted, whole core..	0.45	0.46	0.44	0.445
Extracted, whole core....	0.41	0.44	0.41	0.42
Tracheid length:				
a. Pith section				
1. Earlywood ..(mm.)	1.98	2.04	2.17	2.06
2. Latewood....(mm.)	2.05	2.09	2.41	2.18
b. Bark section				
1. Earlywood...(mm.)	3.06	3.35	2.98	3.13
2. Latewood....(mm.)	3.33	3.52	3.34	3.40
Earlywood, whole core..(mm.)	2.52	2.70	2.57	2.59
Latewood, whole core..(mm.)	2.69	2.81	2.88	2.79
Whole core........(mm.)	2.61	2.75	2.72	2.69
Cell dimensions:				
a. Pith section				
1. Radial section				
a. Cell wall thickness (μ)	3.24	4.08	3.86	3.73

Table 1. (Continued)

Characteristics	Plantation			
	Bogalusa	De Ridder	Idlewild	Average
b. Cell lumen width..(µ)	38.20	27.80	35.30	33.80
2. Tangential section				
a. Cell wall thickness (µ)	3.24	4.22	4.00	3.82
b. Cell lumen width.. (µ)	53.30	40.70	38.40	44.13
b. Bark section				
1. Radial section				
a. Cell wall thickness (µ)	5.85	5.64	5.20	5.57
b. Cell lumen width .. (µ)	35.10	30.00	30.90	32.00
2. Tangential section				
a. Cell wall thickness (µ)	5.64	5.62	5.31	5.52
b. Cell lumen width.. (µ)	33.30	27.30	29.60	30.00
Cell wall thickness, radial (µ)	4.55	4.86	4.53	4.65
Cell wall thickness, tan. . (µ)	4.44	4.92	4.65	4.67
Cell wall thickness, bark (µ)	5.75	5.63	5.26	5.55
Cell wall thickness, pith (µ)	3.24	4.15	3.93	3.78
Cell lumen width, radial (µ)	36.65	28.90	33.10	32.90
Cell lumen width, tan. (µ)	43.30	34.00	34.00	37.10
Cell lumen width, bark (µ)	34.20	28.65	30.25	31.00
Cell lumen width, pith (µ)	45.75	34.94	36.85	39.18
Cell wall thickness, whole core ....(µ)	4.49	4.89	4.59	4.66
Cell lumen width, whole core ....(µ)	39.98	31.55	33.55	35.03

+ At time of measurement all plantations had completed 13 growing seasons.

Table 2. Seed source means over all plantations

Characteristics	Seed sources					
	E. Feliciana	St.Tammany	Vernon (N)	Vernon (S)	Washington	Average
Diameter........inches	6.04	6.17	5.88	6.05	6.12	6.05
Height ....feet	45.60	46.60	45.70	45.80	46.10	46.00
Latewood........percent	30.33	29.67	27.67	30.33	28.67	29.33
Annual ring width..inches	0.203	0.210	0.193	0.200	0.213	0.204
Specific gravity;						
a. Pith section						
1. Unextracted..	0.38	0.38	0.39	0.39	0.37	0.38
2. Extracted....	0.36	0.35	0.36	0.36	0.34	0.35
b. Bark section						
1. Unextracted...	0.51	0.52	0.51	0.52	0.50	0.51
2. Extracted.....	0.48	0.50	0.48	0.50	0.48	0.49
Specific gravity, whole core, unextracted.........	0.45	0.45	0.45	0.46	0.44	0.445
Specific gravity, whole core, extracted.....	0.421	0.424	0.420	0.429	0.408	0.420

Table 2. (Continued)

Characteristics	Seed sources					
	E. Feliciana	St. Tammany	Vernon (N)	Vernon (S)	Washington	Average
Tracheid length						
a. Pith section						
1. Earlywood........ (mm.)	2.04	2.06	2.06	2.06	2.09	2.06
2. Latewood......... (mm.)	2.16	2.18	2.18	2.20	2.20	2.18
b. Bark section						
1. Earlywood........ (mm.)	3.11	3.12	3.12	3.21	3.09	3.13
2. Latewood......... (mm.)	3.35	3.40	3.43	3.49	3.32	3.40
Earlywood, whole core (mm.)	2.58	2.59	2.59	2.64	2.59	2.59
Latewood, whole core (mm.)	2.76	2.79	2.81	2.85	2.76	2.79
Whole core .... (mm.)	2.67	2.69	2.70	2.74	2.67	2.69
Cell dimension:						
a. Pith section						
1. Radial section						
a. Cell wall thickness.. (μ)	3.75	3.80	3.62	3.75	3.71	3.73
b. Width of cell lumen.. (μ)	32.90	33.90	34.00	33.30	35.10	33.80

Table 2. (Continued)

Characteristics		Seed sources					
		E. Feliciana	St. Tammany	Vernon (N)	Vernon (S)	Washington	Average
2. Tangential section							
a. Cell wall thickness	(µ)	3.82	3.91	3.73	3.89	3.78	3.82
b.width of cell lumen	(µ)	43.10	44.20	44.70	42.90	45.80	44.13
b. Bark section							
1. Radial section							
a. Cell wall thickness	(µ)	5.64	5.63	5.56	5.67	5.33	5.57
b. Width of cell lumen	(µ)	31.30	32.20	33.10	31.80	31.30	32.00
2. Tangential section							
a. Cell wall thickness	(µ)	5.60	5.62	5.47	5.69	5.24	5.52
b. Width of cell lumen	(µ)	28.20	28.90	31.60	30.00	31.60	30.00
Cell wall thickness, radial	(µ)	4.79	4.71	4.59	4.71	4.52	4.65
Cell wall thickness, tan.	(µ)	4.71	4.76	4.64	4.79	4.51	4.67
Cell wall thickness, pith	(µ)	3.79	3.85	3.67	3.82	3.74	3.78

Table 2. (Continued)

Characteristics		Seed sources					
		E. Feliciana	St. Tammany	Vernon (N)	Vernon (S)	Washington	Average
Cell wall thickness, bark	(μ)	5.62	5.62	5.51	5.68	5.28	5.55
Width of cell lumen, radial	(μ)	32.10	33.10	33.60	32.60	33.20	32.90
Width of cell lumen, tan.	(μ)	35.70	36.50	38.20	36.40	38.70	37.10
Width of cell lumen, pith	(μ)	39.00	38.90	39.40	38.10	40.50	39.18
Width of cell lumen, bark	(μ)	29.80	30.60	32.40	30.90	31.50	31.00
Cell wall thickness, whole core	(μ)	4.71	4.73	4.59	4.75	4.51	4.66
Width of cell lumen, whole core...............	(μ)	33.90	34.90	34.90	34.60	35.90	35.03

diameter and height have been treated individually.

Diameter. -- The mean diameter for all five sources in the plantations was 6.05 inches (Table 2), and there were no significant differences among seed sources (Table 3). The St. Tammany source had the largest average diameter, 6.17 inches, about two percent greater than the combined mean. The Vernon (N) source had the smallest mean diameter, 5.88 inches, about 4.5 percent less than the combined mean. Crow and Kennedy (1969) reported that the St. Tammany seed source had the largest diameter in the Idlewild plantation at age six.

Mean diameter for plantations ranged from 5.86 inches (De Ridder) to 6.23 inches (Idlewild). The Idlewild plantation had a mean diameter three percent greater than the average, while the De Ridder plantation mean was about three percent smaller than the average (Table 1).

The genotype (seed source) x environment (plantation) interaction was not significant (Table 3) even though the order of performance of the sources was different in each plantation. The absence of significant variation in diameter growth indicates that, for this trait, all five seed sources are about equally adaptable to the various planting sites in the study.

Height. -- The average height of the five seed sources growing at all three sites was fairly uniform (Table 2). The means were 45.6, 45.7, 45.8, 46.1, and 46.6 feet for East

Feliciana, Vernon (N), Vernon (S), Washington, and St. Tammany seed sources, respectively. The analysis of variance indicated that this variation was not significant (Table 4) which is not surprising since the seed sources represent a very limited portion of the range of the species. In other studies which have sampled a much greater portion of the latitudinal range of loblolly pine, highly significant differences in height growth were reported (Zarger 1961, Wells and Wakely 1966, Wells 1969).

There was no significant variation in height among the three plantations (Tables 1 and 4). The mean height for the plantations ranged from 44.5 to 48.0 feet with an average of 46.0 feet. Trees planted in De Ridder were the tallest - about 4.3 percent larger than the combined average. Trees planted in Idlewild were about 3.3 percent shorter than the combined average.

The interaction between plantation and seed source was significant ($P < .05$) (Table 4). Falconer (1960) explained that a specific difference of environment may have a greater effect on some genotypes than on others and all of the sources grown at De Ridder have attained greater height than when grown at Idlewild. Among the seed sources, the St. Tammany provenance had the greatest height (on the average) in all three plantations. This indicated a slight superiority of the St. Tammany material and it appears most adaptable to the different planting locations. In the loblolly pine Southwide Seed Source

Table 3. Analysis of variance for diameter

Sources of variation	D.F.	S.S.	M.S.	F
Plantation	2	17.63	8.82	3.24
Block/Pltn = Error (a)	9	24.47	2.72	
Seed source	4	5.92	1.48	1.76
Plantation x seed source	8	4.24	0.53	<1
Error (b)	36	27.03	0.75 (0.84)1/	<1
Sampling error (b)	540	456.80	0.85	
Total	599	536.09		

1/ Pooled mean square for error (b).

Table 4. Analysis of variance for height

Sources of variation	D.F.	S.S.	M.S.	F
Plantation	2	1293.01	646.51	4.64
Block/Pltn = Error (a)	9	1253.88	139.32	
Seed source	4	82.99	20.75	<1
Plantation x seed source	8	1055.01	131.88	2.63*
Error (b)	36	1807.40	50.21	3.60**
Sampling error (b)	540	7535.50	13.95	
Total	599	13027.79		

* Significant at the 5% level.
** Significant at the 1% level.

Study, Wells (1969) reported a high degree of interaction between planting locations and seed sources which followed a definite geographic pattern. Seed sources from areas with high rainfall and mild winters were tallest but when planted in colder planting locations, these sources were outperformed by those from areas with low summer rainfall and cold winters.

Variation in wood properties

The different wood properties investigated were percentage latewood, width of annual ring, cell dimensions, tracheid length, and specific gravity. These characteristics have been found to vary within an individual tree, between trees, among geographic locations (Rendle 1958b, Kennedy 1961, Zobel *et al*. 1972). Furthermore, these traits have been reported by many authors to be interrelated (Zobel *et al*. 1960, Echols 1958, Larson 1957, Van Buijtenen *et al*. 1961, Squillace *et al*. 1962, Wellwood 1961). Specific gravity, for example, is known to be closely related to percent latewood and cell wall thickness (Echols 1958, Zobel *et al*. 1961b, Mergen *et al*. 1964). The interrelationships between these characters are presented and discussed in more detail in a later section of this dissertation.

Percentage latewood. -- There was a very slight difference in the proportion of latewood among plantations (Table 1) and among seed sources over all plantations (Table 2). These differences were not statistically Significant (Table 5).

Among seed sources, the means ranged from 27.67 percent for the Vernon(N) to 30.33 for the Vernon (S) and East Feliciana seed sources. These results indicated no geographic variation in percentage of latewood in loblolly pine from these five Louisiana sources.

Plantation means ranged from 26.80 to 31.40 percent latewood. The plantation in De Ridder had the highest percentage of latewood - about 8.1 percent greater than the overall average, while the plantation in Bogalusa had the smallest percentage of latewood - about 9.1 percent less than the overall mean.

The seed source x plantation interaction was not significant. However, seed sources growing in the De Ridder plantation have higher percentage latewood, signifying favorable environmental conditions for latewood production at that site.

Geographic variation in the proportion of latewood has not been investigated thoroughly because it is always associated with specific gravity. However, Larson (1957), working with slash pine, reported that the percentage of latewood in this species increased from north to south and from west to east within the species range. In the present study, no definite pattern of geographic variation in percentage latewood was found for the five loblolly pine seed sources.

Width of annual ring. -- Width of annual ring usually decreases from the pith to the bark of coniferous trees.

Table 5. Analysis of variance for percent latewood

Sources of variation	D.F.	S.S.	M.S.	F
Plantation	2	2626.64	1313.32	3.94
Block/Pltn = Error (a)	9	2994.65	332.74	
Seed source	4	759.92	189.98	1.20
Plantation x seed source	8	1242.31	155.28	<1
Error (b)	36	6005.97	166.83	1.05
Sampling error (b)	540	85478.86	158.29	
Total	599	99108.35		

Table 6. Analysis of variance for average width of annual ring

Sources of variation	D.F.	S.S.	M.S.	F
Plantation	2	0.022	0.011	2.32
Block/Pltn = Error (a)	9	0.045	0.005	
Seed source	4	0.016	0.004	3.42**
Plantation x seed source	8	0.010	0.001	1.00
Error (b)	36	0.046	0.001	1.00
Sampling error (b)	540	0.626	0.001	
Total	599	0.763		

** Significant at the 1% level.

The wider annual ring in the pith is characteristic of juvenile wood (Zobel 1971) and is related to physiological aging of the cambium. This trait also varies between trees and geographic locations (Henderson and Petty 1972, Thor and Brown 1962).

The analysis of variance indicated that the differences in width of annual ring among seed sources were highly significant ($P<.01$) (Table 6). The means ranged from 0.193 to 0.213 inches with an average of 0.204 inches (Table 2). The St. Tammany and Washington seed sources consistently had the widest annual ring at all three plantations indicating a possibility of high genetic control for this particular trait. Additionally, there was an east-west geographic trend in variation in the width of annual ring. It decreases from the eastern sources to the western sources (Table 2).

Differences in width of annual ring among plantations were not significant (Table 6). The means were 0.198, 0.202, and 0.212 inches for De Ridder, Bogalusa, and Idlewild plantations, respectively (Table 1). The plantation x seed source interaction was also non-significant.

Cell dimensions

Statistical analyses of the data on cell dimensions revealed that cell wall thickness and width of cell lumen vary among plantations, seed sources, and within an individual tree.

1. Cell wall thickness: There was a pronounced difference in cell wall thickness among seed sources (Tables 2 and 7). The cell wall thickness for the whole core was largest (4.75 microns) in the Vernon (S) seed source and was smallest (4.51 microns) in the Washington seed source. The analysis of variance also indicated a highly significant differences among plantations (Table 7). Plantation means were 4.49, 4.59, and 4.89 microns for Bogalusa, Idlewild, and De Ridder, respectively. These significant results for both seed sources and plantations would mean that cell wall thickness is both environmentally and genetically controlled. The geographic pattern appears to be discontinuous, i.e., no distinct east-west trend was evident as for width of annual ring, above.

The wood near the pith of the tree has been variously referred to as "juvenile wood" or "corewood", and its properties differ from those of wood produced farther from the pith (Zobel et al. 1959). It was found in this study that the cell wall thickness in the pith section and bark section differed significantly (Table 7). The pith section had a cell wall average of 3.78 microns, while the bark section averaged 5.55 microns.

Differences in cell wall thickness of the radial and tangential dimension were not statistically significant. The radial dimension had a mean of 4.65 microns, while the tangential dimension had a mean of 4.67 microns. There was however, a

Table 7. Analysis of variance for cell wall thickness

Sources of variation	D.F.	S.S.	M.S.	F
Plantation	2	13.222	6.611	28.73**
Block/Pltn = Error (a)	9	2.071	0.230	
Seed source	4	3.944	0.986	3.41*
Plantation x seed source	8	4.831	0.604	2.09
Error (b)	36	18.693	0.519 (0.289)1/	1.90
Sampling error (b)	540	147.621	0.273	
Section (pith or bark)	1	379.266	379.366	3930.60**
Cell (tangential or radial)	1	0.081	0.081	<1
Section x cell	1	0.586	0.586	6.07*
Plantation x section	2	33.761	16.880	174.90**
Plantation x cell	2	1.156	0.578	5.99*
Plantation x section x cell	2	0.131	0.066	<1
Seed source x section	4	1.561	0.390	4.04**
Seed source x cell	4	0.095	0.024	<1
Seed source x section x cell	4	0.063	0.016	<1
Plantation x source x section	8	3.631	0.544	4.70**
Plantation x source x cell	8	0.228	0.029	<1
Plantation x source x section x cell	8	0.216	0.027	<1
Error (c)	1755	169.387	0.097	
Total	2399	780.644		

* Significant at the 5% level.
** Significant at the 1% level.
1/ Pooled mean square for error (b).

significant interaction between core section and cell dimensions. The cell wall thickness in both the radial and tangential dimensions of cells in the pith section was considerably smaller than in the bark section (Tables 1 and 2). There was no difference in cell wall thickness between the tangential and radial dimension of cells in either the pith section or bark section. This interaction illustrates that cell wall thickness in the core section was not independent of the cell dimensions (radial or tangential). Larson (1960) had implied that in the juvenile wood the cells most frequently remain thin-walled and are thicker in the mature wood. This cell wall development is dependent upon physiological conditions during the initiation of change.

Significant interactions were also observed for plantation x core section, plantation x cell dimensions, seed source x core section, and plantation x seed source x core section. Other interactions did not show significance (Table 7). The significant interaction between plantation and core section could reflect an influence of environment on wood formation during development of the trees. The difference in cell wall thickness between core sections has already been discussed. In Table 1, differences among plantations in latewood cell wall thickness for both pith and bark sections are evident. The De Ridder plantation had a mean cell wall thickness for both pith and bark sections of 4.89 microns, about six percent higher than the other two

plantations. These observations can be related to environmental conditions favoring a longer duration of latewood production at this planting site. Other authors have reported that changes in cell dimensions of both earlywood and latewood appear to be related to variations in tree spacing (Hiett _et_ _al_. 1960), rate of growth (Pew and Knechtges 1939), and temperature (Van Buijtenen 1958, Larson 1960).

2. Width of cell lumen: A comparison of the values for cell wall thickness and width of lumen indicates the strong negative correlation between these traits. Cells with thicker walls have narrower lumens and vice versa.

Accordingly, width of cell lumen again differed significantly among seed sources (Table 8). The means ranged from 33.9 microns for the East Feliciana seed source to 35.9 microns for the Vernon (N) and Washington seed sources (Table 2).

The variation in width of cell lumen and cell wall thickness of loblolly pine in Louisiana had no distinct geographic pattern. Trees with thicker walls and narrower lumens were found in both the western (Vernon - S) and eastern (St. Tammany) portions of the sampled range, yet trees with wider lumen diameters and thin walls were also found in the eastern part (Washington).

The analysis of variance showed a significant difference in cell lumen diameter among plantations (Table 8). Trees in the

Table 8. Analysis of variance for width of cell lumen

Sources of variation	D.F.	S.S.	M.S.	F
Plantation	2	6357.46	3178.73	113.47**
Block/Pltn = Error (a)	9	252.12	28.01	
Seed source	4	291.27	27.82	3.32*
Plantation x seed source	8	97.05	12.13	<1
Error (b)	36	1283.94	35.66 (21.98)1/	1.69
Sampling error (b)	540	11377.83	21.07	
Section (pith or bark)	1	7604.87	7604.87	449.83**
Cell (tangential or radial)	1	2129.67	2129.67	125.97**
Section x cell	1	4610.94	4610.94	272.74**
Plantation x section	2	824.41	412.20	24.38**
Plantation x cell	2	733.47	366.74	21.69**
Plantation x section x cell	2	964.08	482.04	28.51**
Seed source x section	4	55.03	13.76	<1
Seed source x cell	4	59.69	14.92	<1
Seed source x section x cell	4	49.61	12.40	<1
Plantation x source x section	8	153.64	19.21	1.14
Plantation x source x cell	8	103.11	12.89	<1
Plantation x source x section x cell	8	105.43	13.18	<1
Error (c)	1755	29670.28	16.91	
Total	2399	66723.89		

* Significant at the 5% level.
** Significant at the 1% level.
1/ Pooled mean square for error (b).

De Ridder plantation had the narrowest cell lumen diameter with a mean of 31.55 microns, while trees in the Idlewild and Bogalusa plantations averaged 33.55 and 39.98 microns, respectively. Again, this trend is exactly the opposite of that in cell wall thickness. Trees in the Idlewild and Bogalusa plantations have thinner cell walls and wider lumens than those in the De Ridder plantation.

Variation in width of cell lumen within individual trees was found to be statistically significant. Cell lumen diameter varied not only between pith and bark sections of a core, but also between the tangential and radial dimension of cells (Table 8). Width of cell lumen was widest at the pith section of the cores (38.9 microns) and tangential cell dimension (37.1 microns), narrowest at the bark section (31.0 microns) and radial cell dimension (32.9 microns). This finding agrees with those of Schultze-Dewitze (1955) and Nylinder (1953) who reported that cross-sectional dimensions of the cell lumen decreases from pith to bark and is broader tangentially than radially.

Significant interactions were noted for core section x cell dimension, plantation x core section, plantation x cell dimension, and plantation x section x cell. Other interactions were not significant (Table 8). The core section x cell dimension interaction can be seen more readily in Tables 1 and 2. The cell lumen width decreases from pith toward the bark, is

broader tangentially than radially at the pith section, but narrower at the bark section.

The plantation x core section interaction was highly significant ($P < .01$) for width of cell lumen. In Table 1, it can be seen that trees grown at Bogalusa had wider cell lumen than those grown at the other two plantations. The difference in cell lumen width between pith and bark sections within plantation was very slight, however.

Tracheid length -- In previous studies, variation in tracheid length was found within a tree, between trees, and among geographic origins. In conifers, tracheid length increases from the pith toward the bark and decreases from the base to the top of a tree (Echols 1955, Kramer 1957, Dadswell and Wardrop 1960, Choong et al. 1970). Variation in tracheid length among individual trees and among geographic areas has been found by many authors (Kramer 1957, Zobel et al. 1960, Posey et al. 1970. Dorn 1969).

