To the Graduate Council:

I am submitting herewith a dissertation written by Basil Eugene Pinker entitled "Intertree Competition in Open-Pollinated Progeny Plantations of Virginia Pine (Pinus virginiana Mill.) and White Pine (Pinus strobus L.)." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Edward R. Buckner, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

INTERTREE COMPETITION IN OPEN-POLLINATED PROGENY PLANTATIONS OF VIRGINIA PINE (*PINUS VIRGINIANA* MILL.) AND WHITE PINE (*PINUS STROBUS* L.)

A Dissertation

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ABSTRACT

Dimensional-spatial relationships among trees were utilized to develop a Dimension-Difference Index (DDI) and Distance-Ratio Index (DRI) for estimating intertree competition in white pine (Pinus strobus L.) and Virginia pine (Pinus virginiana Mill.) open-pollinated test plantations. Additional information gathered from a separate spacing study was required in the DDI. Linear regressions of tree dimension on growing space were used to identify effective adjacent competitors of sampled trees and their levels of influence.

Competition was expressed in terms of six measured characteristics: (1) diameter at breast height (dbh), (2) crown diameter, (3) crown area, (4) height, (5) basal area, and (6) volume, plus a derived statistical factor, TREESIZE. Comparisons were made between values of traits adjusted for competitional variance and their unadjusted values.

There were significant differences among stands and families of both white and Virginia pine in competitive influence on most characteristics. The commercially important characteristics of dbh, basal area, and volume were sensitive to competition, and were among the most highly heritable of the characteristics studied. TREESIZE, although useful as an index of commercially important tree characteristics, failed to yield reliable heritability estimates. The DRI appeared to be better than the DDI in estimating competitive influences, and could be made applicable to forest tree improvement plantations of other species and ages.

The overall variance of each measured trait and distribution of variance components were significantly influenced by intertree competition. Most of the competitionally influenced variance occurred in the component of within-plot variances. Upon adjustment for competition, variance within plots was reduced, and this was accompanied by increased percentage contribution to the total variance by replications and replications X families-within-stand-interaction sources. Overall means and the ranking of stand and family means were not influenced significantly by competition. Narrow-sense heritability estimates were both inflated and deflated by competition, suggesting that competition might significantly influence estimates of gain from selection.

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LIST OF SYMBOLS

DBH = diameter at breast height.

CROWN = crown diameter.

BA = basal area.

CA = crown area.

TREESIZE = derived factor from Principle-Component Analysis.

D-COMP = competitive fitness based on DBH.

H-COMP = competitive fitness based on height.

C-COMP = competitive fitness based on crown diameter.

B-COMP = competitive fitness based on basal area.

CA-COMP = competitive fitness based on crown area.

V-COMP = competitive fitness based on volume.

T-COMP = competitive fitness based on TREESIZE.

D-WOUT = DBH adjusted for competition.

H-WOUT = height adjusted for competition.

C-WOUT = crown diameter adjusted for competition.

B-WOUT = basal area adjusted for competition.

CA-WOUT = crown area adjusted for competition.

V-WOUT = volume adjusted for competition.

T-WOUT = TREESIZE adjusted for competition.

Subscript 1 = Dimension-Difference Index.

Subscript 2 = Distance-Ratio Index.

CHAPTER I

INTRODUCTION

Studies of intertree competition examine how designated trees or populations of trees (stands, families, or clones) fare in relation to neighboring trees in the struggle for a common set of limited resources. The influence of competition on any given tree at a specified time may be viewed as the expressed deviation in the size of that tree from the size it might have attained at the same age when grown in a competition-free environment. In cases where open-grown, competition-free progeny trees are not available for comparison, no good estimates of competitional deviation can be obtained. Relative estimates of competitive ability can, however, be derived by examining the dimensional-spatial relationships expressed by trees growing in a highly competitive environment such as a plantation (Mather, 1969).

If every tree in a uniformly spaced, even-aged plantation possessed identical genetic makeup and each was exposed to identical environmental conditions throughout its development, then the observed phenotypic performance of all trees would be the same. In this situation, each tree may be viewed as an equal competitor possessing the same competitive fitness or ability as every other tree (Sakai and Mukaide, 1967). Any deviation from this situation would suggest that either the genetic or environmental characteristics of a plantation, or both, exhibit some degree of variation.