Results of this study showed significant variation in tracheid length within a tree but no significant variation was noted among geographic origins (Table 9). There was however, a significant difference in tracheid length among plantations. In addition, the analysis of variance indicated significant interactions for core section x period (earlywood or latewood), plantation x core section, plantation x period, seed source x

Table 9. Analysis of variance for tracheid length

Sources of variation	D.F.	S.S.	M.S.	F
Plantation	2	381.88	190.94	5.03*
Block/Pltn = Error (a)	9	342.59	38.06	
Seed source	4	60.25	15.06	1.36
Plantation x seed source	8	196.19	24.52	2.22*
Error (b)	36	398.25	11.06	2.28*
Sampling error (b)	540	2618.19	4.84	
Core section (pith or bark)	1	32833.80	32833.80	2122.26**
Period (latewood or earlywood)	1	912.17	912.17	602.65**
Core section x period	1	149.70	149.70	98.90**
Plantation x core section	2	1151.93	575.98	380.53**
Plantation x period	2	168.40	84.20	55.63**
Plantation x section x period	2	10.29	5.14	3.39**
Seed source x core section	4	72.03	18.01	11.89**
Seed source x period	4	9.59	2.39	1.60
Seed source x section x period	4	5.27	1.32	≤ 1
Plantation x source x section	8	96.82	12.10	7.99**
Plantation x source x period	8	8.71	1.09	≤ 1
Plantation x source x section	8	18.22	2.28	1.51
Error (c)	1755	2656.42	1.51	
Total	2399	42090.73		

* Significant at the 5% level.

** Significant at the 1% level.

core section, plantation x core section x period, and plantation x seed source x core section.

In the present study, the significant difference in tracheid length among plantations and the non-significant difference among seed sources suggest a strong degree of environmental control of this trait. The plantation means were 2.61, 2.75, and 2.72 mm. for Bogalusa, De Ridder, and Idlewild, respectively. The seed source means were 2.67, 2.67, 2.69, 2.70, and 2.74 mm . for East Feliciana, Washington, St. Tammany, Vernon (N), and Vernon (S) seed sources, respectively. The differences in tracheid length among plantations were much greater than the differences among seed sources.

Although geographic differences were not statistically significant, there seems to be a weak clinal trend in tracheid length variation along an east-west and north-south transect. Seed sources from the western part of the State have longer tracheids than seed sources from the east, and the northern seed source (Vernon - N) had shorter tracheids than the southern seed source (Vernon - S). A decrease in tracheid length in loblolly pine populations from south to north was reported by Zobel et al. (1960a) in a study of seed sources collected from the entire Atlantic Coastal Plain. A similar geographic trend was found by Whitesell et al. (1966) in loblolly pine from Maryland and Delaware.

Significant differences were observed in tracheid length between the pith section and bark section (Tables 1 and 9). The pith section had an average tracheid length of 2.11 mm., while the bark section had an average of 3.27 mm. It had been earlier reported that tracheids are shortest near the pith and longest near the bark in conifers (Anderson 1952, Choong et al. 1970). Kennedy (1957) explained that, of the two factors causing variation in fiber length, the length of the initiating cell in the cambium is more important in coniferous trees than the elongation of the young daughter cell after differentiation.

Tracheid lengths in the latewood were significantly longer than the tracheid lengths in the earlywood. Latewood had an average tracheid length of 2.79 mm., while earlywood had an average tracheid length of 2.59 mm. There seems to be some difference of opinion with respect to whether the tracheid length of the latewood differs from that of the earlywood. Gerry (1916) reported that the latewood tracheids of Douglas-fir and southern pines were shorter than earlywood tracheids; but Jackson and Greene (1957) did not find any difference between latewood and earlywood tracheids in southern pines. Other investigators (Bissett and Dadswell 1950, Anderson 1951, Dadswell and Wardrop 1960) have indicated that latewood tracheids were slightly longer than the earlywood tracheids.

Specific gravity. -- Most investigators who have studied specific gravity of loblolly pine have reported large variation

Table 10. Analysis of variance for specific gravity

Sources of variation	D.F.	S.S.	M.S.	F
Plantation	2	0.348	0.174	47.28*
Block/Pltn = Error (a)	9	0.033	0.004	
Seed source	4	0.118	0.029	5.89**
Plantation x seed source	8	0.096	0.012	2.40*
Error (b)	36	0.205	0.006 (0.005)1/	1.14
Sampling error (b)	540	2.677	0.0049	
Core section (pith or bark)	1	10.295	10.295	9969.11**
Extraction, methods of	1	0.433	0.433	418.93**
Core section x extraction	1	0.006	0.006	5.59*
Plantation x core section	2	0.055	0.027	26.56**
Plantation x extraction	2	0.004	0.002	2.14
Plantation x section x extraction	2	0.0006	0.0003	<1
Seed source x core section	4	0.013	0.003	3.15*
Seed source x extraction	4	0.0015	0.0004	<1
Seed source x section x extraction	4	0.0012	0.0003	<1
Plantation x source x section	8	0.0298	0.0037	3.62**
Plantation x source x extraction	8	0.001	0.00013	<1
Plantation x source x core x extraction	8	0.0008	0.0001	<1
Error (c)	1755	1.812	0.00103	
Total	2399	16.1308		

* Significant at the 5% level.
** Significant at the 1% level.
1/ Pooled mean square for error (b).

within trees, among trees, and among geographic origins. Results obtained from this study were no exception.

Analysis of variance (Table 10) indicated significant differences in specific gravity among plantations, seed sources, and between core sections. Significant interactions were also obtained for the plantation x seed source, plantation x core section, core section x extraction, seed source x core section, and plantation x seed source x core section.

Highly significant differences were found among seed sources (Table 10). The average extracted specific gravities (whole core) for the different seed sources were 0.429, 0.424, 0.421, 0.420, and 0.408 for Vernon (S), St. Tammany, East Feliciana, Vernon (N), and Washington seed sources, respectively (Table 11). The most westerly seed source (Vernon - S) had the highest average specific gravity, while the Washington parish seed source had the lowest.

Significant differences were also obtained among plantations. The mean specific gravities (extracted) for the different plantations were 0.44, 0.41, and 0.41, for De Ridder, Bogalusa, and Idlewild, respectively. All seed sources had higher specific gravity in the De Ridder plantation, indicating environmental conditions favoring the development of denser wood (Table 11).

The early moisture stress during the active growing period in trees in De Ridder plantation could have initiated prolonged

Table 11. Comparison of wood specific gravity (extracted) of seed sources within plantation

Seed sources	Plantation			
	Bogalusa	De Ridder	Idlewild	Mean
East Feliciana	0.417	0.427	0.419	0.421
St. Tammany	0.417	0.439	0.418	0.424
Vernon (N)	0.403	0.448	0.407	0.420
Vernon (S)	0.426	0.450	0.411	0.429
Washington	0.393	0.428	0.403	0.408
Mean	0.411	0.438	0.411	0.420

production of latewood but less diameter growth. Diameter growth, which depends mainly on the products of current photosynthesis, slows or ceases during periods of extreme moisture stress and reaccelerates when the soil is recharged by rain. During the period when diameter growth slows down, more of the carbohydrates are incorporated into the cell walls resulting in the production of thick-walled cells.

The interaction between plantation and seed source was significant ($P<.05$) (Table 10). This interaction is most noticeable in the lower specific gravity of trees from the Washington seed source grown in all plantations and the relatively higher specific gravity of trees from the Vernon (S) and St. Tammany seed sources when grown everywhere except in the Idlewild plantation. In the De Ridder plantation, the average specific gravity of the local seed source was noticeably higher than that of the non-local sources. The same was true with the "local" sources at the other plantations (Table 11) although the differences were very small.

The interaction between plantation and seed source indicates both environmental and genetic control of specific gravity. Goggans (1961) pointed out that environmental factors can affect specific gravity considerably, but when one examines those environmental factors that the practicing forester can control within a given stand it is evident that the practical significance of the environmental effect becomes much less. In another report,

Zobel et al. (1972) stated that although specific gravity is a complex characteristic affected by percent latewood, wall thickness and cell size, it is inherited rather strongly, with a narrow-sense heritability between 0.50 and 0.65. This enables good genetic gains to be obtained by selection and breeding of desired parents.

The difference in specific gravity between the pith and bark sections was highly significant (Table 10). Mean specific gravity (extracted) for the pith section was 0.37, while the bark section was 0.50. This significant difference was expected as it had been reported by several authors (Panshin et al. 1964, Goggans 1961, Zobel and Mc Elwee 1958a) that within the stem of conifers, specific gravity of wood tends to increase from the pith toward the bark.

A significant difference was also found in specific gravity between the extracted and unextracted samples (Table 10). This illustrates that extractives tend to mask the actual specific gravity of the wood. Posey et al. (1970) advised to use only the specific gravity of extractive-free wood for comparisons in seed source studies because of the strong environmental influence on variation in extractive content.

The core section x extractions interaction was significant at the 0.05 level. This interaction resulted because the difference between the means of the extracted and unextracted

specific gravities in the bark section was higher than the difference between the means of the same specific gravities in the pith section.

Discussion

Results of this investigation have shown that very little geographic variation in growth and wood properties existed among the five Louisiana seed sources of loblolly pine grown in three plantations. Only specific gravity and associated characteristics (cell wall thickness, width of annual ring, and lumen diameter) showed significant genetic variation. Close examination of the data revealed strong environmental influences on the different traits studied. These were evident in the highly significant differences among plantations.

Although statistical tests did not show significant differences among seed sources in diameter and height, there was an indication that these growth traits were genetically controlled to a certain extent as evidenced by the consistently higher growth rate of the St. Tammany seed source when planted in all three plantations (Table 2). There are conflicting ideas on the degree of genetic control of diameter and height growth because these traits are very much affected by the environment (Young and Kramer 1952). On the other hand, Van Buijtenen (1963) reported that height and diameter growth are moderately genetically controlled in loblolly pine.

The significant differences among seed sources in width of annual ring, specific gravity, and cell dimensions are quite surprising considering the fact that seed sources were sampled from a very limited geographical range with almost no differences in latitude. These results however, indicated that these wood properties are genetically controlled to a much greater degree than height or diameter growth rate. Many other investigators have shown that, in loblolly pine specific gravity is very strongly genetically controlled. Zobel et al. (1972) found two loblolly pine trees growing side by side which differed in wood specific gravity.

Variation in width of annual ring appeared to follow a continuous pattern of geographical variation, decreasing from east to west. Seed sources from the eastern part of the State have wider ring width than sources in the western part of the State. In a provenance test of loblolly pine in Tennessee, Thor and Brown (1962) also found significant differences in width of annual ring among six seed sources but no geographical pattern of variation was observed.

Specific gravity and cell dimensions followed the same general geographic pattern of variation. This was expected, because these traits are highly correlated (correlation among growth and wood properties is discussed later in this paper). The most westerly seed source (Vernon - S) had the highest

average specific gravity in all three plantations, while the Washington parish seed source had the lowest.

This trend, although weak, would further support evidence that, for specific gravity and related traits, geographic strains of loblolly pine do exist in Louisiana. In an earlier study, Crow (1961) had reported that there are genetic differences in fusiform rust resistance among geographical sources from Louisiana. Bishop (1972) had also found significant variation in certain morphological characteristics among five Louisiana seed sources of loblolly pine planted in southeastern Louisiana. What may have contributed to this variation, according to Bishop, was the possibility of shortleaf-loblolly pine introgression. It could then be possible that the higher specific gravity of the western seed source was also due to this introgression. (It will be noted that wood specific gravity of shortleaf pine is higher than loblolly pine). In western Louisiana, shortleaf pine is much more abundant than in southeastern Louisiana. Therefore, it is very likely that more shortleaf-loblolly introgression has occurred in western Louisiana than in southeastern Louisiana. This phenomenon could explain the geographic variation in wood properties found among loblolly pine seed sources in this study.

Analyses of variance revealed differences in growth and wood properties among seed sources due to environmental influences , i.e., planting site. These influences were more

pronounced on tracheid length, specific gravity, cell dimensions and were less pronounced in percentage latewood, width of annual ring, and growth rate. As mentioned earlier, due to the unique location of seed sources and plantations, variations in latitude, elevation, photoperiod, temperature, and soils were minimized. One major climatic variable that was not uniform among the three plantation sites was seasonal distribution of rainfall. Therefore, these precipitation patterns at the three sites were investigated to determine if seasonal moisture relations could possibly help to explain some of the differences found in this study.

Precipitation records for the 13-year period since the source tests have been established revealed fairly large differences in seasonal rainfall distribution among the three planting sites (Tables 12, 13, and 14). The amount of rainfall in the early growing season ("Spring" - March, April, May) was highest at the Idlewild plantation and lowest at De Ridder, and the pattern is reversed for late season precipitation ("Autumn"- October, November, December), i.e.,rainfall during this three-month-period was highest at De Ridder and lowest at Idlewild. A comparison of "Summer" (June, July, August) precipitation indicated a relatively "dry" period at the De Ridder plantation during these three months compared with the Idlewild and Bogalusa plantations.

To more closely examine the effect of the variable rainfall distribution among plantations on the relationship of height

Table 12. Monthly precipitation (inches) and average by years in the Bogalusa plantation for the period 1958 - 1971

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1958	5.63	3.87	7.86	5.26	5.57	3.68	9.19	6.91	12.58	1.15	2.89	2.10
1959	5.88	7.76	2.22	4.25	12.97	7.74	6.82	4.57	2.93	8.27	3.10	3.76
1960	4.97	7.28	3.88	3.29	4.20	.44	6.46	11.21	.85	2.91	1.58	3.60
1961	8.72	12.31	8.87	2.79	3.15	9.09	4.42	2.91	6.95	1.59	14.66	13.18
1962	10.19	.40	3.86	7.67	2.80	5.72	1.09	2.30	4.56	4.40	1.03	4.27
1963	3.67	4.41	1.69	.97	1.35	7.97	6.44	4.56	3.50	.22	4.08	4.23
1964	6.44	5.54	10.91	8.23	3.99	3.01	5.16	3.65	1.97	6.66	6.24	6.69
1965	4.84	8.22	4.28	.93	1.52	4.73	6.07	13.80	4.85	1.08	1.17	4.92
1966	9.64	16.02	1.53	5.15	6.58	4.21	2.22	6.95	3.47	.98	1.82	3.21
1967	3.01	4.77	1.63	7.87	11.29	2.96	5.16	3.81	4.68	1.45	.63	9.87
1968	3.14	3.19	2.46	3.34	1.39	1.90	5.81	3.24	3.40	.53	6.79	9.54
1969	.77	4.53	6.51	9.33	7.42	3.20	5.96	2.64	.36	3.13	2.88	4.16
1970	2.99	3.05	4.03	2.47	5.97	4.07	7.82	9.00	.69	10.57	2.21	6.90
1971	3.01	5.14	4.24	1.19	2.78	4.64	8.72	2.77	10.41	.82	2.96	11.88
Mean	5.18	6.36	4.32	4.39	5.01	4.13	5.91	5.60	3.74	3.62	3.85	6.63

Table 13. Monthly precipitation (inches) and average by years in the De Ridder plantation for the period 1958 - 1971

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1958	-	-	-	-	-	-	-	7.70	17.64	-	5.29	2.08
1959	3.21	6.52	2.57	6.23	2.38	2.39	6.42	5.32	2.74	3.80	2.33	3.72
1960	5.87	5.59	2.18	2.29	.71	4.84	2.78	3.70	1.79	7.18	2.85	10.10
1961	7.62	8.74	5.49	1.28	3.39	11.19	2.72	5.54	.69	10.03	8.05	8.38
1962	4.05	2.49	2.78	2.93	2.99	6.38	1.75	3.23	3.84	2.92	5.96	4.97
1963	3.45	3.56	.84	.77	3.78	5.29	6.33	3.67	3.07	.01	7.40	4.61
1964	4.80	2.40	5.29	8.91	4.39	1.16	4.81	2.82	3.73	.15	6.58	6.32
1965	4.77	3.72	2.72	.46	5.27	1.72	3.84	2.58	4.70	.74	4.10	7.61
1966	7.53	7.55	.67	6.39	4.42	2.89	2.19	9.04	5.54	6.33	9.48	4.94
1967	1.82	4.94	2.26	9.49	5.99	3.17	5.22	1.85	1.19	4.49	.19	15.46
1968	6.35	3.46	4.00	7.83	4.68	8.07	3.20	4.68	3.35	2.22	5.33	7.50
1969	1.09	5.72	4.94	5.75	6.05	1.45	5.47	2.39	1.87	1.72	2.14	7.56
1970	1.62	2.91	3.76	3.60	3.00	1.29	3.67	2.35	7.36	10.82	2.32	3.09
1971	1.51	5.52	4.70	.67	4.15	3.25	4.88	5.64	4.03	2.27	4.95	13.65
Mean	3.84	4.84	3.25	4.35	3.94	3.84	4.75	3.56	3.75	3.33	4.90	7.53

Table 14. Monthly precipitation (inches) and average by years in the Idlewild plantation for the period 1958 - 1971

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1958	4.82	3.89	6.23	4.32	3.32	5.80	4.19	6.80	6.48	1.51	1.87	1.59
1959	6.40	8.13	3.36	5.15	5.73	4.94	8.18	4.84	3.39	4.22	6.99	6.64
1960	5.87	4.04	2.63	1.48	1.92	1.47	2.68	14.00	.37	6.34	1.41	5.72
1961	7.72	9.79	15.07	2.28	2.78	2.78	7.19	3.08	10.40	.57	8.42	9.37
1962	10.01	1.93	2.38	12.83	4.76	5.82	2.71	3.47	1.59	1.55	1.06	3.31
1963	6.90	3.40	2.83	.45	5.25	5.02	3.81	5.88	2.15	.02	4.02	4.43
1964	6.85	4.49	11.61	8.93	2.24	3.55	9.45	3.04	2.52	10.80	6.12	4.54
1965	1.84	5.85	5.34	.05	3.08	3.52	4.42	4.15	5.77	1.56	4.14	6.27
1966	9.10	14.61	2.52	6.32	3.99	2.82	5.99	4.72	3.19	2.84	2.44	1.78
1967	3.68	4.88	3.38	9.72	8.75	2.44	5.88	6.54	1.93	1.80	.31	6.96
1968	3.01	3.50	3.25	3.09	7.63	2.35	5.07	2.99	3.10	2.33	4.38	8.69
1969	1.40	5.90	6.16	7.42	7.32	.69	8.69	2.23	2.98	5.41	.68	6.29
1970	2.78	2.29	5.19	3.15	3.38	4.35	7.27	4.87	5.31	8.28	2.06	5.99
1971	3.39	4.40	5.01	1.39	8.97	4.61	6.83	4.32	10.17	.96	3.77	13.34
Mean	5.30	5.63	5.29	4.79	5.10	3.50	6.01	4.94	4.07	3.59	3.52	6.40

and diameter growth and wood properties found in this study, and to determine the growth responses and sensitivity of the individual seed sources to these patterns, regression and correlation analyses were conducted.

Using long-term precipitation records from "Climatography of the United States No. 86-14 (Louisiana)" it was possible to determine the "normal" precipitation levels for each seed source during each of the three-month periods previously designated as spring, summer, and autumn. These data were then used to arrive at a value of the percent "normal" precipitation during the periods for each seed source growing at each of the three plantations during the 13-year period of the study (Table 15). These values were obtained by dividing the 13-year mean precipitation at each planting site by the "normal" precipitation values for each seed source.

$$\text{Percent "normal" precipitation} = \frac{\text{13-year } \bar{x} \text{ precipitation at planting site}}{\bar{x} \text{ for seed origin}} \times 100$$

Percent "normal" precipitation for the seed source was used as the independent variable in subsequent regression analyses.

Growth and wood property data were converted to a percentage of the average performance at all three planting sites for each individual seed source at each plantation by dividing the seed source mean at each planting site by the overall mean for each seed source multiplied by 100.

Table 15. Percent "normal" precipitation of seed sources at the three plantation locations for the period 1958 - 1971

March, April, and May (spring):

Seed sources	Plantations		
	Bogalusa	De Ridder	Idlewild
East Feliciana	92	77	102
St. Tammany	83	67	91
Vernon (N)	90	76	99
Vernon (S)	90	76	99
Washington	82	69	91

June, July, and August (summer):

Seed sources	Plantations		
	Bogalusa	De Ridder	Idlewild
East Feliciana	92	71	85
St. Tammany	85	66	78
Vernon (N)	114	89	106
Vernon (S)	114	89	106
Washington	87	67	80

October, November, December (autumn):

Seed sources	Plantations		
	Bogalusa	De Ridder	Idlewild
East Feliciana	119	132	114
St. Tammany	113	125	108
Vernon (N)	101	112	97
Vernon (S)	101	112	97
Washington	109	108	104

$$\text{Percent mean performance} = \frac{\bar{x} \text{ of seed source at planting site}}{\bar{x} \text{ of seed source on all sites}} \times 100$$

These converted data provide a more objective and uniform value for analysis of seed source growth responses to deviations from the "normal" moisture levels than would the actual values for growth and wood properties. These data are expressed as percentages of the seed source means in Table 16 and 17 and they were used as the dependent variable in the regression analyses.

Examination of the data for height and diameter growth for all five seed sources at the three planting sites revealed an inverse or negative relationship between height and diameter growth (Table 1). Seed sources grown at the De Ridder plantation averaged highest in height growth and lowest in diameter growth, while the same sources grown at Idlewild had the largest diameter and the smallest average height. Trees in the Bogalusa seed source test were intermediate in both characteristics.