Analysis of variance generally provides the basis for evaluating performance of selected progeny in forest tree improvement plantations (Namkoong, 1979; Sakai and Hatakeyama, 1963). The total variance, however, often includes some portion of variation due to intertree interaction. That is, some portion of the total phenotypic variance exhibited by a plantation shows up because trees, due to their proximity to one another, influence each other as they utilize the limited available resources (Hamblin and Rosielle, 1978; Mather, 1969; Sakai and Mukaide, 1967). Whether or not these intertree interactions contribute significantly to the analytical evaluations of progeny performance, or to estimates of heritability, depends on how much of the total variance they make up and how they are distributed among the genetic and environmental components of variance (Donald, 1963; Sakai, 1955; Tauer, 1975).

Competition among trees may be estimated by isolating the portion of total variance in the genetic and environmental factors that results from intertree spacing (Mather, 1969). On an individual-tree basis, competitive fitness is estimated by determining the deviation in the expressed performance of each tree from that which it might have attained if it and all trees with which it effectively interacts were equal competitors (Sakai and Mukaide, 1967).

Objectives

The objectives of this study were:

1. To develop a method of estimating intertree competition in established, open-pollinated, progeny test plantations.

2. To analyze and evaluate the expressed competitive abilities among selected stands and among halfsib families of two native tree species of economic importance in Tennessee; white pine (Pinus strobus L.) and Virginia pine (Pinus virginiana Mill.).

3. To examine the influence of intertree competition in young study plantations on the distribution of derived variance components and on estimates of heritability.

4. To isolate the portion of total variance influenced by intertree competition and to determine its contribution to expressed rankings of stand and family means of measured characteristics.

These objectives were established to determine whether or not intertree competition is detectable and of sufficient importance in forest tree improvement plantations to affect analytical evaluations of progeny performance.

CHAPTER II

LITERATURE REVIEW

The study of intergenotypic competitive interactions in plants has received considerable attention in recent years (Adams et al., 1973). Plant breeders in particular have been interested in intergenotypic competition because of its effect on phenotypic performance and the evaluation of genotypes (Allard and Adams, 1968). Studies have shown that planting select mixtures of crop varieties, having favorable interactions of genotype, can result in increased yields beyond that expected from pure stand, single variety plantings (Brim and Schutz, 1968; Schutz and Brim, 1967). In addition, population geneticists have found that intergenotypic interactions may play a crucial role in the maintenance of polymorphisms since they result in frequency-dependent selection (Allard and Adams, 1968; Mather, 1969; Schutz et al., 1968).

Although mathematical models have been developed for the genetic analysis of competition (Sakai, 1955; Griffing, 1967), they have rarely been used. Plant breeders and geneticists have generally ignored the potential importance of intergenotypic competition in genetic parameter estimation. In classical plant breeding theory, it has been assumed simply that individuals do not interact (Gallais, 1976). Perhaps the reason for this, in part, is the complexity of available models for the analysis of competition (Hamblin and Rosielle, 1978).

A large part of the complexity and confusion that surrounds the topic of interplant competition appears to stem from how different investigators have chosen to define competitive interactions in specific experimental situations. Rennie (1974) suggested that competition may have different meanings to ecologists, geneticists, and agronomists, depending on whether the processes of competition, the results of competition, or the relationships among competing individuals are being considered. Whereas ecologists often are concerned with competition at the interspecific level and how it affects the organization and development of communities of various kinds, geneticists are interested in the effects of competition at the intraspecific level on the makeup of populations. Agronomists and foresters in particular are concerned with the manner in which competition influences crop yields (Harper, 1961). At the finer levels of restricting growing space, competition control has been used frequently as a major silvicultural tool (Namkoong, 1979). However, since competition is the same biological process in all cases, one definition should suffice (Milne, 1961).

According to Rennie (1974), the following definition, drawn from Odum (1959) and Milne (1961), applies equally well to all biological sciences.

> Competition is a process in which two or more organisms in proximity interact for a portion of an environmental factor which is not available in supply sufficient to meet their combined demands.