Availability of moisture greatly affects shoot and cambial growth of trees. As internal water deficits develop in trees, cambial and shoot growth slows or ceases and accelerates or resumes with increased water availability. Kozlowski (1972) reviewed the literature pertaining to the effects of seasonal soil moisture patterns on height and diameter growth of forest trees. Findings of several studies on different species have shown that, in areas with abundant spring soil moisture,

Table 16. Growth data expressed as percentage of the seed source means

	Plantation		
Diameter:			
Seed sources	Bogalusa	De Ridder	Idlewild
East Feliciana	101	97	102
St. Tammany	98	96	106
Vernon (N)	100	98	102
Vernon (S)	100	97	103
Washington	99	96	105
Height:			
East Feliciana	102	99.5	98.5
St. Tammany	101.5	101.5	97
Vernon (N)	97	110.5	92.5
Vernon (S)	97	106	97
Washington	97.5	106	96.5

Table 17. Wood property attributes expressed as percentage of seed source means

Seed sources	Plantation: Bogalusa	De Ridder	Idlewild
Width of annual ring:			
East Feliciana	103	94	103
St. Tammany	95	95	110
Vernon (N)	98	98	104
Vernon (S)	100	100	100
Washington	98.5	98.5	103
Latewood:			
East Feliciana	95.6	108.8	95.6
St. Tammany	91	104.5	104.5
Vernon (N)	80	112	108
Vernon (S)	92	109	99
Washington	98	101	101
Specific gravity:			
East Feliciana	100	102	98
St. Tammany	98	103	99
Vernon (N)	96	107	97
Vernon (S)	99	105	96
Washington	94	103	103

Table 17. (Continued)

Tracheid length:			
	Plantation		
Seed sources	Bogalusa	De Ridder	Idlewild
East Feliciana	95	105	100
St. Tammany	99	100	101
Vernon (N)	96	100	104
Vernon (S)	98	102	100
Washington	97	104	99
Cell wall thickness:			
East Feliciana	94	103	103
St. Tammany	101	101	98
Vernon (N)	97	105	98
Vernon (S)	95	107	98
Washington	97	104	99
Width of cell lumen:			
East Feliciana	117	90	93
St. Tammany	113	91	96
Vernon (N)	115	88	97
Vernon (S)	114	89	97
Washington	113	91	96

seasonal height growth of many species is controlled by precipitation during the preceding season (Motley 1949, Hustich 1948, Tryon 1957). In contrast to height growth, diameter growth depends mainly on the products of current photosynthesis and is therefore much more sensitive to environmental factors, particularly moisture stress, during the current growing season.

A significant positive relationship (r^2 = 0.66) between diameter growth response of seed sources and "normal" or above "normal" levels of precipitation during the spring period (March, April, May) was found (Figure 4). Non-significant relationships were found when growth data were plotted over summer (positive correlation, Figure 5) and autumn (negative correlation, Figure 6) precipitation. Young and Kramer (1952) found that, in loblolly pine, diameter and height growth begin at about the same time, and the results of the present study suggest that adequate moisture during the period March through May is more critical for diameter growth than are moisture levels later in the growing season. As seen in Table 15, over the 13-year-period of this study, the most optimal precipitation levels for all seed sources early in the growing season occurred at the Idlewild plantation, and each of the five sources attained their greatest diameters on this site (Table 16). Conversely, trees grown at the De Ridder plantation were exposed to rather severe moisture stress (on the average) during the spring, and here

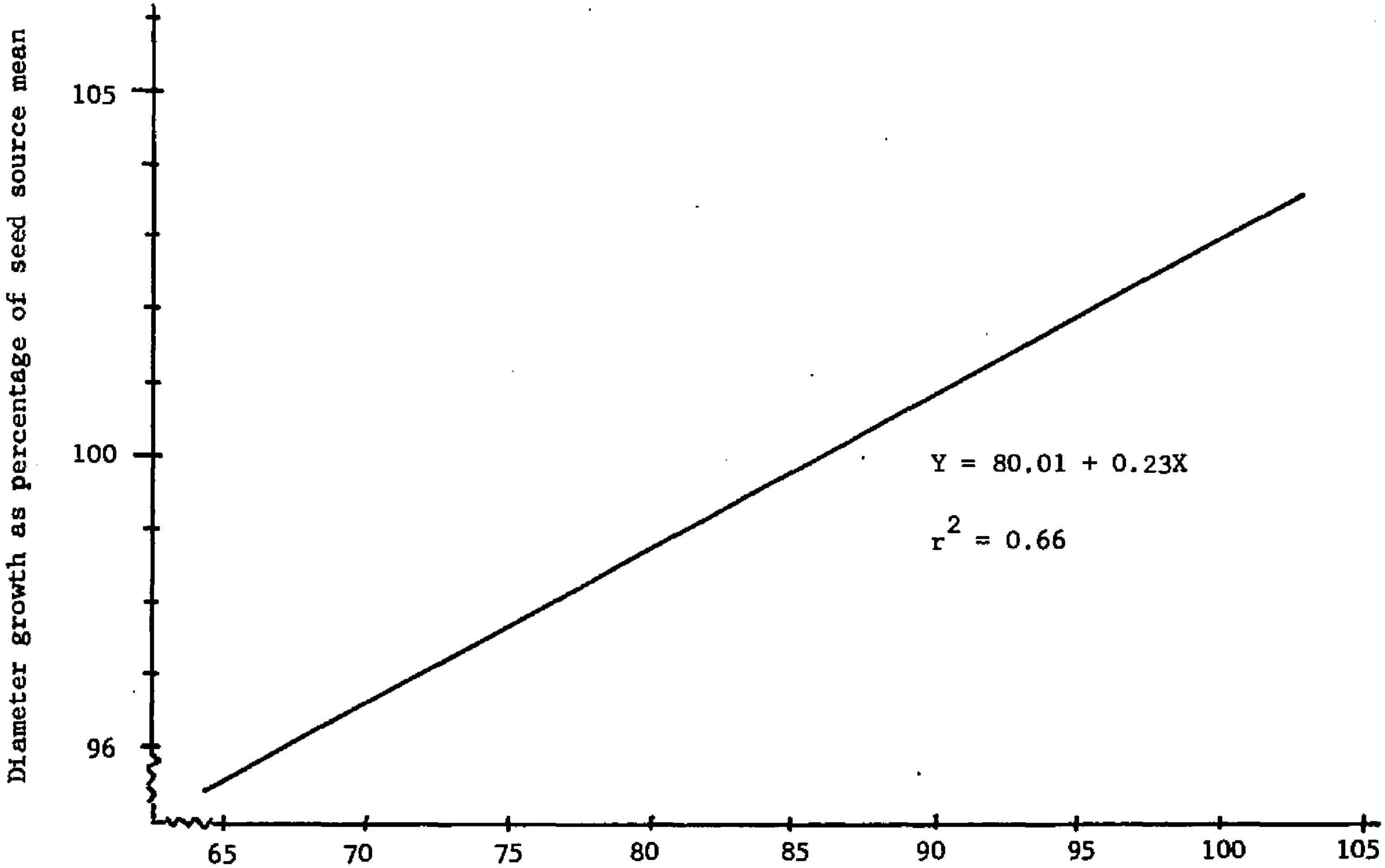

Figure 4. Relationship between diameter growth and spring precipitation of seed source means.

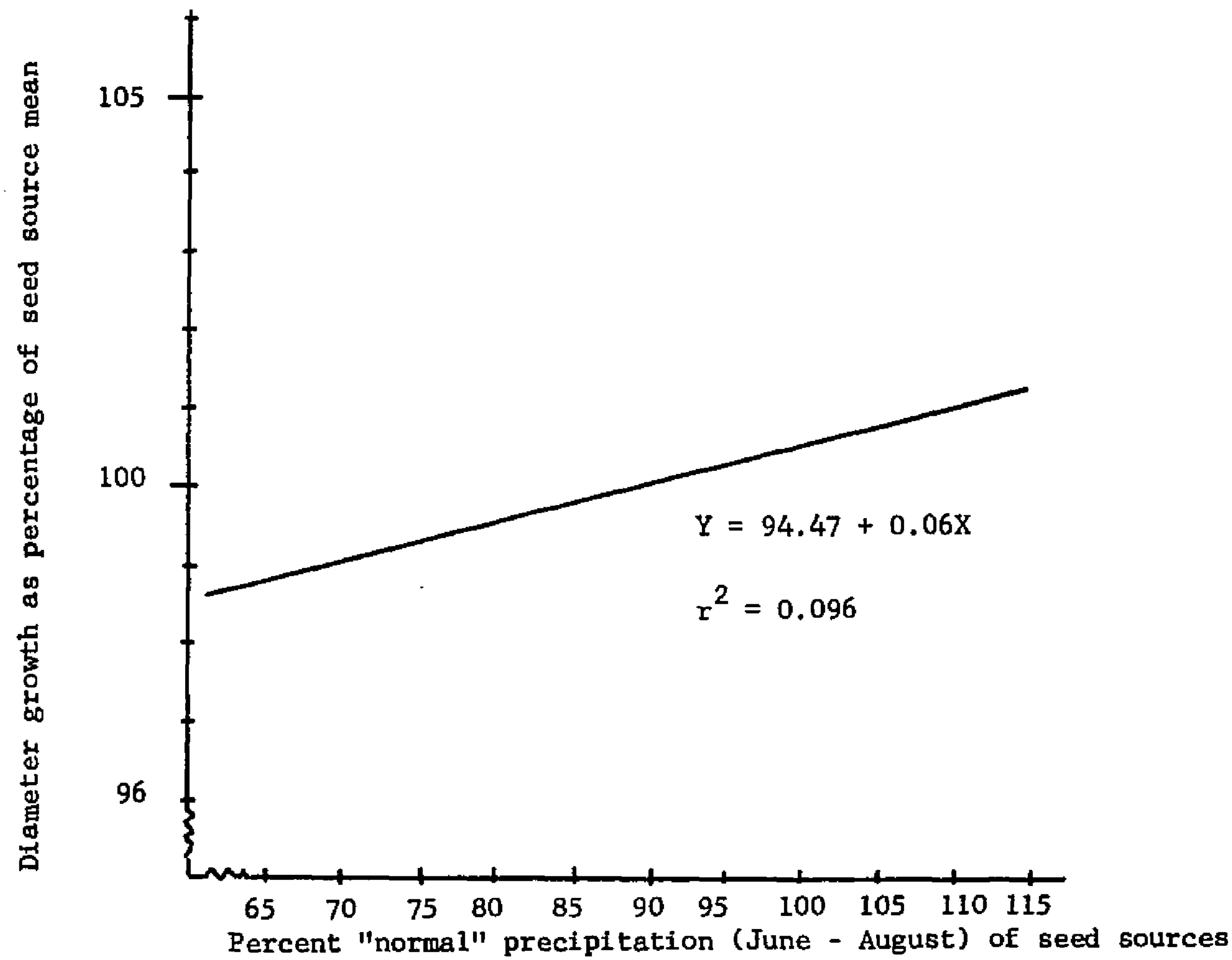

Figure 5. Relationship between diameter growth and summer precipitation of seed source means.

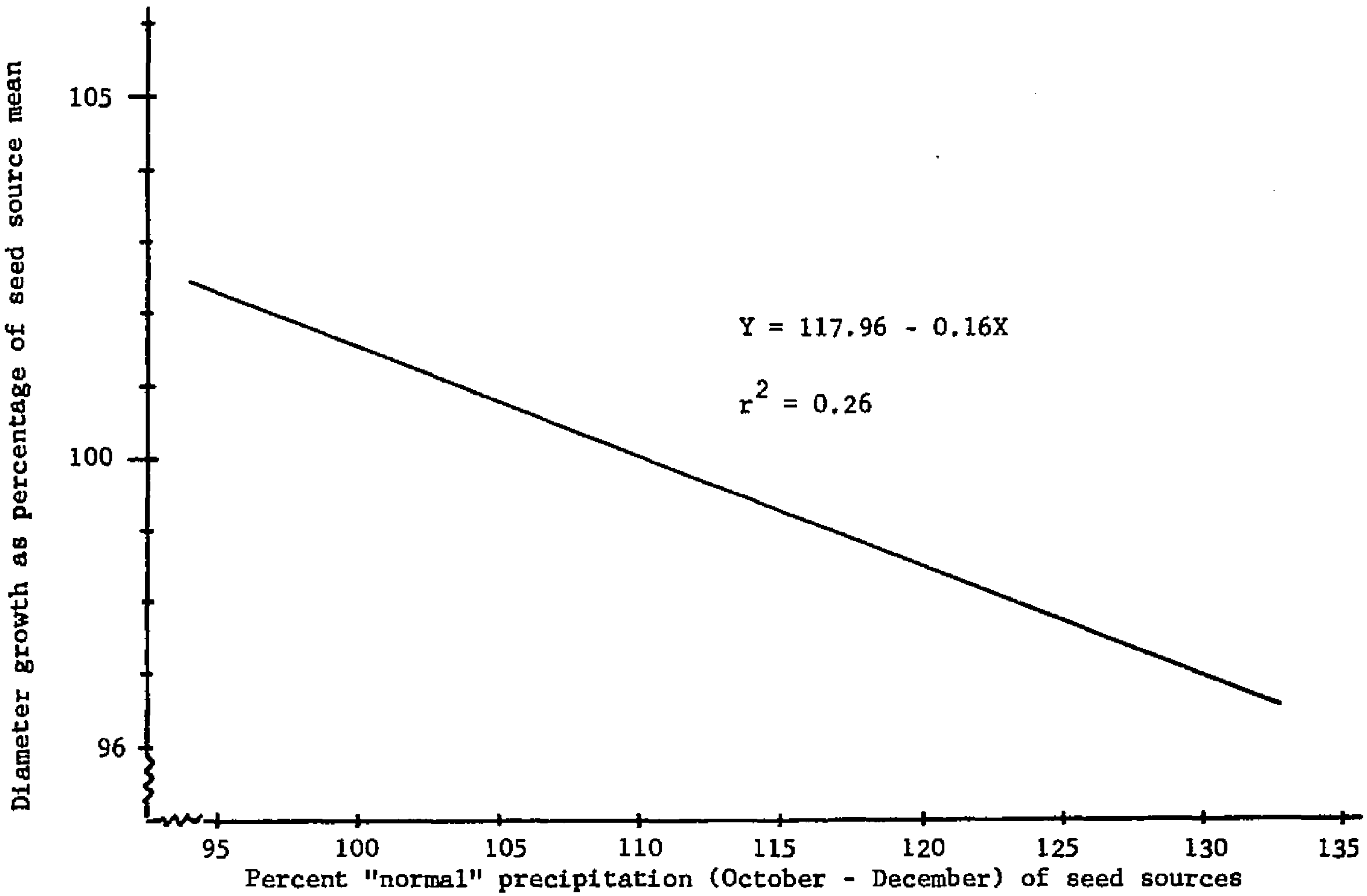

Figure 6. Relationship between diameter growth and autumn precipitation of seed source means.

the seed sources averaged only 90 to 95 percent of their diameter growth at Idlewild. Differences in precipitation during June, July, and August were not as pronounced among the plantations as they were early in the growing season and, during this period, the Bogalusa plantation recieved the greatest amount of precipitation (Figure 5 and Table 15). Apparently, despite heavy autumn rainfall at the De Ridder plantation, available moisture during this period had little or no effect on annual diameter growth rate (Figure 6).

Correlations of height growth responses of seed sources with precipitation levels revealed a positive relationship only with autumn (October, November, and December) data (Figure 9). While this relationship was not significant ($r^2 = 0.18$) it represents some indication of favorable response to late season rainfall and soil moisture recharge. Height growth was negatively correlated with spring and summer precipitation levels (Figures 7 and 8), suggesting that moisture stress during summer has much less effect on height growth than on diameter. All five sources attained their greatest mean height at the De Ridder plantation despite the comparatively severe spring and summer moisture deficits at this site.

A possible cause of the better height growth of seed sources in the De Ridder plantation was the late rainfall which favored formation of large terminal buds in autumn and elongation of these throughout the winter until the first flush of growth in

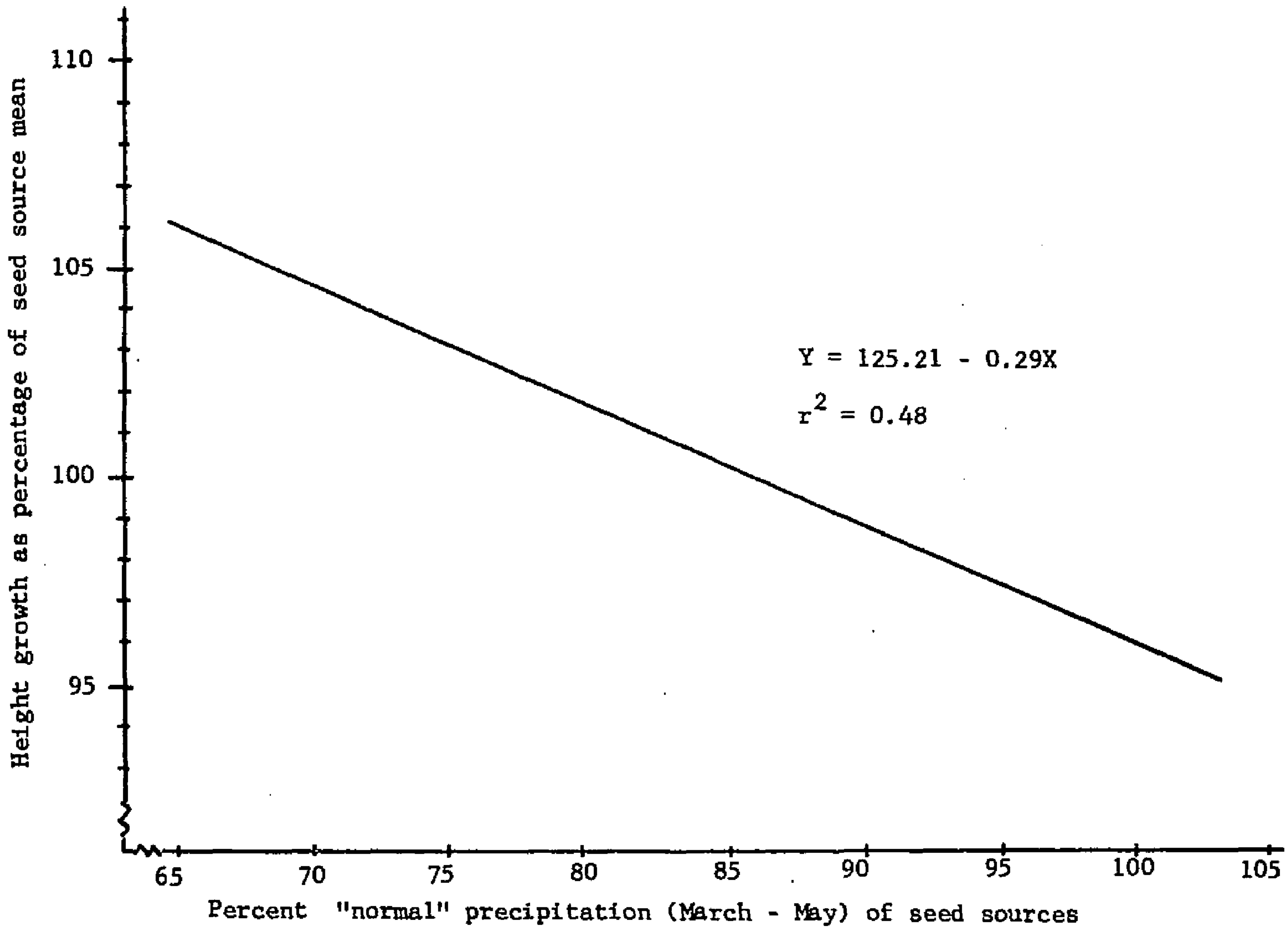

Figure 7. Relationship between height growth and spring precipitation of seed source means.