Plant competition is considered to be a passive process, while in animals competition is usually thought of as being active (Gause, 1934).

According to Namkoong (1979), intergenotypic competition has been defined as "any departure in plant performance exhibited when a plant is competing against other genotypes rather than in a pure [clonal] stand." The departure in plant performance observed is not restricted in a directional sense by this definition and, therefore, may occur in a negative or positive fashion. Schutz and Brim (1967) further defined three intergenotypic competition effects which are based on the size and sign of the linear regression coefficients obtained for the regression of a measured trait in the test genotype on the number of individuals in the competing genotype. Complementation occurred when the regression coefficient for a specific genotype pair was of equal magnitude and of opposite sign when compared to its reciprocal. Overcompensation was in effect when the sum of these regression coefficients was greater than zero, and undercompensation occurred when the sum of the regression coefficients was less than zero.

Linear responses of test genotypes to the relative frequency of competitor genotypes were demonstrated in soybeans (Glycine max (L.) Merr.) by Schutz and Brim (1967) and in barley (Hordeum sativum L.) by Sakai (1957). When overcompensating responses occur, the potential for increasing yields exists (Harper, 1965). Such overcompensation has been observed in genotypic mixtures of lima beans (Phaseolus limensis Mcfad.) by Allard (1961), of wheat (Tritichum aestivum L.) by Jensen and Federer (1964, 1965), of oats (Avena sativa L.) by Smith et al. (1970), and those of soybeans by Schutz and Brim (1967, 1971). Adams et al. (1973) reported overcompensating responses between genotypic families of

loblolly pine (Pinus taeda L.) seedlings, and Tauer (1975) observed similar interactions between clones of black cottonwood (Populus trichocarpa Torr. and Gray).

The majority of research concerning intergenotypic competitive interactions has involved species which are primarily self-pollinators, and little information is available on interclass interactions in outcrossing species (Adams et al., 1973). Similarly, little is known of the importance of interfamily competition in open-pollinated stands of forest trees at the intraspecific level (Stahl, 1977).

There are two basic approaches to determining estimates of intergenotypic competition in plant populations. The first and most accurate method is to grow different genotypes in pure stands and mixtures and measure the increment or decrement of growth or yield of a given genotype due to mixing. Most, if not all, intraspecific competition studies dealing with annual or short-lived plants have been patterned after this general approach (Sakai et al., 1966).

A second method for obtaining estimates of intergenotypic competition is to examine plantations already in existence and attempt to partition out suitable variance components by means of intricate statistical manipulations (Sakai et al., 1966; Sakai and Mukaide, 1967). This method has both advantages and disadvantages, but, when feasible, is more applicable to forest tree breeding programs which are of long-term nature. A major obstacle to this approach is the obvious fact that the plantations to be evaluated were not intentionally designed and

planted for the purpose of studying competition (Sakai et al., 1966; Stahl, 1977).

Steneker and Jarvis (1963) examined the correlation between the growth of individual trees and the collective growth of several trees growing in proximity to those individuals and suggested that this correlation might reveal the intertree competition in a forest. Sakai et al. (1966) used this approach to evaluate intergenotypic competition in plantations of Cryptomeria japonica D. Don, but restricted the correlations of measured traits to randomly sampled pairs of adjacent trees.

Several indices describing the competitive status of individual trees have been proposed for application in growth models for tree and stand simulation (Adlard, 1974). These include:

1. The mean distance to various numbers of neighboring trees or distance to the ith closest neighbor (Clark and Evans, 1954; Thompson, 1956).

2. Available growing space, defined by polygons whose vertices are determined by the intersection of bisectors of the straight-line distances to surrounding trees (Brown, 1965; Jack, 1967).

3. Available growing space, defined by polygons whose areas are proportional to the dimensions of the centered trees (Moore et al., 1973; Pelz, 1978).

4. Overlapping competitive-influence zones in which circular areas are proportional to individual tree dimensions (Gerrard, 1968; Opie, 1968; Bella, 1971; Keister, 1971).

The proportional polygons (No. 3) and overlapping areas of competitive-influence zones (No. 4) are the most accurate indices, with the polygonal areas being easier to calculate than overlapping influence zones (Adlard, 1974).

Agronomists and foresters generally view plant competition in terms of stand density. Numerous plantings at different densities have been established to determine which densities maximize yield per unit area (Harper, 1961). Experimental designs which have been used in long-term competition studies with forest trees include Nelder's design (Nelder, 1962) and block plantings of pure and mixed genotype stands (Goddard and Rockwood, 1978). Other designs such as the hexagonal plots reported by Tauer (1975) or the nonsystematic design (Lin and Morse, 1975), which promises to overcome shortcomings of Nelder's design, could also be used with forest plantings. Experiments of these types, however, make no attempt to examine the finer details of competition, such as the separation of spacing effects from direct interactions or separating above- and below-ground competition (Rennie, 1974).

Hayashi and Sakai (1967) observed that competitive effects were cumulative over years in Cryptomeria japonica D. Don suggesting that competitive interactions may be of particular importance in perennials. Donald (1963) reported that competitive response may change with environment and this was observed by Tauer (1975) in experiments on black cottonwood clones. Tauer also noticed changes in the rankings of treatment means of select clonal pairs over time indicating that trees,

unlike annual plants, may require at least several years of growth before their final competitive relationships are concretely established.

The potential importance of intergenotypic competition is perhaps most clearly demonstrated by its effect on estimates of genetic parameters (Hamblin and Rosielle, 1978). Estimates of genetic parameters in forest trees have been obtained by two different methods. The first approach is to obtain estimates of environmental variance in a clonal population. Then, by subtracting the environmental variance from the phenotypic variance of a seed-propagated population, genetic variance or covariance may be estimated. The second method involves computing the components of between-family and within-family variance by the method of analysis of variance under the assumption of random mating. From these, the genetic variance and genetic covariance are then estimated (Sakai and Hatakeyama, 1963).

Both of these methods have limitations in general application. The first assumes that environmental variations in two separate forests are equal, which is not likely to be true. In addition, species which are not easily propagated vegetatively cannot be analyzed (Sakai and Hatakeyama, 1963). In the second method, Mather and Jinks (1971) suggested that the best designs for genetic interpretation are fully randomized designs. Hamblin and Rosielle (1978) have shown in experiments with agricultural crops that these designs are inadequate in at least two situations. The first situation occurs when the characteristic studied is markedly affected by competition and the experiment is carried out at average field-crop densities. Under these conditions,

competitive effects may invalidate the interpretation of genetic parameters in a pure-culture situation. The second situation occurs when the characteristic studied is markedly affected by genotype-density interactions and the experiment is performed at low densities. Genetic interpretations at low density may have little meaning under conditions of high plant density.

A third method of genetic parameter estimation was developed by Shrikhande (1957) and does not require the raising of progeny. In using this method, Sakai and Mukaide (1967) introduced a component of variance, in addition to genetic and environmental components, which accounted for intertree competition. Improvements in this methodology have been suggested (Huhn, 1969, 1970); however, numerous implicit assumptions continue to restrict its general applicability.

Several theoretical and analytical models have been proposed which incorporate interplant competition as a factor in the estimation of genetic parameters and the processes of natural and artificial selection. These range from versions which consider simplistic cases of true-breeding lines and dominant-recessive alleles (Mather, 1969) to generalized quantitative versions expressing means, variances, covariances and heritabilities as functions of environmental, additive, and sometimes numerous interplant interaction effects (Griffing, 1967; Gallais, 1976; Huhn, 1975; Sakai and Mukaide, 1967). The complexity of taking competitive effects into consideration is evident in even the simplest cases (Mather, 1969), whereas, the broad generalized models rely heavily on simplifying assumptions to reduce these complexities

(Gallais, 1976; Huhn, 1975). Such limitations make these methods of questionable value for practical evaluation of performance in progeny test plantations.

Observed effects of intergenotypic competition on estimated genetic parameters may be summarized as follows:

1. The mean competitive effect tends to be small in comparison to the mean genetic effect (Simmonds, 1962; Trenbath, 1974).
2. The effects of competition on variances, however, are large in both the additive and dominance components. Cases of both inflation and deflation of expected progeny (F_2) variances have been observed (Hamblin and Rosielle, 1978).