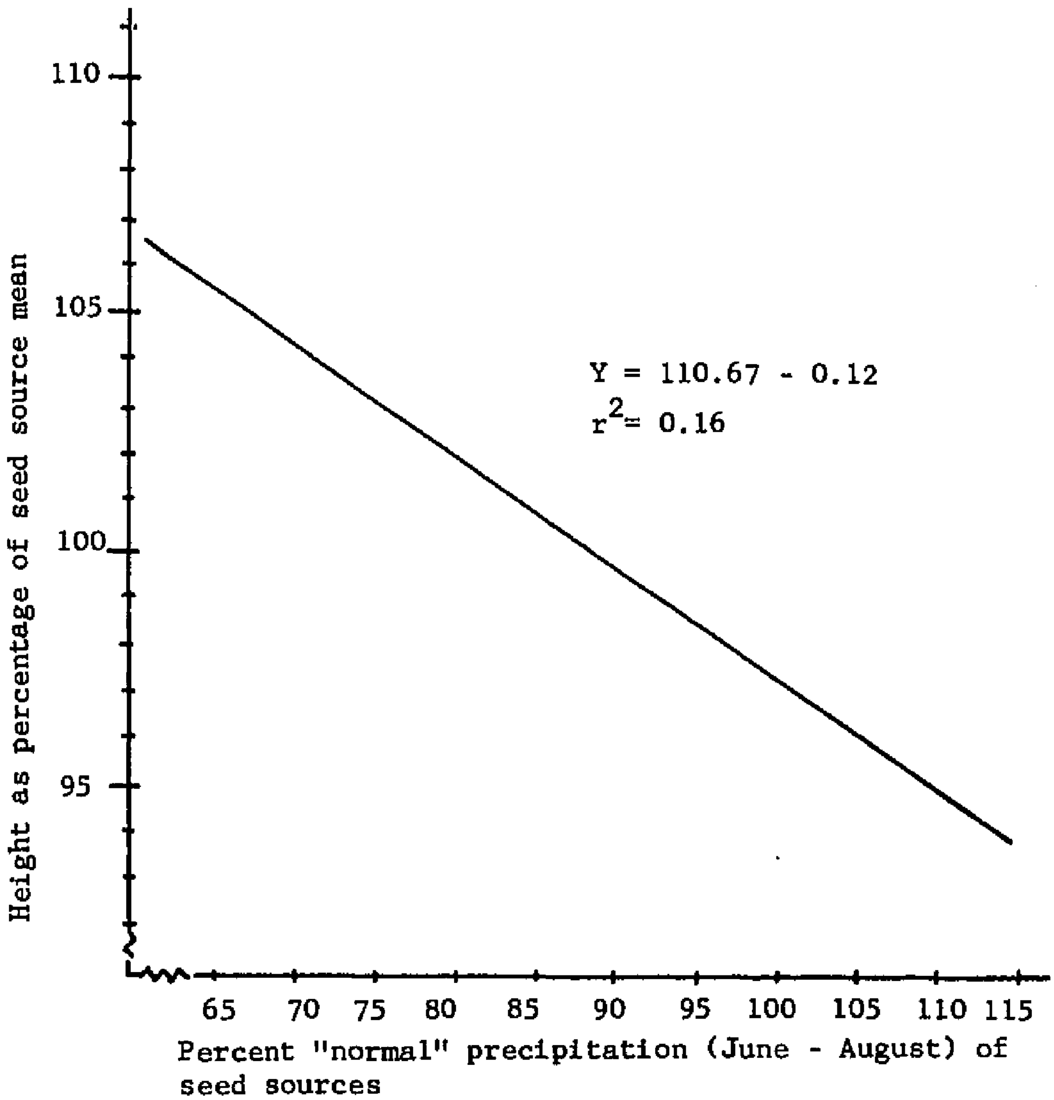

Figure 8. Relationship between height growth and summer precipitation of seed source means.

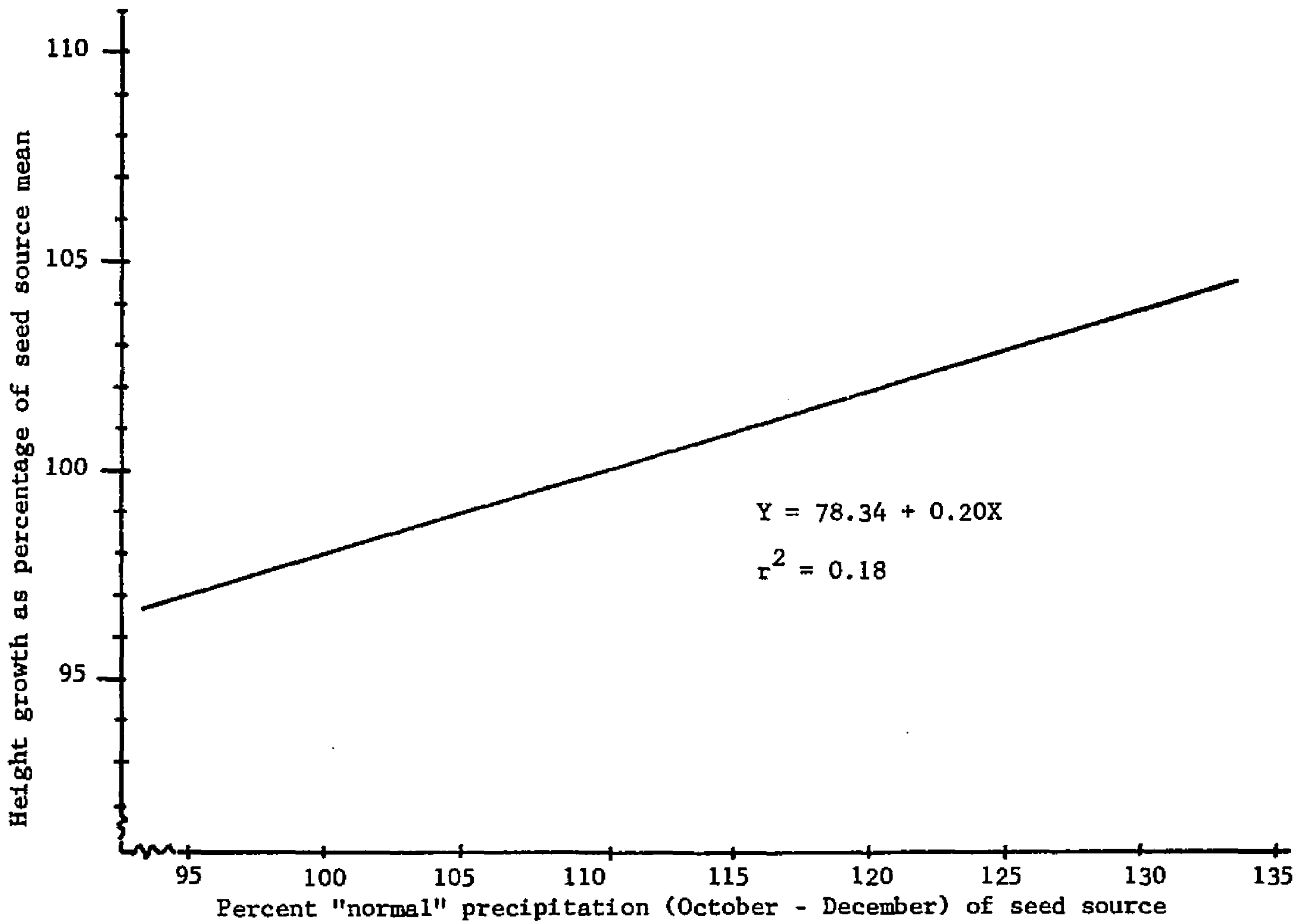

Figure 9. Relationship between height growth and autumn precipitation of seed source means.

the spring. Also, increased moisture would favor a longer period of growth which could be extended until low temperature become limiting. Loblolly pine is a recurrently flushing species which makes about five to eight flushes for five months or more out of the year, usually starting in March and ending in September but sometimes extending to late October (Kramer 1943, Boyer 1970).

These shoot flushes and the ultimate length of the internode are correlated with the size of the bud and the number of shoot primordia that were present in the bud. Adequate moisture induces formation of large buds, subsequently large shoots with many needle fascicles are produced. Bengtson et al. (1967) reported a close correlation between terminal bud length of slash pine and subsequent height growth both in the spring ($r = 0.97$) and for the whole year ($r = 0.91$). Hanover (1963) reported a close correlation between terminal bud length and subsequent total seasonal elongation of ponderosa pine. In loblolly pine, Boyer (1970) found significant correlations among lengths of initial buds, succeeding shoots, and final buds for terminal shoots of seedlings and saplings. He reported further that on lateral shoots of seedlings, the first flush provided 61 percent of all new growth. Most of the new growth on seedling terminal came from the second and third growth flushes.

Since large buds have already been produced before the

first flush of growth, the moisture stress that occurred during spring and summer at De Ridder would not have much marked effect on the first flush and subsequent flushes of growth. It is only when drought continues throughout the period of growth that the expansion of primordia in the buds and subsequent internode elongation may be inhibited (Kozlowski 1971). In the De Ridder plantation, however, increased precipitation was noted in July (Table 13) which could have initiated long shoot flushes. And because of the unusually high precipitation in November following the relatively dry months of September and October this might have resulted in another spurt of growth.

It can then be hypothesized that the seasonal rainfall pattern at the De Ridder plantation, while unfavorable for diameter growth because of moisture stress earlier in the season, was conducive to height growth because of relatively abundant water in the late fall (October, November, December). This may have caused more prolonged growth flushes and most certainly would influence the formation of larger terminal buds in the winter, which would produce a vigorous growth flush the following spring.

The hypothesis presented above are based only upon correlations of height and diameter growth with precipitation patterns and experimental data from this study are not available

to support them. However, there appears to be ample support in the literature for these theories which provide a logical explanation for the dramatic differences in height and diameter growth at the different planting sites. The relationship with seasonal precipitation also illustrates the sensitivity of growth, especially cambial growth, to moisture stress.

Analyses of variance for the different wood properties have shown strong environmental variation in specific gravity, tracheid length, and cell dimensions, and relatively small environmental influence in percentage latewood and width of annual ring. Examination of these traits revealed that all five seed sources have high values for specific gravity, tracheid length, cell wall thickness, and percentage latewood, and low values for width of annual ring and width of cell lumen in the De Ridder plantation. The opposite was found in the Bogalusa and Idlewild plantations (Table 17).

When specific gravity, percentage latewood, and cell wall thickness were individually correlated with precipitation during the different seasons, all followed the same trend, i.e., these traits showed positive correlations with autumn precipitation and negative correlations with spring and summer precipitation (Figures 10 - 18). This uniform trend again confirms the results of previous studies which have shown that these traits are very strongly correlated, and whatever environmental factors affect one will also affect the others.

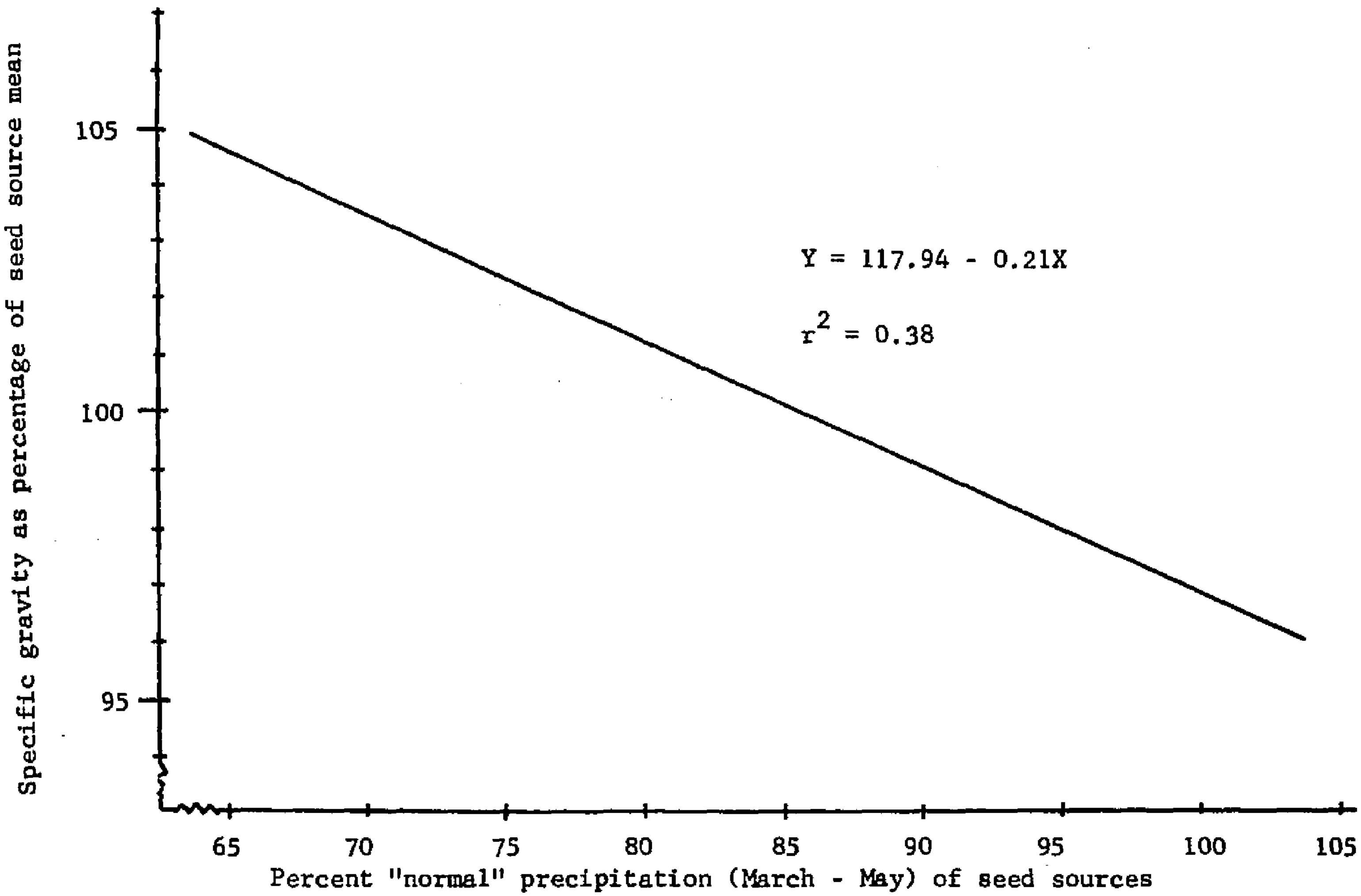

Figure 10. Relationship between specific gravity and spring precipitation of seed source means.

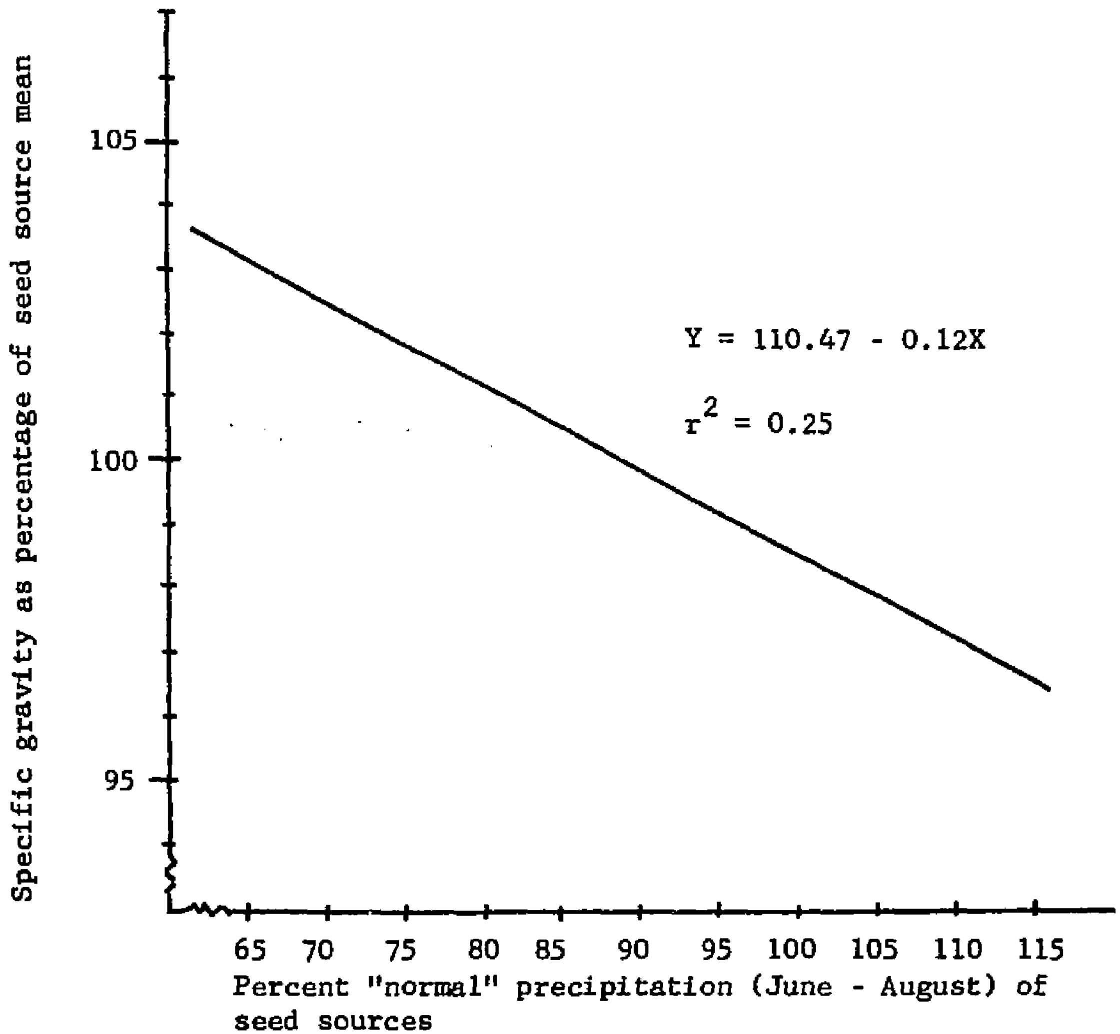

Figure 11. Relationship between specific gravity and summer precipitation of seed source means.

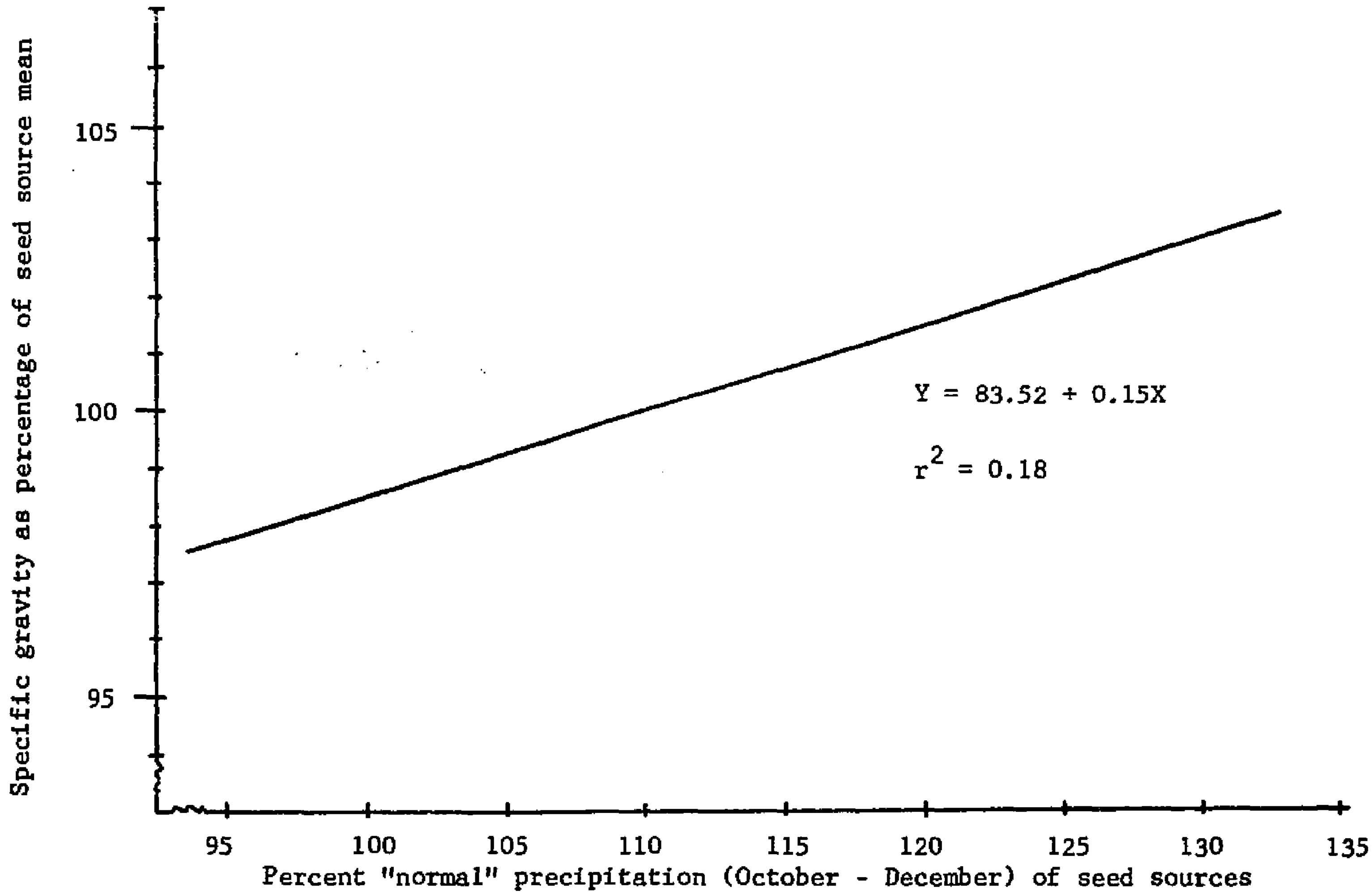

Figure 12. Relationship between specific gravity and autumn precipitation of seed source means.