A problem therefore occurs in the use of such common measurements as heritabilities since these are based on estimated variance components.

Obtaining heritability estimates without considering the effects of competition might result in over- or underestimation of genetic advances from selection. This could lead to situations in which excessive attention is paid to parents or crosses where competitive effects have increased heritability estimates, or to rejection of parents or crosses where heritability estimates have been decreased due to competition. In both cases the efficiency of selection is reduced (Hamblin and Rosielle, 1978).

When working with species that have large generation intervals, such as forest trees or other perennial plants, it is important to obtain heritability estimates as early as possible in the breeding program (Huhn, 1975). If early selection of individuals is to be

effective, techniques which accurately assess the confounding effects of interplant competition on genetic parameter estimation must be developed, preferably ones that can correct for competitive effects or incorporate them into the selection procedure to the tree breeder's advantage (Hamblin and Rosielle, 1978). Fluctuating responses evident in experiments with young perennial species suggest that long-term field studies are needed to assess the influences of competition on productivity over the complete rotation period (Tauer, 1975).

CHAPTER III

METHODS AND PROCEDURES

Study Area

Three plantations located at the Highland Rim Forestry Field Station near Tullahoma, Tennessee, were used for this study. Two of these plantations, a white pine and a Virginia pine open-pollinated heritability study were examined in detail for intertree competitive effects.

The white pine heritability study, established in 1970, is composed of the offspring of ten parent trees selected from each of 13 natural stands in Georgia, North Carolina, and Tennessee (see Table 1). At the time of establishment, a total of 12,800 seedlings representing 128 open-pollinated families were planted in a randomized complete block design with ten replications.

The Virginia pine test, established in 1967, consists of open-pollinated progeny from most of the 15 parent trees selected from each of 12 stands in Tennessee and Kentucky (see Table 2). This plantation also has 128 families represented in a randomized complete block design with ten replications.

Both the Virginia pine and white pine plantations conform to a rectangular spacing regime. Family row plots are separated from neighboring plots by a distance of 2.44 meters (8 feet), and trees within row plots are positioned 1.22 meters (4 feet) apart. In

Table 1. Locations of Natural Stands of White Pine from Which Parent Tree Selections Were Made

Stand Number	Stand Location
1	Monroe Co., Tenn.
2	Polk Co., Tenn.
3	Fannin Co., Ga.
4	Cherokee Co., N.C.
5	Madison Co., N.C.
6	Cocke Co., Tenn.
7	Unicoi Co., Tenn.
8	Unicoi Co., Tenn.
9	Transylvania Co., N.C.
10	Carter Co., Tenn.
11	Scott Co., Tenn.
12	Morgan Co., Tenn.
13	Anderson Co., Tenn.

Table 2. Locations of Natural Stands of Virginia Pine from Which Parent Tree Selections were Made

Stand Number	Stand Location
1	Clifton, Tenn.
2	Dawson Springs, Ky.
3	Sewanee, Tenn.
4	Rock Island, Tenn.
6	Wartburg, Tenn.
7	Pineville, Ky.
8	London, Ky.
9	Morehead, Ky.
10	Etowah, Tenn.
11	Vonore, Tenn.
12	Newport, Tenn.
13	Elizabethton, Tenn.

comparison to a uniform spacing of 1.83 x 1.83 meters (6 x 6 feet), this scheme provides for diminished competition among families while competition among trees within a family is accentuated.

Supplementary data utilized in the development of one of the competition indices examined in this investigation were collected from a Species-Spacing Comparison Study. This plantation, established in 1966, consists of four species of pine, loblolly (Pinus taeda L.), shortleaf (Pinus echinata Mill.), Virginia and white, each planted at four different spacings in a split-plot experimental design. Spacings of 1.83 x 1.83 meters (6 x 6 feet), 2.74 x 2.74 meters (9 x 9 feet), 3.66 x 3.66 meters (12 x 12 feet), and 4.57 x 4.57 meters (15 x 15 feet) are represented.