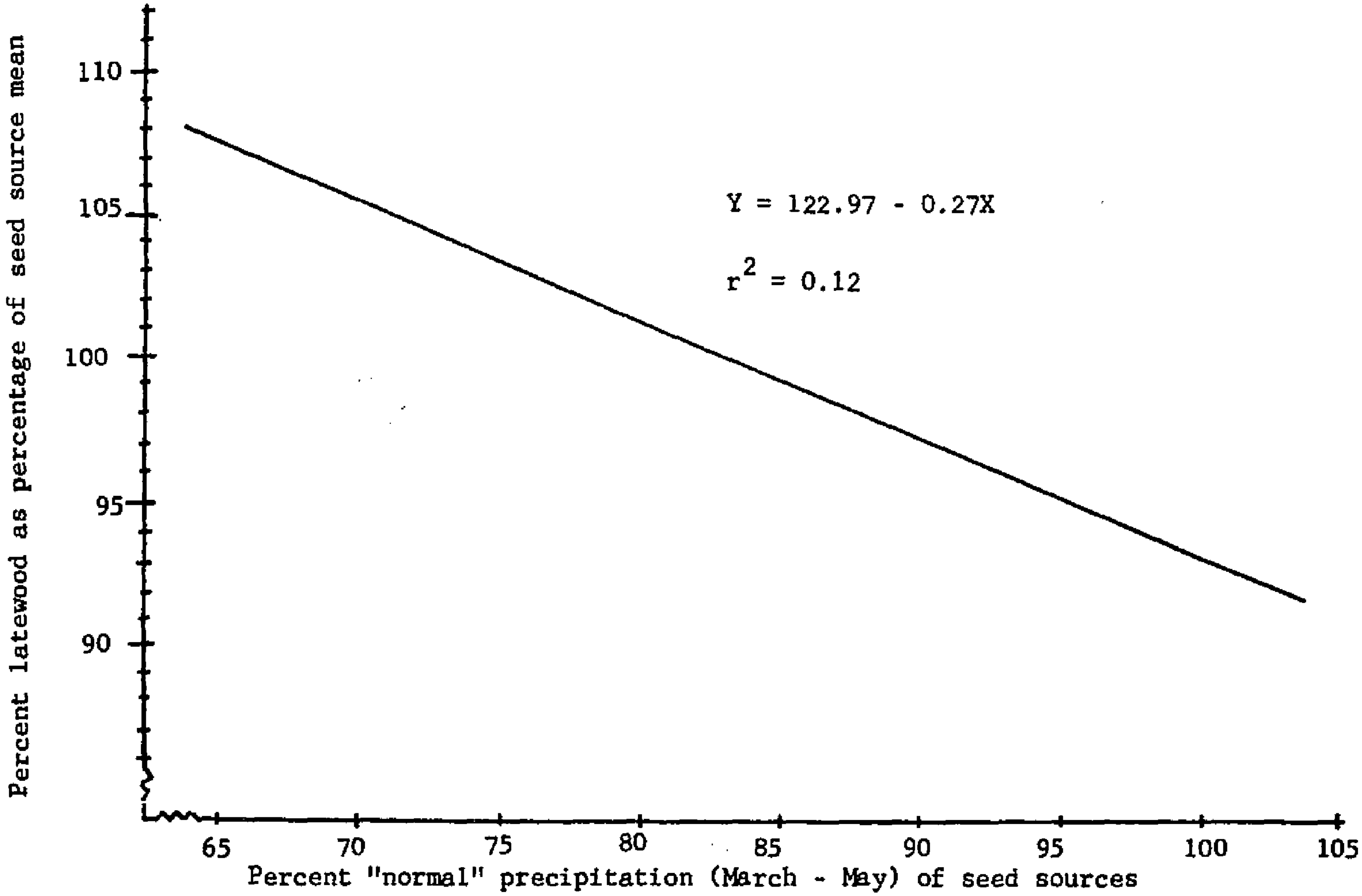

Figure 13. Relationship between percent latewood and spring precipitation of seed source means.

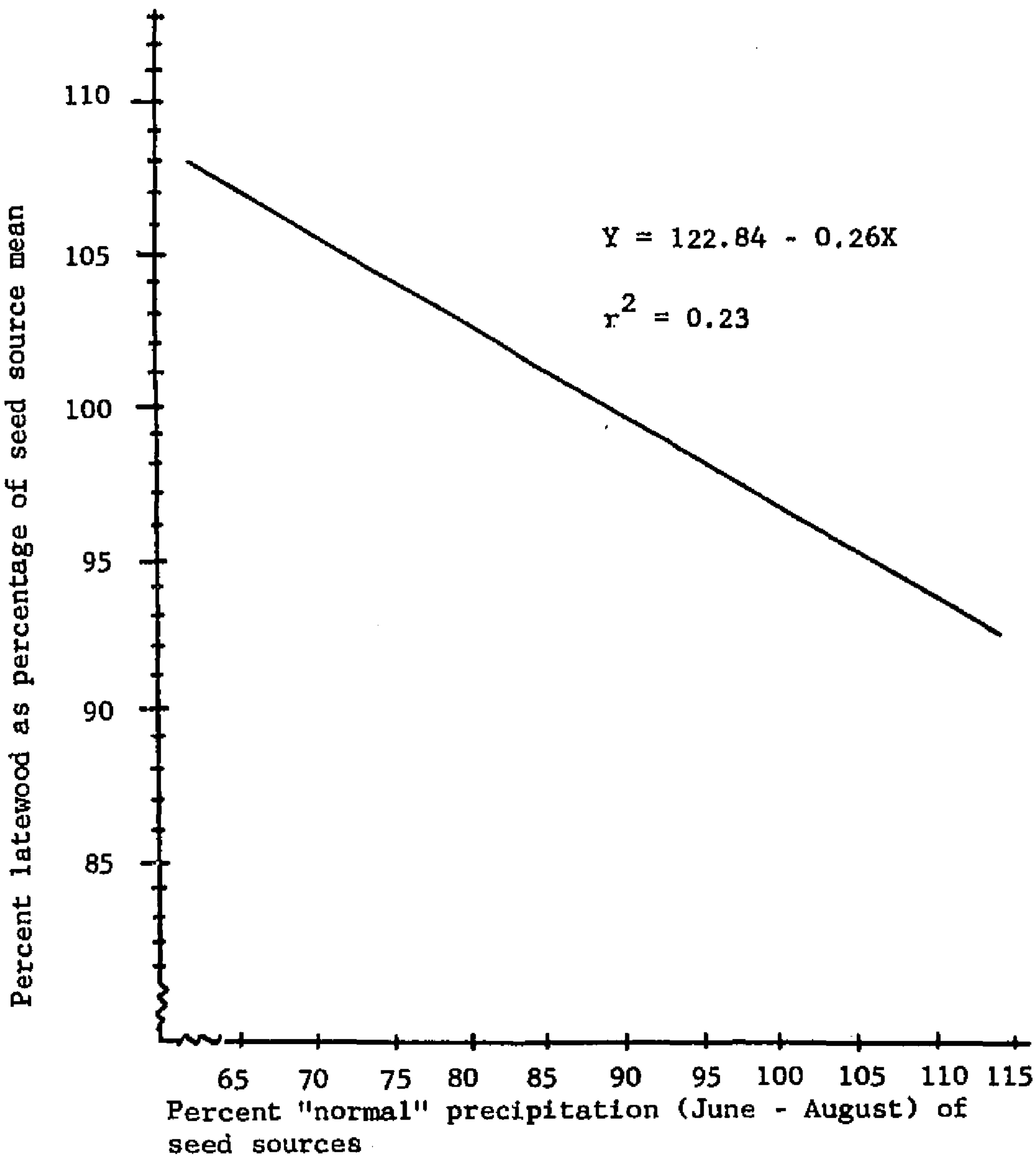

Figure 14. Relationship between percent latewood and summer precipitation of seed source means.

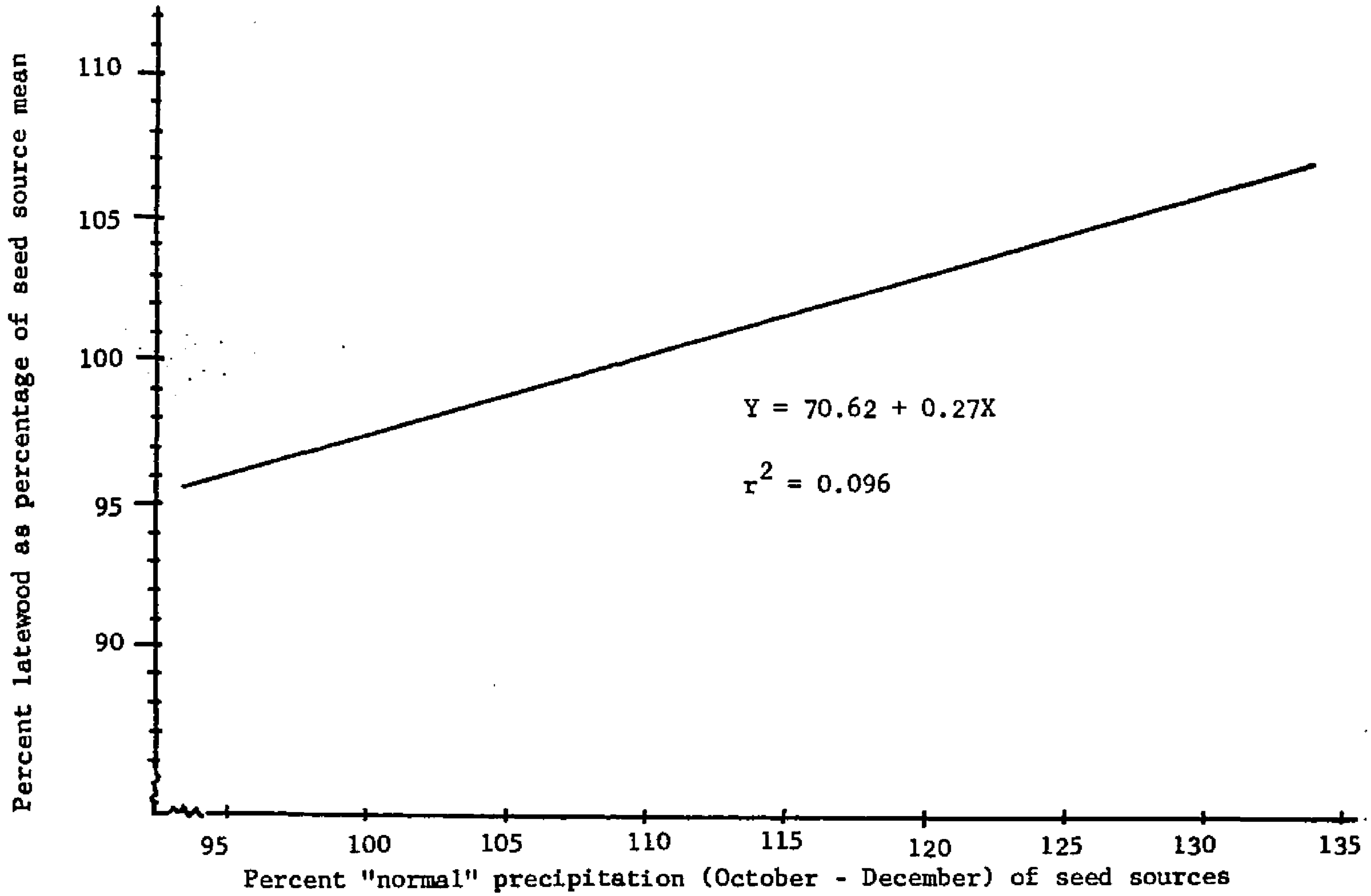

Figure 15. Relationship between percent latewood and autumn precipitation of seed source means.

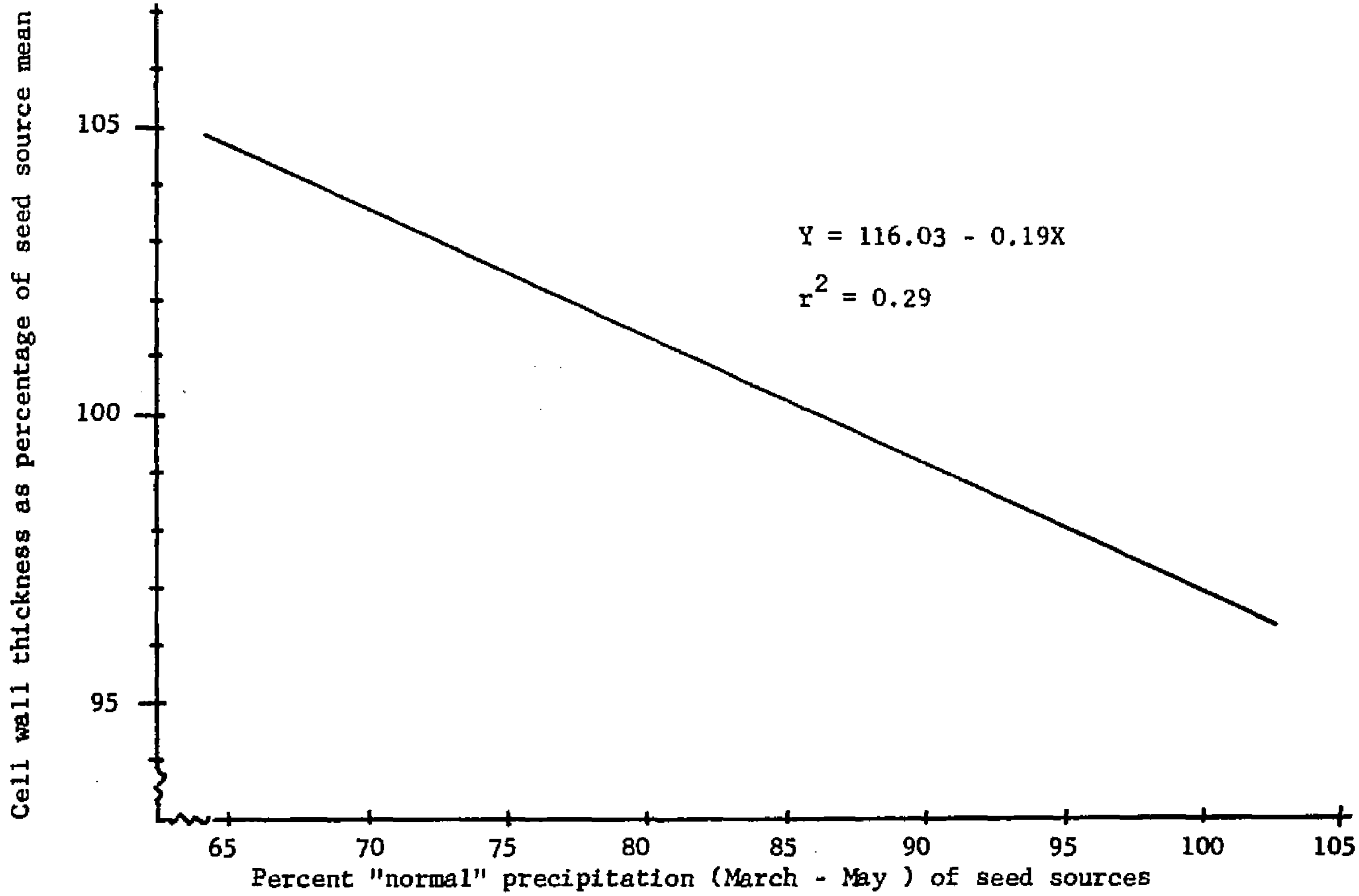

Figure 16. Relationship between cell wall thickness and spring precipitation of seed source means.

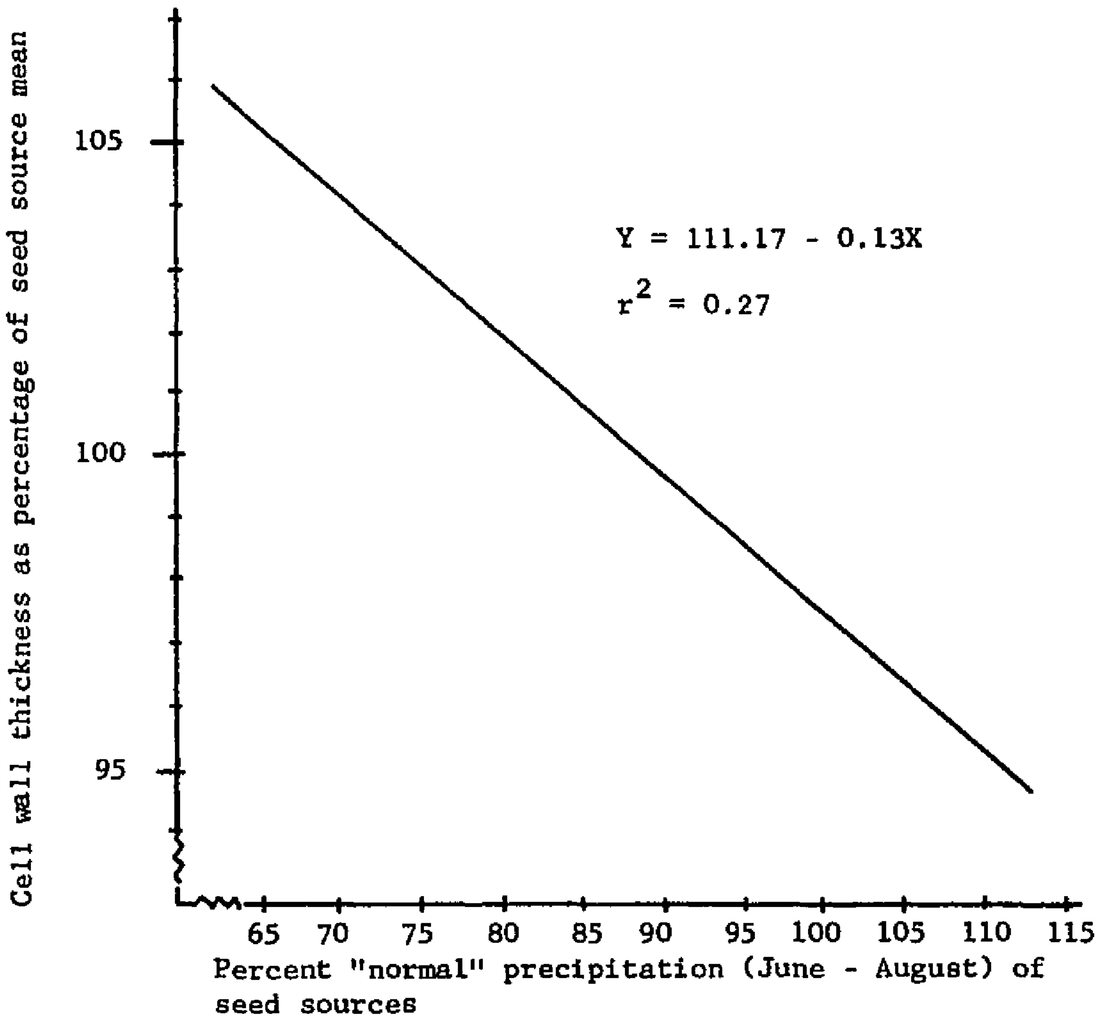

Figure 17. Relationship between cell wall thickness and summer precipitation of seed source means.

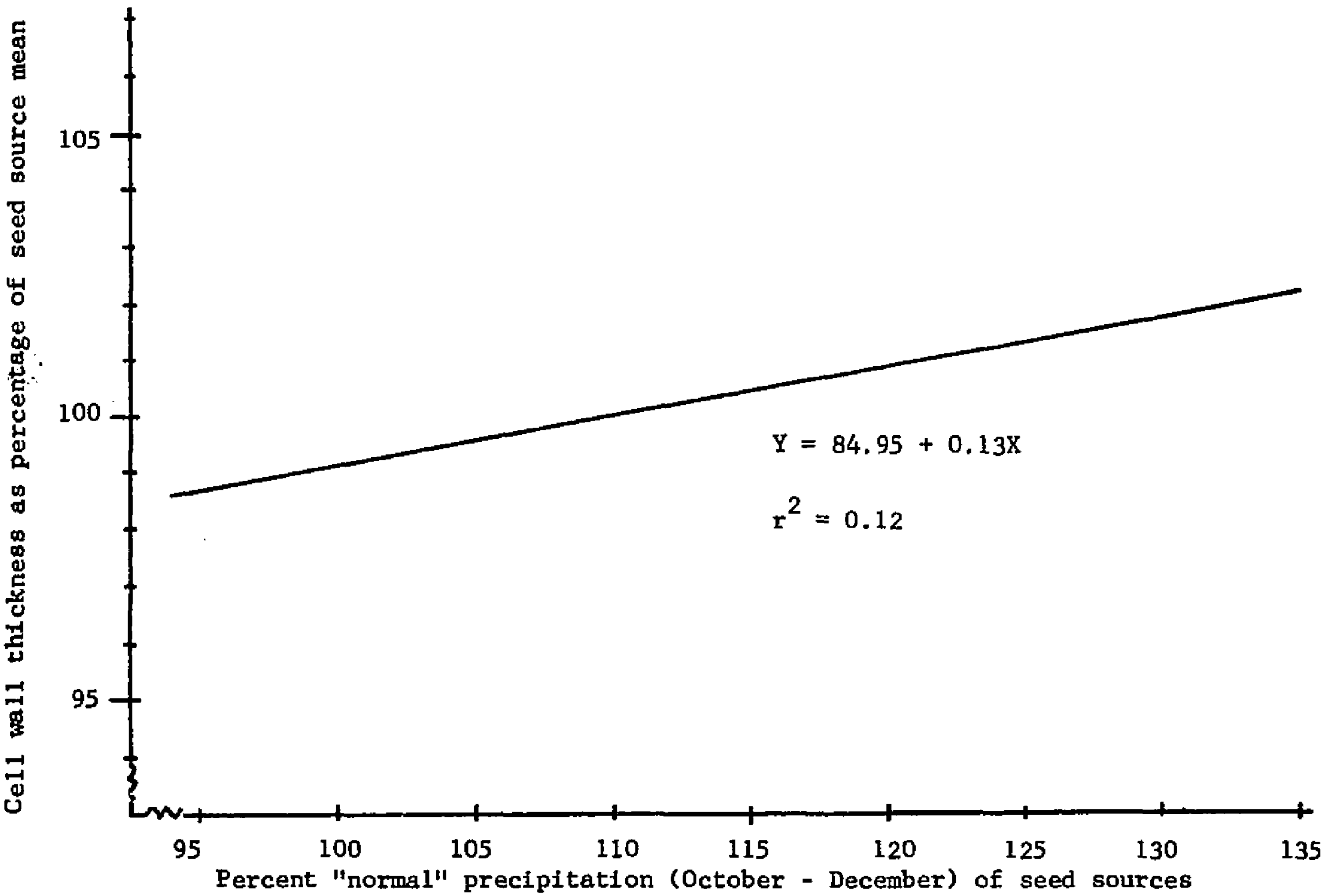

Figure 18. Relationship between cell wall thickness and autumn precipitation of seed source means.

One of the environmental factors that most affects specific gravity (hence, percentage latewood and cell wall thickness) is soil moisture. Reports on the relationship between moisture and specific gravity are rather confusing and sometimes contradictory, however. In explaining some of the environmental variations encountered in Mississippi, Wheeler and Mitchell (1959) concluded that rainfall has an effect on specific gravity, and that this effect is more pronounced in loblolly pine. Zahner (1955) stated that plentiful soil moisture and dense wood seem to be related. However in a later study, Zahner (1962), found a higher percentage of latewood in growth rings of loblolly pine trees grown under dry conditions. Others (Wellwood 1960, Klem 1957, Larson 1957, Jayne 1958) indicated that coniferous trees growing on good sites generally tend to produce lower density wood than those growing on poor sites. Whitesell et al.(1966) noted that loblolly pine trees grown in Maryland and Delaware on poorly drained soils have slightly higher specific gravities than trees growing on better drained sites.

In the present study, specific gravity was correlated with seasonal rainfall patterns at the planting sites. The positive correlations of autumn precipitation with specific gravity ($r = 0.42$), percentage latewood ($r = 0.31$), and cell wall thickness ($r = 0.35$) and the negative correlations with spring and summer precipitation suggest that October to December was the period of effective rainfall with respect to latewood

formation and March to May the period of effective rainfall with respect to earlywood formation in trees in all three plantations. This phenomenon, however, was more pronounced in the De Ridder plantation than in the other two plantation sites. Spring and summer precipitation at De Ridder was very much lower than at either Bogalusa or Idlewild but autumn precipitation at De Ridder was higher which would in effect induce a longer duration of production of latewood with thick-walled cells and hence, high specific gravity. The early moisture stress at the De Ridder plantation prompted early formation of latewood which possibly continued until late November. Rainfall distribution during the summer months was almost the same at the three sites which could further enhance latewood production at De Ridder. In loblolly pine, once the formation of latewood has begun, it cannot be reversed to the formation of earlywood by late-summer rains (Larson 1957). Smith and Wilsie (1961) found that large amounts of latewood were formed in Pinus taeda during years of low moisture stress, further emphasizing the influence of ample water supply in prolonging latewood growth. The positive correlation of percent latewood with autumn moisture supply confirmed that reported by Foil (1961), Young (1952), and Van Buijtenen (1958).

It has been suggested that cell wall thickening, which is a feature of latewood formation, depends largely on the amount of photosynthate available, which in turn depends directly on

moisture avaialability and other environmental factors (Larson 1960, 1969, Richardson 1964). During periods of rapid shoot growth and leaf development, most of the photosynthate is mobilized and used in these rapidly growing centers and only a small amount is transported basipetally. Thus, thin walled cells are produced. However, upon cessation of terminal growth, which is caused by abrupt change in moisture supply, low temperature or short photoperiod, the current photosynthate is shunted or reshuttled into the bole and incorporated into cell walls resulting in production of thick-walled cells (Kozlowski 1971).

Variation in width of cell lumen was related more to earlywood formation which accompanies rapid shoot growth and needle formation. Correlation of width of cell lumen with seasonal precipitation revealed positive correlations with spring (r = 0.32), Figure 19) and summer (r = 0.54, Figure 20) and a negative correlation with autumn precipitation (Figure 21). These correlations suggest that spring and summer precipitation were most critical in earlywood formation, while autumn precipitation was not. It can be noted that all sources planted in Bogalusa and Idlewild have wider-lumened cells than those planted in De Ridder. The low water stress during the active growing period in these areas obviously caused formation of more earlywood than latewood. According to Larson (1962), large diameter, springwood cells are produced during

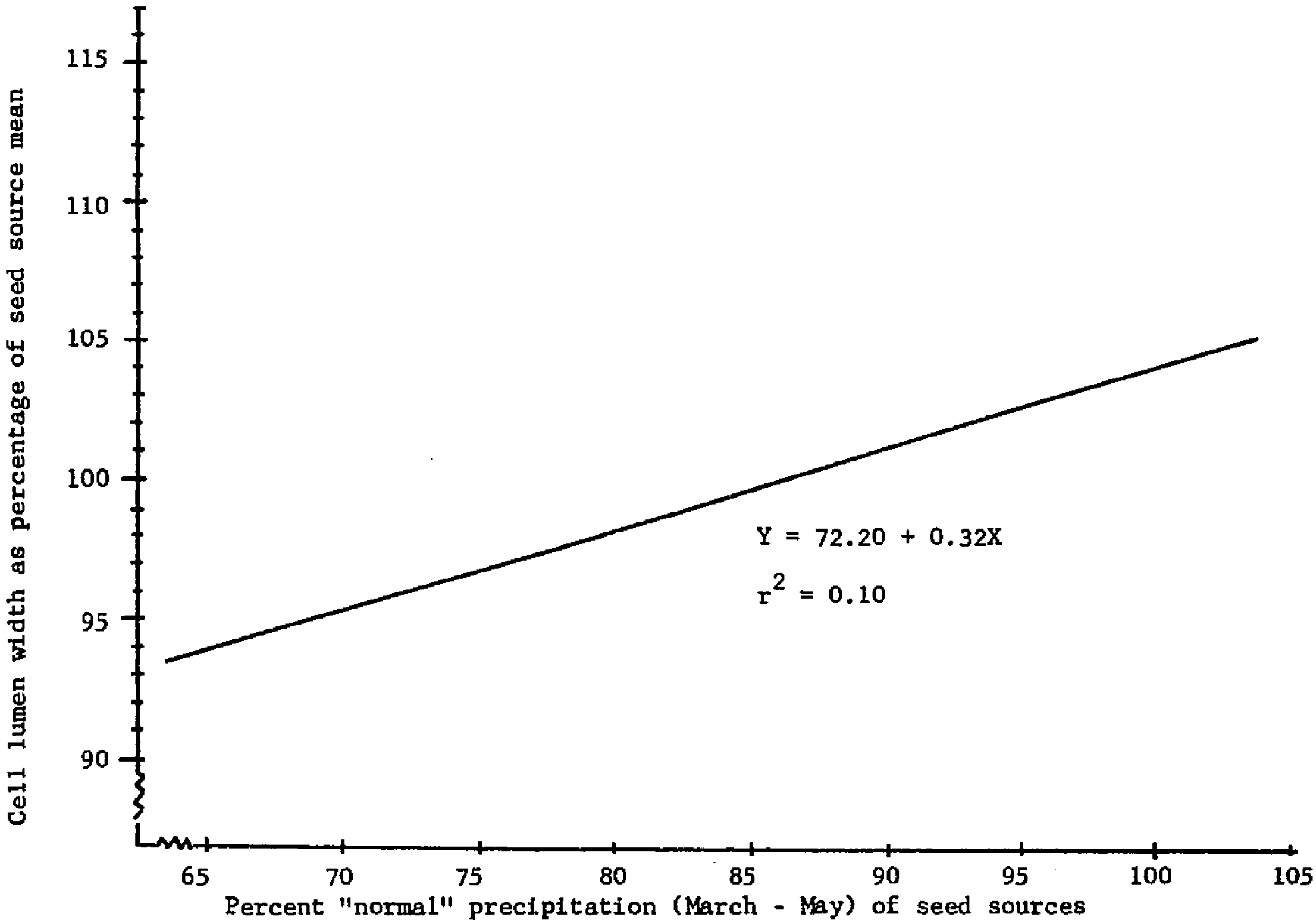

Figure 19. Relationship between cell lumen width and spring precipitation of seed source means.

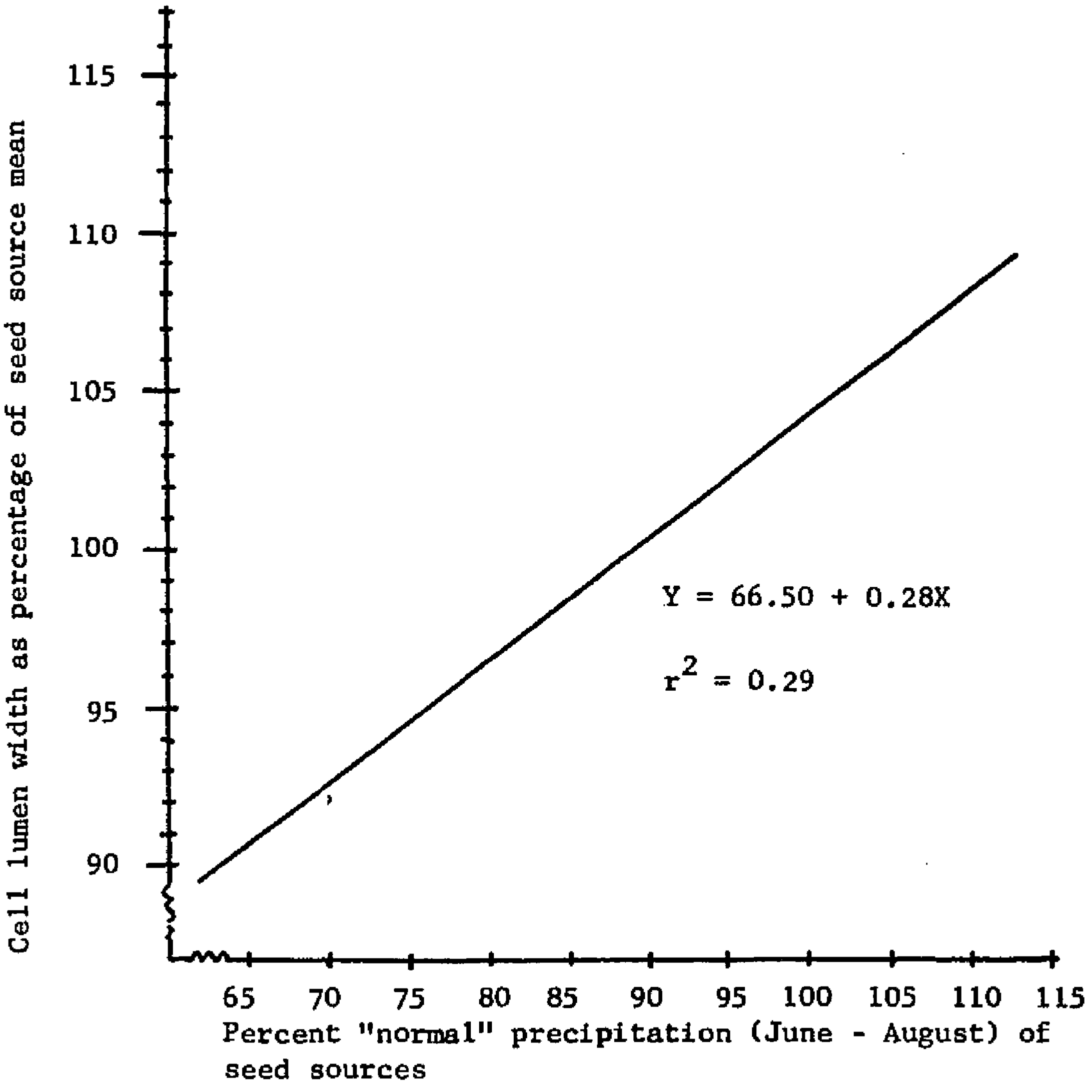

Figure 20. Relationship between cell lumen width and summer precipitation of seed source means.

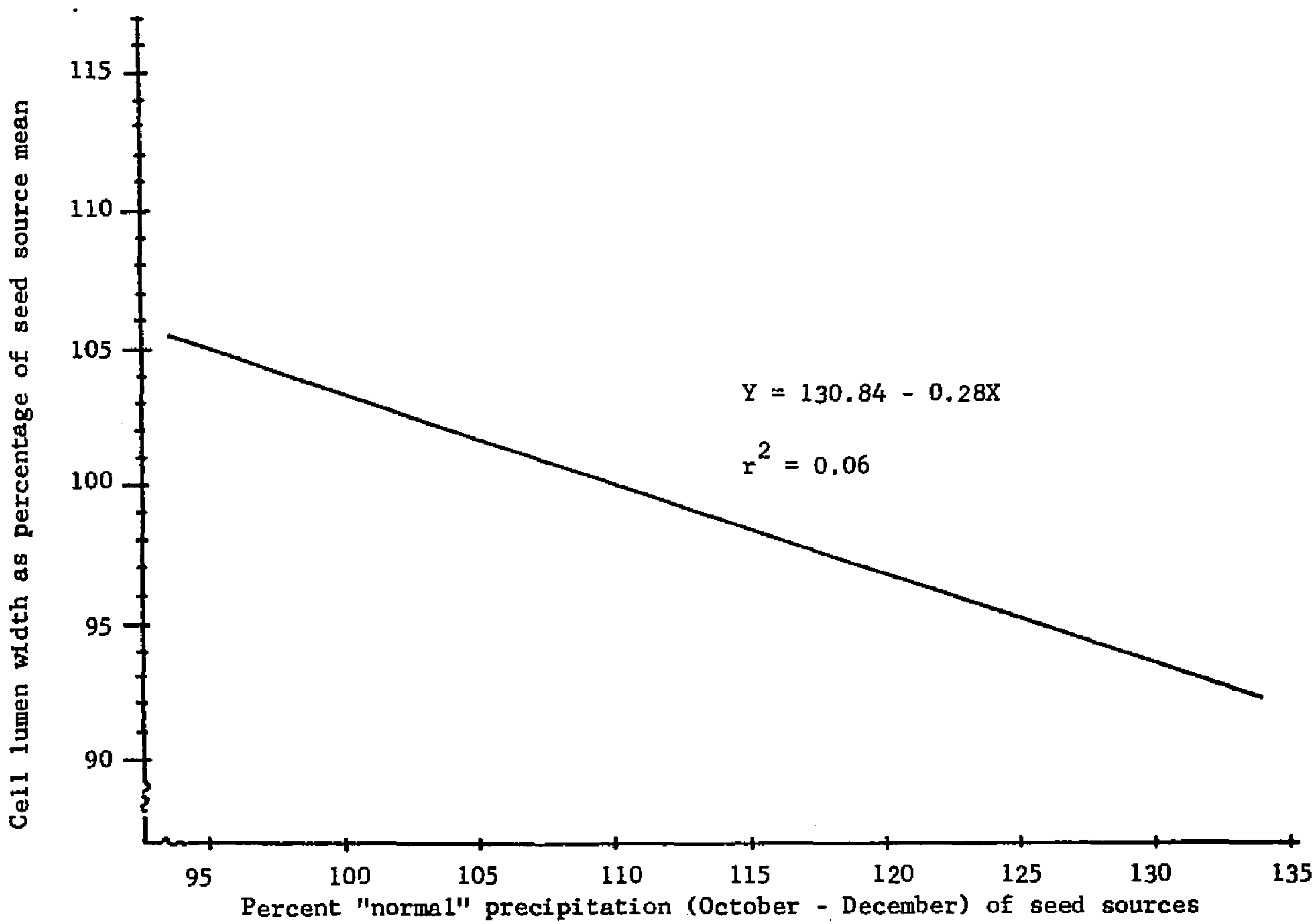

Figure 21. Relationship between cell lumen width and autumn precipitation of seed seed source means.

the period of active elongation and high auxin synthesis. This in turn resulted in wider width of annual ring and greater diameter (Table 1).

When width of annual ring was correlated with precipitation, a significant positive correlation ($r = 0.62$, Figure 22) was obtained for spring months, a positive but non-significant correlation ($r = 0.19$, Figure 23) for summer and a negative correlation for autumn (Figure 24). As in the results for width of cell lumen and diameter, these correlations indicated spring and summer rainfall to be most effective in ring formation, while autumn precipitation was not effective. According to Gaumann (1928), *Picea* and *Abies* species have produced 95 percent and 86 percent, respectively, of their annual increment by mid-July. Bannan (1955) reported that *Thuja orientalis* produces 70 to 80 percent of its growth ring by the beginning of July. In the Bogalusa and Idlewild plantations greater amounts of precipitation during the spring and summer favored the production of wide-celled xylem resulting in wider ring widths of trees with a lower percentage of latewood, while in De Ridder where spring and summer precipitation was low, narrower annual rings were formed with more latewood.

The cause and development of annual rings is a physiological complex that is beyond the scope of this study. The differences in annual ring width among plantations could have been caused not only by the availability of water or the lack of it, but

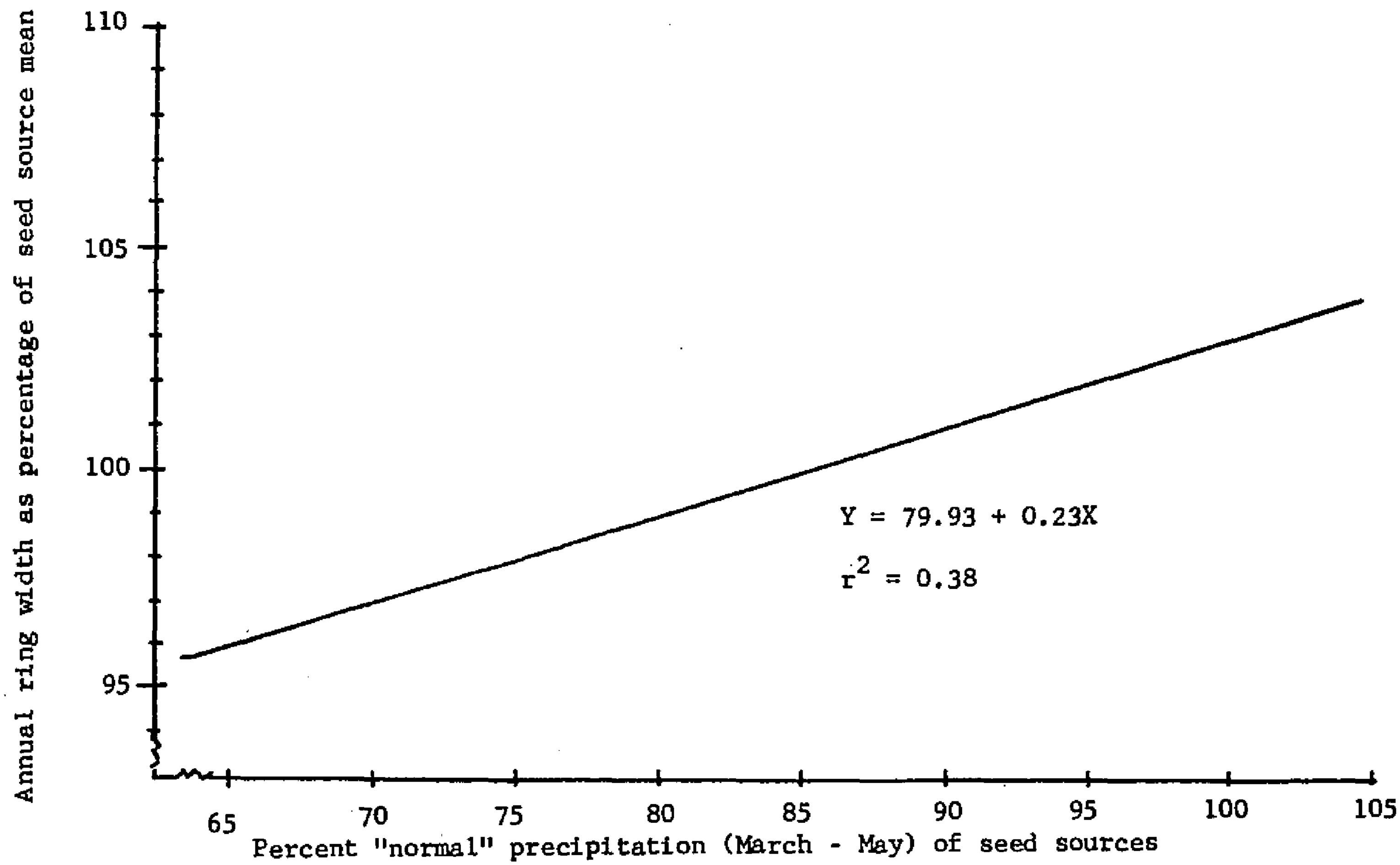

Figure 22. Relationship between annual ring width and spring precipitation of seed source means.

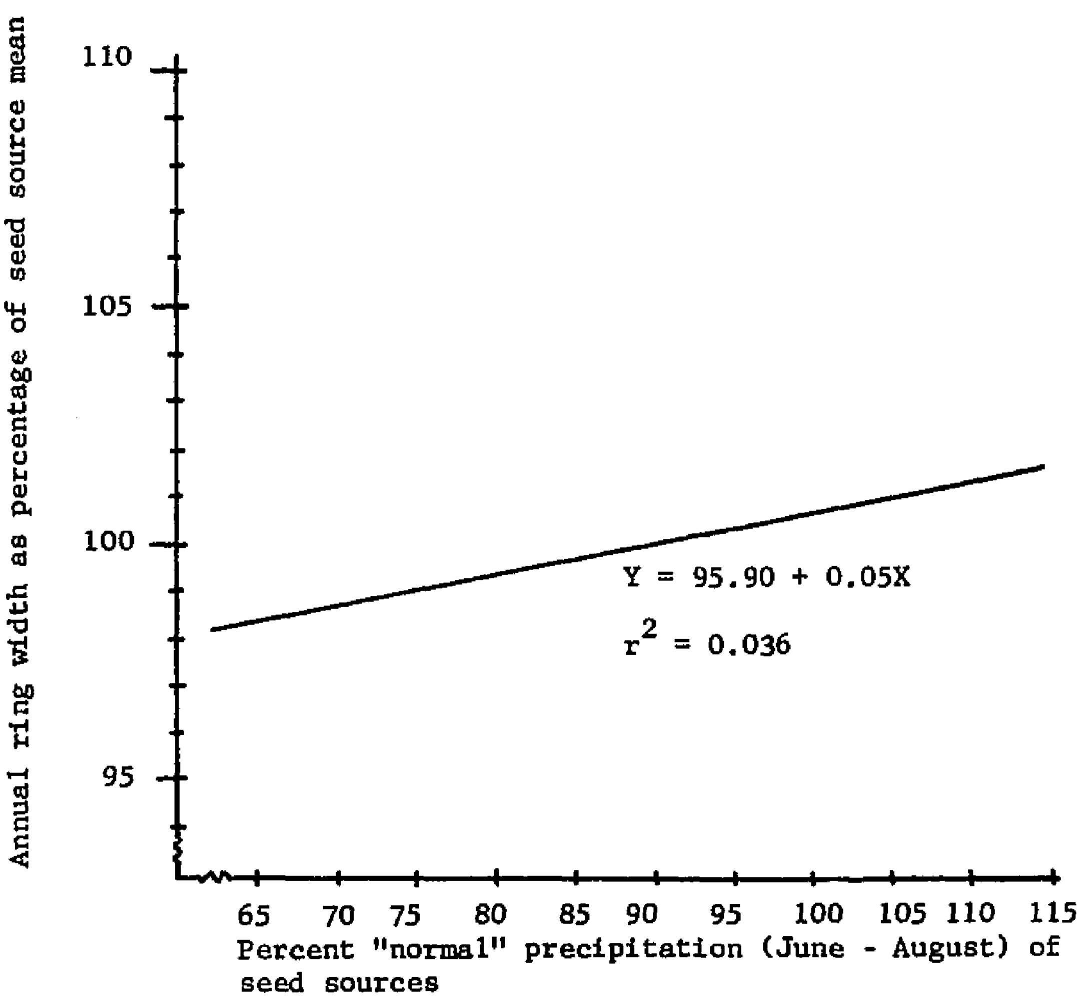

Figure 23. Relationship between annual ring width and summer precipitation of seed source means.

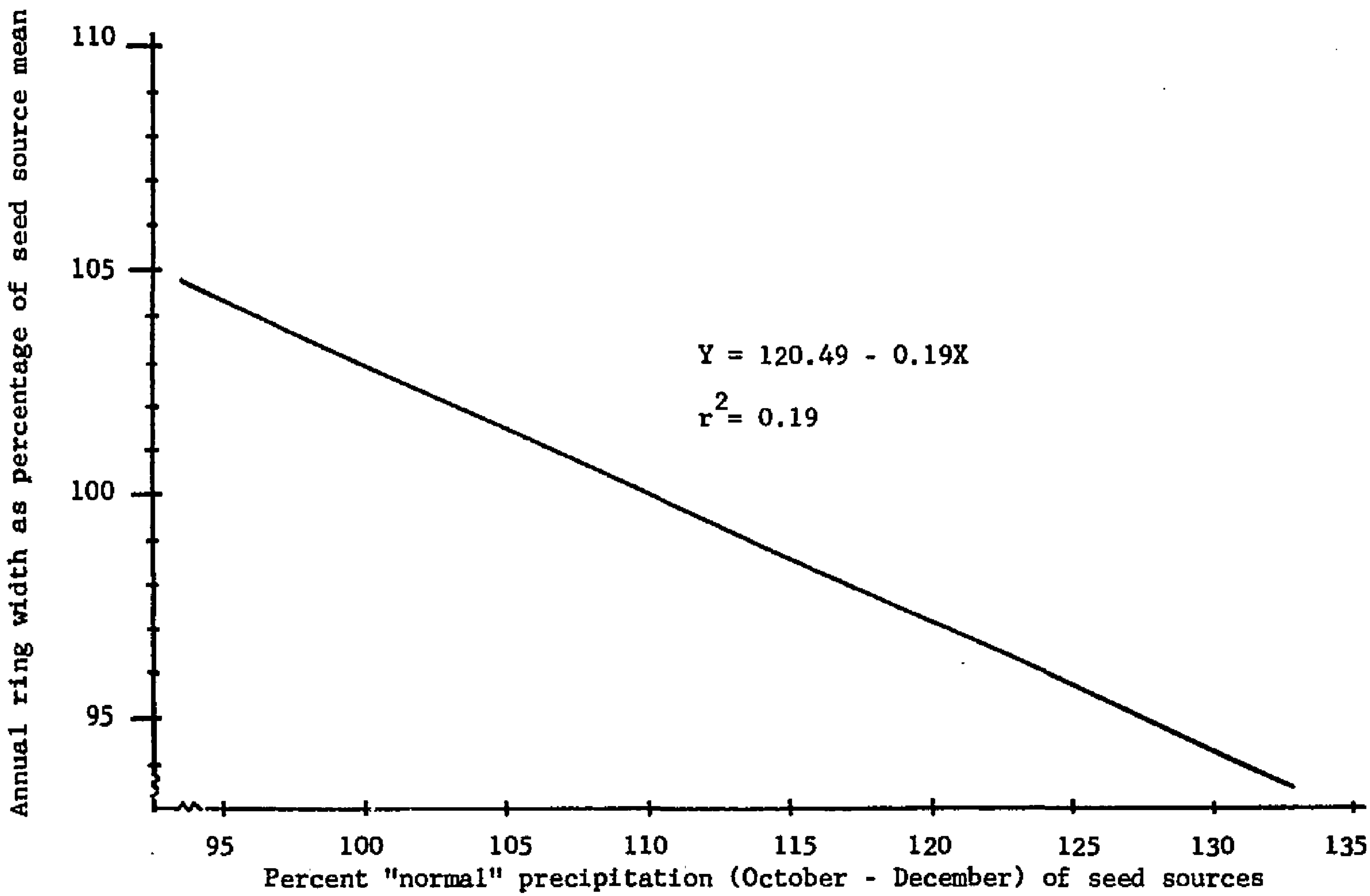

Figure 24. Relationship between annual ring width and autumn precipitation of seed source means.

also by the complex components of environment such as light intensity, temperature, soil fertility, basal density, etc..

Several other arguments have been advanced as to the control of annual ring formation. During the past decade a considerable body of evidence has accumulated supporting the hormonal control of growth ring formation (Larson 1960, Wareing 1958). According to these authors, this concept relates the production of high levels of diffusible and basipetally transported auxin associated with shoot extension and leaf development with the formation of large diameter cells (earlywood), and the cessation of shoot growth accompanied by reduced levels of diffusible auxin with the initiation of latewood formation. Thus, any environmental effect such as drought or temperature would affect growth ring formation indirectly through its effect on shoot growth and leaf extension and the subsequent levels of auxin produced.

Virtually nothing is known about the environmental component of tracheid length variation in the southern pines because meaningful, controlled experiments have yet to be undertaken (Koch 1972). The present study, even though it was not conducted in a manner to be considered "controlled" has indicated environmental variation in tracheid length (Table 9). Correlation analyses of tracheid length with precipitation revealed positive correlation ($r = 0.17$, Figure 27) with autumn and negative correlations with spring (Figure 25) and summer (Figure 26)

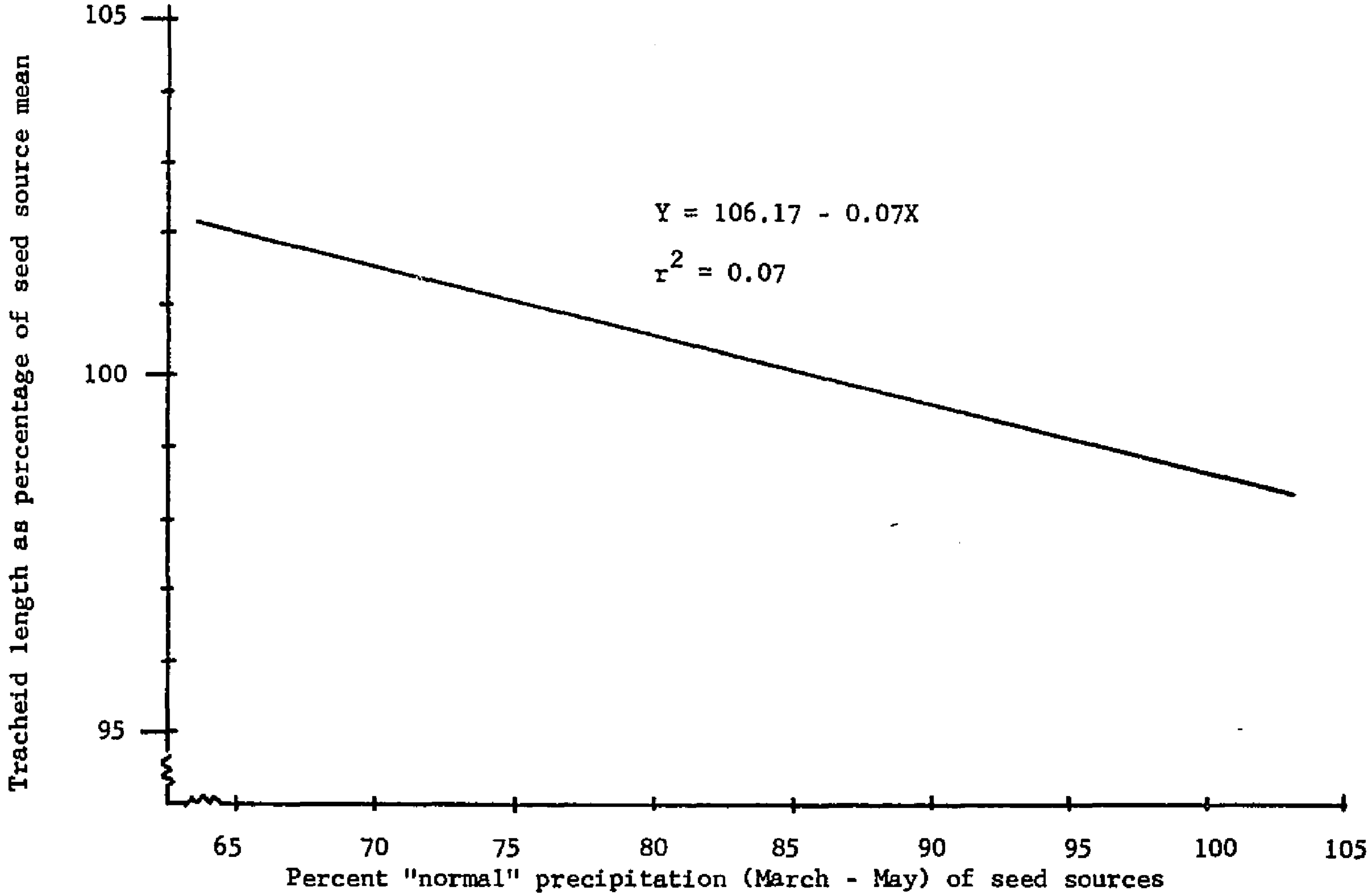

Figure 25. Relationship between tracheid length and spring precipitation of seed source means.

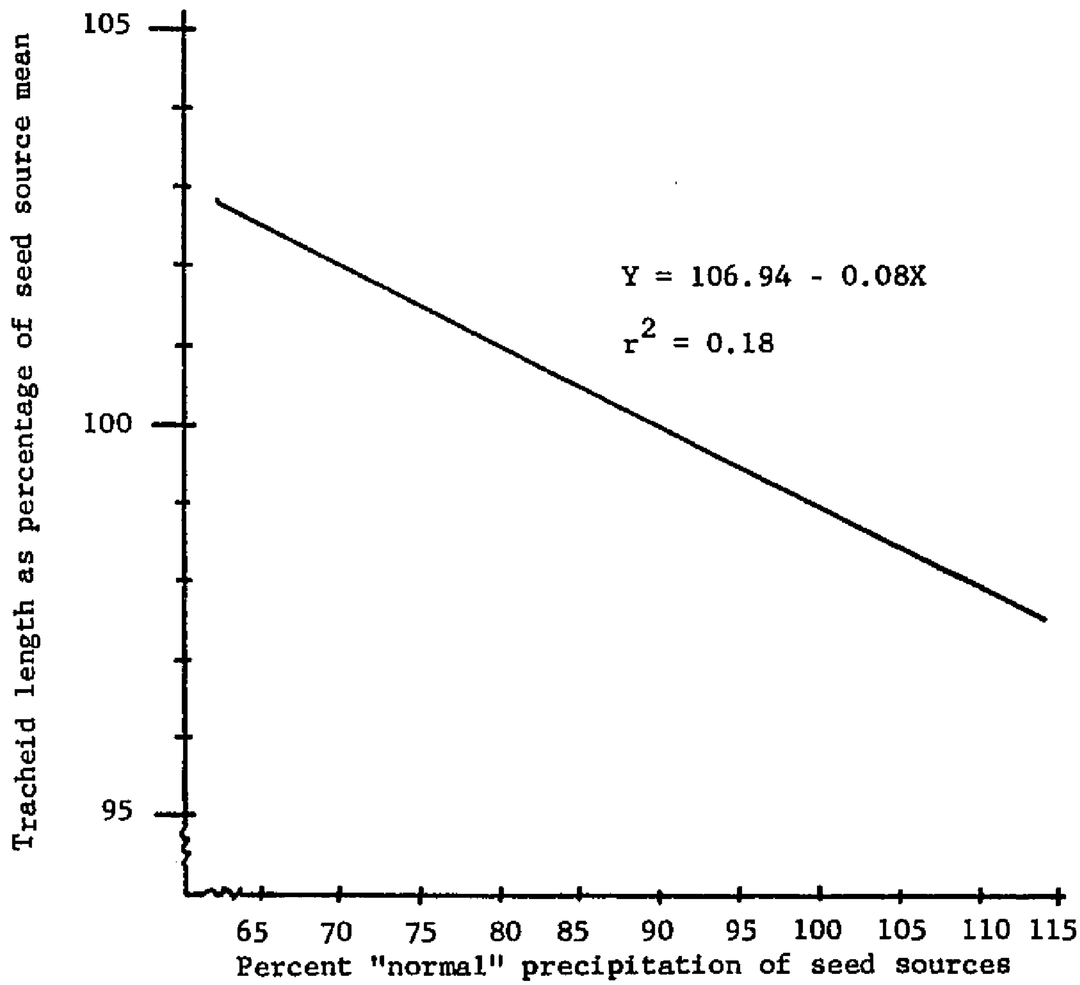

Figure 26. Relationship between tracheid length and summer precipitation of seed sources means.

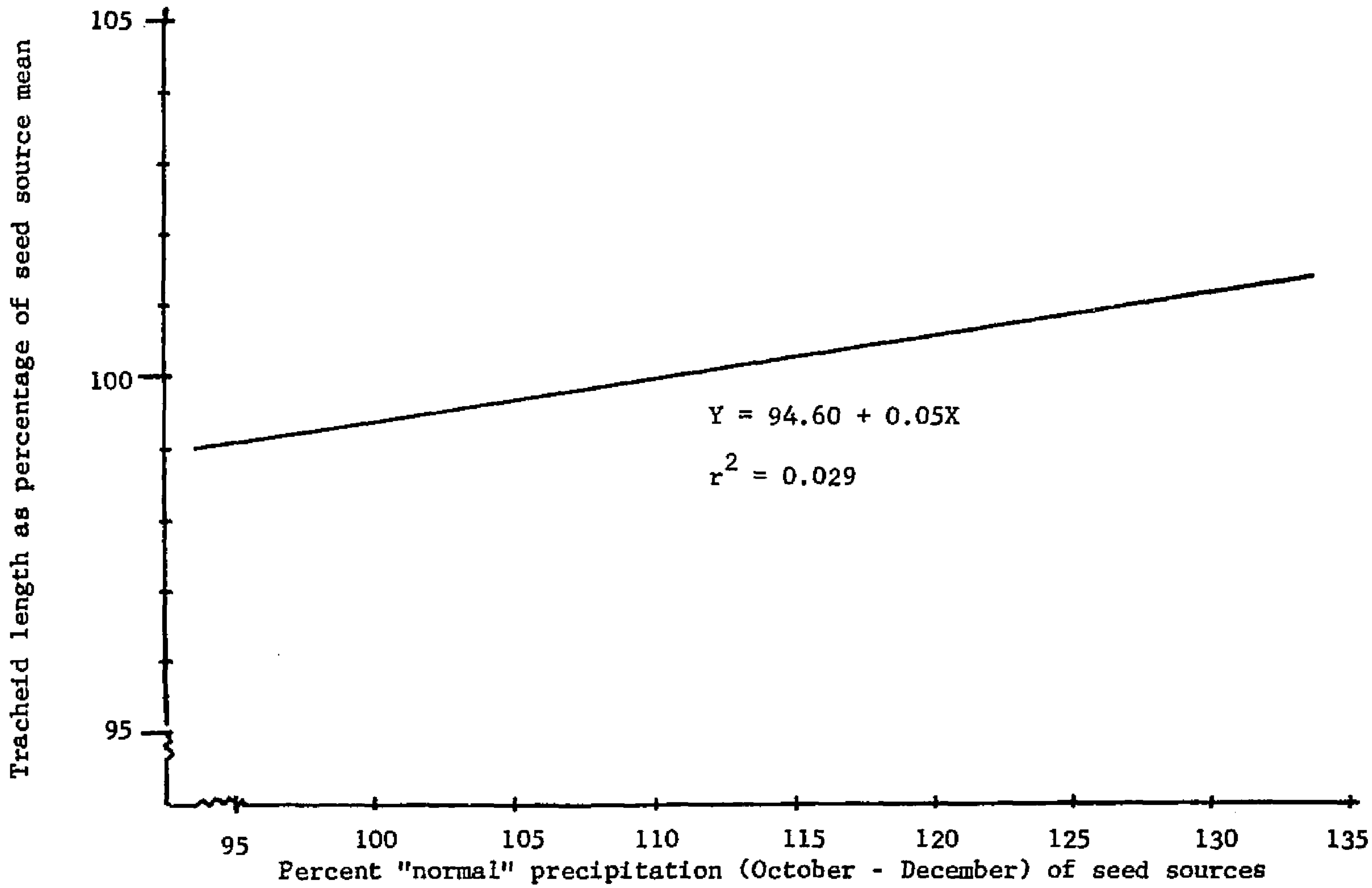

Figure 27. Relationship between tracheid length and autumn precipitation of seed source means.

precipitation. These correlations suggested autumn precipitation was more critical in tracheid length elongation.

The tracheid length correlations were quite similar to the trend shown for height growth, suggesting that the two processes may be similarly affected by the environment. As mentioned earlier, adequate fall precipitation favors the production of large terminal buds. Consequently, the initial cells laid out could be larger than those of smaller buds. According to Kennedy (1957) of the two factors causing variation in fiber length, the length of the initiating cell in the cambium is more important in coniferous trees than is the elongation of the young daughter cells after differentiation. It is evident that cambial initials in fast growing trees divide rapidly anticlinally to keep pace with the rapid rate of circumferential growth. Therefore, when a tree is increasing rapidly in diameter, the average length of daughter cells produced by the cambium might be expected to shorten, due to the fact that large number of cambial initials have divided anticlinally. Similarly, a tree growing slowly in diameter would not increase in circumference at a rapid rate, and as a result, fewer cambial cells would need to divide anticlinally. Such a tree could be expected to have tracheids of greater length, since cambial initials on the whole remain long. This may explain the longer tracheids in trees with greater height but smaller diameter as observed in the trees grown in the De Ridder plantation.

Correlation

To maximize genetic gain through selection for wood properties and growth characteristics, it is necessary to determine whether the various economic characteristics under selection are interdependent, (i.e., inherited as a unit) or whether each one varies without affecting the others. Therefore, all possible correlations were calculated among the six wood properties and two growth characteristics of the loblolly pine trees in this study.

The simple correlation coefficient for each variable is tabulated in Table 18. Significant correlation coefficients are underlined. The results are presented and discussed below. All extremely small correlations was ignored in the discussion.

Proportion of latewood.-- This wood property was significantly correlated with specific gravity and latewood cell wall thickness. Its relationship with cell wall thickness (r = 0.08) was not as strong as its relation with specific gravity (r = 0.12). No definite relationship was established with tracheid length. The negative correlation with width of cell lumen, although not significant, suggests that cell lumens were narrower in the latewood portion of the wood. The positive correlation of percent latewood with cell wall thickness and specific gravity, and its negative correlation with width of cell lumen seemed further to indicate that as latewood tracheid area became larger,

Table 18. Correlation coefficients of several wood and growth characteristics for 13-year-old loblolly pines in Louisiana+≠

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2	-.05																				
3	.08	.05																			
4	.10	.03	.95																		
5	.09	.16	.35	.35																	
6	.12	.08	.36	.37	.89																
7	.01	-.03	.15	.16	.03	.06															
8	.02	-.02	.19	.20	.09	.13	.67														
9	-.01	.14	-.07	-.03	-.14	-.13	.15	.03													
10	.01	.16	-.08	-.04	-.17	-.16	.25	.16	.72												
11	.10	.11	.88	.85	.75	.69	.12	.18	-.12	-.14											
12	.13	.07	.87	.91	.66	.72	.15	.20	-.08	-.10	.94										
13	.09	.11	.19	.22	.19	.21	.15	.18	.15	.16	.23	.26									
14	-.05	.06	-.18	-.19	-.22	-.27	-.11	-.21	.10	.02	-.23	-.26	-.46								
15	.09	.10	.17	.20	.19	.21	.16	.19	.16	.16	.21	.25	.94	-.47							
16	-.06	-.10	-.06	-.10	-.18	-.20	-.12	-.09	-.19	-.15	-.13	-.16	-.62	.42	-.67						
17	.08	-.02	.24	.23	.05	.05	.15	.14	-.11	-.07	.19	.20	-.01	.01	-.04	.07					
18	-.01	.06	-.05	-.08	-.02	-.03	00	.01	-.07	-.08	-.04	-.07	-.15	.20	-.16	.15	-.03				
19	-.03	00	.21	.22	.07	.09	.13	.13	-.04	00	.18	.20	.04	-.03	.04	.02	.83	-.09			
20	-.06	-.03	-.18	-.10	-.13	-.10	-.11	-.12	-.15	-.12	-.16	-.19	-.13	-.08	-.14	.08	-.27	.16	.34		
21	-.04	.83	.10	.08	.17	.10	00	-.02	.12	.11	.16	.10	.14	.06	.13	-.12	.02	.06	.02	-.05	
22	.01	.39	.21	.20	.19	.16	.13	.24	-.08	.02	.24	.22	.11	-.15	-.13	-.05	-.11	-.04	-.08	-.09	.49

+ Underlined correlations are significant ($P < .05$).

≠

1 = Proportion of latewood.

2 = Average width of annual ring.

3 = Specific gravity, unextracted, bark section.

4 = Specific gravity, extracted, bark section.

5 = Specific gravity, unextracted, pith section.

6 = Specific gravity, extracted, pith section.

7 = Tracheid length, latewood, bark section.

8 = Tracheid length, earlywood, bark section.

9 = Tracheid length, latewood, pith section.

10 = Tracheid length, earlywood, pith section.

11 = Specific gravity, unextracted, whole core.

12 = Specific gravity, extracted, whole core.

13 = Cell wall thickness, radial dimension, pith section.

14 = Width of cell lumen, radial dimension, pith section.

15 = Cell wall thickness, tangential dimension, pith section.

16 = Width of cell lumen, tangential dimension, pith section.

17 = Cell wall thickness, radial dimension, bark section.

18 = Width of cell lumen, radial dimension, bark section.

19 = Cell wall thickness, tangential dimension, bark section.

20 = Width of cell lumen, tangential dimension, bark section.

21 = Diameter.

22 = Height.

width of cell lumen decreased and the wall thickness of cells increased. This increase was sufficient to result in an increase of specific gravity, even though the number of tracheids per unit areas was decreasing. The relationships between these characteristics are significant because they suggest that if selections are made for increased latewood percentage, an increase in specific gravity will also be obtained.

Width of annual ring. -- Average width of annual ring represents the average radial growth increment of a tree. Its high positive correlations with diameter ($r = 0.83$) and height ($r = 0.39$) were expected. In the pith section, the width of annual ring was also highly correlated with specific gravity, tracheid length in both earlywood and latewood,and cell dimensions. No significant correlation was found with other wood characteristics.

The significant but low correlation of annual ring width with specific gravity in the pith section ($r = 0.16$) would indicate that while specific gravity increases in annual ring width up to the 7th ring, no relationship exists from the 8th ring outward. It is generally recognized that, in conifers, more uniform ring widths are formed with higher specific gravity as the tree ages. This would therefore account for the lack of a correlation between annual ring width and specific gravity in the bark section. Additionally, during the early growth of the tree, wider rings are formed with an increasing amount

of latewood. In the present study, this relationship ceased at the eighth ring from the pith.

A significant relationship between annual ring width and tracheid length in the pith section was obtained (r = 0.14, latewood, and 0.16, earlywood), indicating that during juvenile growth, as annual ring width increases, so does tracheid length.

Specific gravity. -- A very strong relationship between unextracted and extracted specific gravity was obtained (r = 0.94). This high correlation means that although both can be used as indicators of solid wood material, the extracted specific gravity is preferred because extractions merely add "bulk" to the cell and extractive content varies widely within the tree. The relationship of specific gravity in the pith section to the bark section (i.e., wood near tree center to that near the bark) was highly significant ($P<.01$), showing that specific gravity of the bark section was indicative of specific gravity of the whole tree. Also, this relationship would indicate that specific gravity is under rather strong genetic control because it remains fairly uniform even with seasonal variation in environment. Stonecypher and Zobel (1966) reported narrow-sense heritabilities of 0.73 and 0.72 for five-year-old and two-year-old loblolly plantations, respectively. In a progeny test of slash pine, Goddard and Cole (1966) reported a significant correlation between parent and progeny. Based on the half-sib progenies, heritability of specific gravity

was 0.43.

Extracted specific gravity of the bark section showed a strong positive correlation with tracheid length in the latewood (r = 0.16) and earlywood (r = 0.20) of the bark section. Extracted specific gravity of the pith section however, showed a significant negative correlation with tracheid length in the latewood (r = - 0.13) and earlywood (r = - 0.13) of the pith section. Furthermore, this relationship was reflected in the extracted specific gravity of the whole core which was significantly positively correlated with tracheid length in the bark section and significantly negatively correlated with tracheid length in the pith section. These relationships suggest that, as tracheid length increases, there is a corresponding increase in specific gravity. Apparently, trees with longer tracheids have higher specific gravity. This result contrasts with the negative correlation between tracheid length and specific gravity in loblolly pines found by Zobel et al. (1960, 1961), but supports the findings of Echols (1958) who found that an increase in tracheid length was accompanied by an increase in specific gravity in Scots pine. In a third study, Kramer (1957) found no relationship between tracheid length and density in loblolly pine.

Trees with high specific gravity will have cells with thicker walls and narrower lumens than trees with lower specific gravity, In this study, specific gravity and cell wall

thickness in the bark section were highly correlated. The correlation coefficient for cell wall thickness in the radial dimension was 0.23 and in the tangential dimension, 0.22. The relationship between specific gravity and cell wall thickness of the pith section was also strong. The correlation coefficient for cell wall thickness in the radial dimension was 0.22 and at the tangential dimension it was 0.20. Conversely, negative correlations were obtained between specific gravity and width of cell lumen at both the bark and pith sections. These relationships seem to indicate that the increase in specific gravity is attributed to thick-walled cells with narrow lumens, but this relationship is also affected by the proportion of latewood. The negative correlation between specific gravity and width of cell lumen showed that specific gravity generally decreased as tracheids grew larger in cross-sectional lumen area.

The relationship of specific gravity and growth rate was significant but rather weak. Correlation coefficients for specific gravity with height were 0.24 (unextracted) and 0.22 (extracted), while with diameter, correlation coefficients were 0.16 and 0.10 with unextracted and extracted, respectively. According to Koch (1972), growth rate of plantation trees, when manipulated with changing environment, may not be closely related to wood specific gravity. Yao (1970), considering all height and radial positions in loblolly pines, concluded that unextracted wood specific gravity was positively correlated with number of rings per

inch in the range three to eight rings per inch; in wood more than eight rings per inch, however, specific gravity was generally unrelated to growth rate. Others (Miller 1959, Gilmore et al. 1961) also failed to find any significant correlation between diameter growth and specific gravity.

The positive relationships between specific gravity and proportion of latewood, width of annual ring, tracheid length in the bark section, cell wall thickness, and growth rate, suggests that selection of loblolly pine seed sources for higher specific gravity may be economically feasible and advantageous.

Tracheid length. -- Tracheid length is a characteristic of great importance to the pulp and paper industry. Like specific gravity, it is now being considered in selecting trees for tree improvement.

Table 18 show a strong positive correlation between latewood and earlywood tracheid lengths in both the pith and bark section. Earlywood and latewood tracheid length does not differ very much within a growth ring even though large differences are found between tracheids of the pith and the bark section (Table 2). In agreement with the literature (Dadswell and Wardrop 1960, Anderson 1951, and Choong et al. 1970), both earlywood and latewood tracheids near the pith were shorter than those near the bark.

Cell wall thickness was measured only in the latewood of both pith and bark sections. Significant positive correlations between latewood tracheid length and latewood cell wall thickness of the bark and pith sections were obtained. Cell wall thickness (radial dimension) of the bark section had a correlation coefficient of 0.15, while in the tangential diameter, r = 0.13. Correlation coefficients for the pith section were 0.15 and 0.16 for the radial and tangential dimensions, respectively.

Negative correlations between tracheid length and width of cell lumen at both the pith and the bark sections were obtained. For the bark section, correlation coefficients for width of cell lumen were - 0.11 in the radial and - 0.12 in the tangential dimensions; for the pith section, they were - 0.10 in the radial and - 0.19 in the tangential dimensions, respectively. These results and the significant positive correlations between cell wall thickness and tracheid length in both the pith and bark sections indicate that longer tracheids (in the latewood) have thick walls and narrow lumens. This is in accord with the findings of Zobel et al. (1961) and Goggans (1962) who reported that in loblolly pine, longer tracheids have thicker walls.

The significant correlations of tracheid length with diameter and height are more difficult to explain. When growth rate was expressed in terms of diameter, many researchers (Hata 1949, Echols 1958, Zobel et al. 1960, Thor 1964) reported that the relationship was negative; others either found a

positive correlation (Kennedy and Smith 1960, Posey et al. 1969, Choong et al. 1970) or no relationship (Stairs et al. 1966, Zobel et al. 1969). When height was used to express growth rate, Echols (1958) and Dorn (1968) reported a strong correlation with tracheid length in Scots pine. In this study, the correlations were not clear either. Tracheid length in the pith section was positively correlated with diameter, but tracheid length in the bark section was not. Also, tracheid length in the bark section was positively correlated with height but tracheid length in the pith section was negatively correlated.

Cell wall thickness.-- While there was no correlation between the latewood cell wall thickness in either the radial or tangential dimensions of the pith and bark sections, significant negative correlations were found between cell wall thickness and width of cell lumen in both pith and bark sections. The lack of a significant relationship for cell wall thickness between the pith and the bark sections indicates indicates that the tendency for production of thicker-walled tracheids developed early in the life of the tree. The significant negative correlation between cell wall thickness and width of cell lumen is an indication that an increase in wall thickness is accompanied by a decrease in the width of cell lumen. There was no relationship between the radial and tangential dimensions for cell wall thickness and width of cell lumen in this study which agrees with the findings of

Zobel et al. (1961).

The relationships between cell wall thickness and diameter and height were quite erratic. The correlation coefficient was significant for diameter when correlated with cell wall thickness in the pith section but not significant when correlated with cell wall thickness in the bark section. These findings suggest that early increase in diameter caused a corresponding increase in cell wall thickness in latewood but this effect disappeared as the tree aged. Taras (1965) observed the variation in wall thickness and cell diameter with distance from the pith at breast height in slash pine. He reported that in latewood, wall thickness increased fairly rapidly for the first 10 years, then increased slowly, finally leveling off at about age 22.

Width of cell lumen.-- There were positive correlations between cell lumen width of the pith section and that of the bark section, which indicates that the size of the lumen is related at various radial locations at a given height. This indicates a strong degree of genetic control in lumen cells because in spite of age and seasonal differences they remained uniformly the same.

The relationship of width of cell lumen with diameter and height was quite inconsistent. A negative correlation was obtained between width of cell lumen in the pith section and diameter, but no significant correlation was found between the

width of cell lumen of the bark section and diameter. Significant negative correlations were also found between width of cell lumen in both pith and bark section with height. These correlations would mean that trees in this study which grew taller produced narrow lumened cells, which is probably related to the pattern observed in the De Ridder plantation where all of the seed sources made better height growth and also produced a higher proportion of latewood.

Diameter and height.-- These two growth characteristics were strongly correlated as expected because of the young age of the trees. According to A.B. Crow (personal communication) there is no age limit at which this relationship ceases in loblolly pine. The relationships found when diameter and height were correlated with wood properties have been discussed above. Height and diameter growth were positively correlated with annual ring width, specific gravity, tracheid length, and cell wall thickness, but negatively correlated with cell lumen width.

SUMMARY AND CONCLUSIONS

This study was initiated to determine the geographical variation in wood and growth characteristics of loblolly pine trees from local Louisiana seed sources, to investigate seed source-environment interaction, and to test for correlations between wood properties and growth characteristics.

The geographic seed sources used in this study were selected by Professor A.B. Crow of the Louisiana State University, School of Forestry and Wildlife Management in 1956 in East Feliciana, St. Tammany, Vernon (North), Vernon (South), and Washington parishes in Louisiana. The seed source tests were established in 1958-59 with 1-0 seedlings in plantations located in Vernon Parish (West Louisiana Experiment Station, De Ridder), East Feliciana Parish (Idlewild Plantation, Clinton), and Washington Parish (Lee Memorial Forest, Bogalusa). The plantations were designed as randomized blocks with four replications using a 6' x 6' spacing.

Oversize increment core samples were taken at breast height from 10 trees per source in each block. The diameters (dbh) and total heights of the sampled trees were also measured.

From each core sample the following wood properties were measured: percentage latewood, width of annual ring, specific gravity (unextracted and extracted), tracheid length, and tracheid cross-sectional dimensions (cell wall thickness and

width of cell lumen).

A split plot analysis of variance was used to evaluate the geographic variation and genotype-environment interaction in diameter, height, percentage latewood, and width of annual ring. A split-split plot analysis of variance was used in analyzing specific gravity, tracheid length, and cross-sectional cell dimensions. Simple correlation analyses were conducted to determine the relationships between wood properties and growth characteristics.

Regression and correlation analyses were made on the 13-year precipitation data for a plantation site (expressed as percentage of the "normal" precipitation of the seed sources) and the growth or wood characteristic (expressed as percentage of the seed source means) to evaluate the effects of seasonal moisture conditions on differences among seed sources at the different planting sites.

Analyses of variance for growth revealed non-significant differences in diameter and height growth among seed sources and among plantations. There was however, an indication that these growth traits were genetically controlled to a certain extent as evidenced by the consistently higher growth rate of the St. Tammany seed source when planted in all three planting sites.

Analyses of variance for the different wood properties indicated significant differences in annual ring width, specific gravity, cell wall thickness, and cell lumen width among seed

sources, and also significant differences in tracheid length, specific gravity, and cell dimensions among plantations. Percentage latewood did not show any significant differences either among seed sources or among plantations.

Variation in annual ring width appeared to follow a continous pattern of geographical variation, decreasing from the east to west. The easternmost seed sources, St. Tammany and Washington, had annual ring widths of 0.210 and 0.213 inches, respectively, while the westernmost seed source, Vernon (N) had an annual ring width of 0.193 inches.

Specific gravity, cell wall thickness, and cell lumen width did not follow a definite pattern of geographical variation. High specific gravity was found in a westerly seed source (Vernon - S) and also an easterly seed source (St. Tammany). The average extracted specific gravities (whole core) for the different sources were 0.429, 0.424, 0.421, 0.420, and 0.408, for Vernon (S), St. Tammany, East Feliciana, Vernon (N), and Washington seed sources, respectively. Cell wall thickness followed the same pattern of variation as specific gravity, i.e., cell wall thickness was largest (4.75 microns) in the Vernon (S) seed source and was smallest (4.51 microns) in the Washington seed source. For cell lumen width, the Washington seed source has the widest (35.9 microns) and East Feliciana seed source had the narrowest (33.9 microns).

Although geographic differences in tracheid length were not significant, there seems to be a clinal trend in variation along an east-west and north-south transect in Louisiana.

Within a tree, specific gravity, cell wall thickness, percentage latewood, and tracheid length increased from pith to bark, while annual ring width decreased from pith to bark.

Significant seed source-plantation interactions were obtained for height, specific gravity, and tracheid length.

Analyses of variance revealed differences in growth and wood properties among seed sources due to environmental influences, i.e., planting site. These influences were more pronounced on tracheid length, specific gravity, cell dimensions and were less pronounced in percentage latewood, width of annual ring, and growth rate.

Due to the unique location of seed sources and plantations, variations in latitude, elevation, photoperiod, temperature, and soils were minimized. One major variable that was not uniform among the three planting sites was seasonal distribution of rainfall. Therefore, these precipitation patterns were investigated to determine if seasonal moisture relations could possibly explain some of the differences in growth and wood properties among seed sources. Regression and correlation analyses were made on these seasonal precipitation and growth and wood characteristics.

Regression analyses of the different growth and wood properties on the seasonal precipitation revealed positive relationships for autumn precipitation with height, cell wall thickness, percentage latewood, specific gravity, and tracheid length; and positive relationships for spring and summer precipitation with diameter, annual ring width, and cell lumen. These results suggest that autumn precipitation was critical for height growth and production of higher density wood (high in percentage latewood and thick-walled cells), while spring and summer precipitation were critical for diameter growth and the production of wider annual rings and wide-lumened xylem (earlywood) in loblolly pines in Louisiana.

In the De Ridder plantation, where moisture stress began early in the growing season but more precipitation occurred later in the growing season (autumn), trees of all seed sources grew taller but had a low rate of diameter growth, were higher in wood specific gravity (high percentage latewood and thicker cells) and had longer tracheids. On the other hand, in the Idlewild and Bogalusa plantations where moisture stress was lower, seed sources had larger diameters, wider annual rings but were lower in wood density.

Apparently, the seasonal rainfall pattern at the De Ridder plantation, while unfavorable for diameter growth because of moisture stress earlier in the season, was conducive to height

growth because of relatively abundant water in the fall. This late-season precipitation may have prolonged the production of growth flushes and most certainly influenced the formation of longer terminal buds in the winter, which would produce a more vigorous growth flush the following spring. Also, it was evident that early moisture stress at this site had initiated early formation of latewood and late-season rainfall prolonged the production of these thick-walled cells, resulting in higher density wood.

Specific gravity was positively correlated with percentage latewood, annual ring width, cell wall thickness, tracheid length (in the bark section), diameter, and height. It was negatively correlated with width of cell lumen and tracheid length (at the pith section). These correlations would indicate that an increase in width of annual ring, proportion of latewood, cell wall thickness and tracheid length contribute to increased specific gravity. Also, loblolly pine trees in this study that made good height growth also had higher specific gravity.

Tracheid length was positively correlated with the width of annual ring, diameter, and cell wall thickness of the latewood. It was negatively correlated with width of cell lumen.

Other correlations showed that cell wall thickness was positively correlated with proportion of latewood, specific

gravity, tracheid length, and negatively correlated with width of cell lumen. This negative correlation with cell lumen indicates that cell lumen width decreases with the thickening of the cell wall.

Annual ring width, diameter, and height growth were strongly positively correlated as expected because of the young age of the trees.

From the results of this study, the following conclusions can be drawn:

1. Very little geographic variation in growth and wood properties existed among the five Louisiana seed sources. Only annual ring width, specific gravity, and cell dimensions showed significant variation. Among the five seed sources, the St. Tammany seed source had a consistently higher growth rate (diameter and height) at all sites. The Vernon (S) seed source was highest in specific gravity. Therefore, selection for growth rate would favor the St. Tammany source, while selection for specific gravity would favor the Vernon (S) source. The St. Tammany source also ranked second in specific gravity.
2. The non-significant result for tracheid length among seed sources and the significant plantation variation would indicate that tracheid length of loblolly pines in Louisiana is more strongly controlled by environmental

factors than genetics. Therefore, selection of individual trees rather than seed sources would be a more efficient means of obtaining genetic gain in this trait.

3. There is some possibility that the genetic diversity in wood properties observed in this study may be attributed to shortleaf-loblolly pine introgression. Shortleaf pine has higher specific gravity than loblolly pine and the higher specific gravity of trees from the Vernon (S) seed source could indicate that more introgression has occurred in that area. Results of this study support the evidences presented by Hare and Switzer (1969) for more frequent introgression with shortleaf pine in western than in eastern loblolly pine.

4. The differences in performance of seed sources among the three planting sites can be attributed to a great degree to differences in rainfall distribution among the three plantations. Precipitation in De Ridder during the spring and summer months was very much lower than the precipitation during the same period in Bogalusa and Idlewild, while autumn precipitation was higher in De Ridder than in Bogalusa and Idlewild. These conditions have favored production of more latewood and narrower growth rings in trees planted in the De Ridder plantation and more earlywood and wider annual rings in trees in the Bogalusa

and Idlewild plantations. Furthermore, the environmental conditions at De Ridder were conducive to greater height growth of trees at this site.

5. Autumn precipitation is critical for height growth and and extended latewood production, while spring and summer precipitation have more effect on diameter growth and earlywood production in loblolly pine in southern Louisiana.
6. An increase in percentage latewood, cell wall thickness, and tracheid length will cause an increase in specific gravity. These wood properties were found to be highly positively correlated in this study.
7. In the pith section, width of annual ring was found to be correlated with specific gravity, tracheid length, and cell wall thickness but no correlation was found with these properties in the bark section.
8. Annual ring width is very highly correlated with diameter and height.

Suggestions for future study:

One of the obvious applications of the results of this study is the use of the St. Tammany seed source for reforestation in southern Louisiana. This source grew well at all planting locations and had wood of high specific gravity. However, these

early results could be misleading and many changes may occur as the plantations mature. It would be worthwhile therefore, to conduct a similar study at a later date to verify whether the slight superiority of the St. Tammany source is maintained as the trees grow to harvest. Some other characteristics which could be given special consideration in a later study are bole straightness, amount of compression wood, and extractive content.

In general, the genetic variation in growth and wood characteristics of the five loblolly pine sources was not pronounced. Only specific gravity, annual ring width, and cell dimensions varied among the seed sources. Together with tracheid length, these wood traits were also strongly affected by environmental factors. Diameter and height growth rate and percentage latewood did not show any significant genetic or environmental variation but differences were apparent. It would be interesting to investigate these differences by conducting a progeny test of the selected trees in the different seed sources to see whether these differences are genetically controlled.

Another interesting aspect of study would be to investigate the possibility of introgression with shortleaf pine in the western populations of loblolly pine in Louisiana.

Another study might be designed to investigate the relationship between seasonal precipitation and terminal bud size of the different trees planted at the different plantations to determine

whether the size of the buds formed has a direct influence on the number of growth flushes in loblolly pine. Also, it would be of interest to investigate the effect of moisture on tracheid elongation and differentiation.

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EXAMINATION AND THESIS REPORT

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Major Field: Forestry

Title of Thesis: Genetic and Environmental Factors Affecting Growth and Wood Properties of Loblolly Pine Seed Sources in Louisiana

Approved:

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VITA

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