The three plantations, located within a few hundred yards of each other, were established on flat terrain at an average elevation of 300 meters (1000 feet). The soil is Dickson silt loam with an impervious fragipan at a depth of 46 centimeters (18 inches). Mean annual precipitation is 135 centimeters (53 inches), and the mean daily temperature ranges from 5.3°C (41.5°F) in January to 25.3°C (77.6°F) in July with an average of 196 frost-free days (Nelson and Zillgitt, 1969).

Characteristics Measured

Competition could influence all measurable tree characteristics. In this study, the following characteristics were measured and evaluated.

1. Height - measured to the nearest half meter from the surface of the ground to the top of the crown.

2. DBA - diameter at breast height [1.37 meters (4.5 feet)] of the bole, measured to the nearest centimeter.

3. Crown Diameter - crown width measured to the nearest half meter from the drip lines, in two directions (the second direction perpendicular to the first). This was calculated as the geometric mean ($\sqrt{C_1 C_2}$) of the two directional crown diameters to provide an estimate of diameter more accurate than the arithmetic mean in cases where the horizontal cross sectional area of the crown is more nearly elliptical than circular (Husch et al., 1972).

From these measurements, three additional characteristics were computed.

4. Basal Area (BA) in m^2.

5. Crown Area (CA) in m^2.

6. Volume of solid wood in m^3.

The formulas used to derive these values are given below.

$$BA(m^2) = \left(\frac{\pi}{10000}\right)\left(\frac{DBH(cm)}{2}\right) = 0.00007854(DBH(cm))^2$$

$$CA(m^2) = \pi\left(\frac{\text{crown diameter(m)}}{2}\right)^2 = 0.7853982(\text{crown diameter(m)})^2$$

For Virginia pine:

$$\text{volume}(ft^3) = 0.002056 + 0.00218664(DBH(in))^2(\text{height(ft)})$$

(Goebel and Warner, 1966)

Converted to metric,

$$\text{volume}(m^3) = (0.002056 \times 0.0283168) + (0.00218664 \times 0.0144)$$
$$(\text{DBH(cm)})^2(\text{height(m)})$$

For white pine, the formula for the volume of a cone was used:

$$\text{volume}(m^3) = 0.00003926991(\text{DBH(cm)})^2(\text{height(m)})$$

On both the white pine and Virginia pine data, a Principle-Component Factor Analysis was performed with varimax rotation on all six variables. From this a single factor highly correlated with the original variables was derived for each species. This factor was made positive over its entire range by adding a constant equal to twice the absolute size of the greatest negative deviation encountered to all derived factor coefficients. The factor (TREESIZE) was then included with the above as an additional variable for estimating overall tree size.

Preliminary Study

Each individual tree in the plantations studied was assumed to be competing to some degree with some of its closest neighbors. To arrive at a value estimating competitive fitness or ability of any given tree, it was first necessary to determine with which neighboring trees it was effectively competing and to what extent.

Data on all variables and characteristics included in the main study were collected from a sample of white pine and Virginia pine trees

growing in the Species-Spacing Study plantation. Measurements were made in December of 1981 when the trees were fifteen years of age. Sampling was controlled to assure that all four of the original closest neighbors were still surviving. For example, all measured trees in the 1.83 x 1.83 meter (6 x 6 foot) spacing had no fewer than four surviving trees spaced no farther than 1.83 meters (6 feet) from them. Similarly, all measured trees at all spacings had a full configuration of closest neighbors (Figure 1). Trees whose closest neighbors included border trees were not measured. The purpose of this sampling approach was to obtain the best possible estimate of tree performance at each of the spacings represented.

An attempt was made to measure one hundred trees of each species at each spacing level distributed throughout the plantation. For white pine, this goal was achieved and a balanced sample of data from 400 trees was collected. In Virginia pine, however, survival was poor in two of the four replications, especially at the wider spacings. As a result, not enough trees with a full configuration of neighbors were present to obtain a sample completely balanced with respect to spacing. An unbalanced sample of 312 measured Virginia pine trees that fully met sampling criteria was collected.

To determine if trees at all spacings were effectively competing, data from both species were analyzed using Duncan's New Multiple Range Test. Significant differences at the .05 probability level were obtained between trees grown at the 4.57 x 4.57 meter (15 x 15 foot) spacing and trees grown at all closer spacings in all characteristics

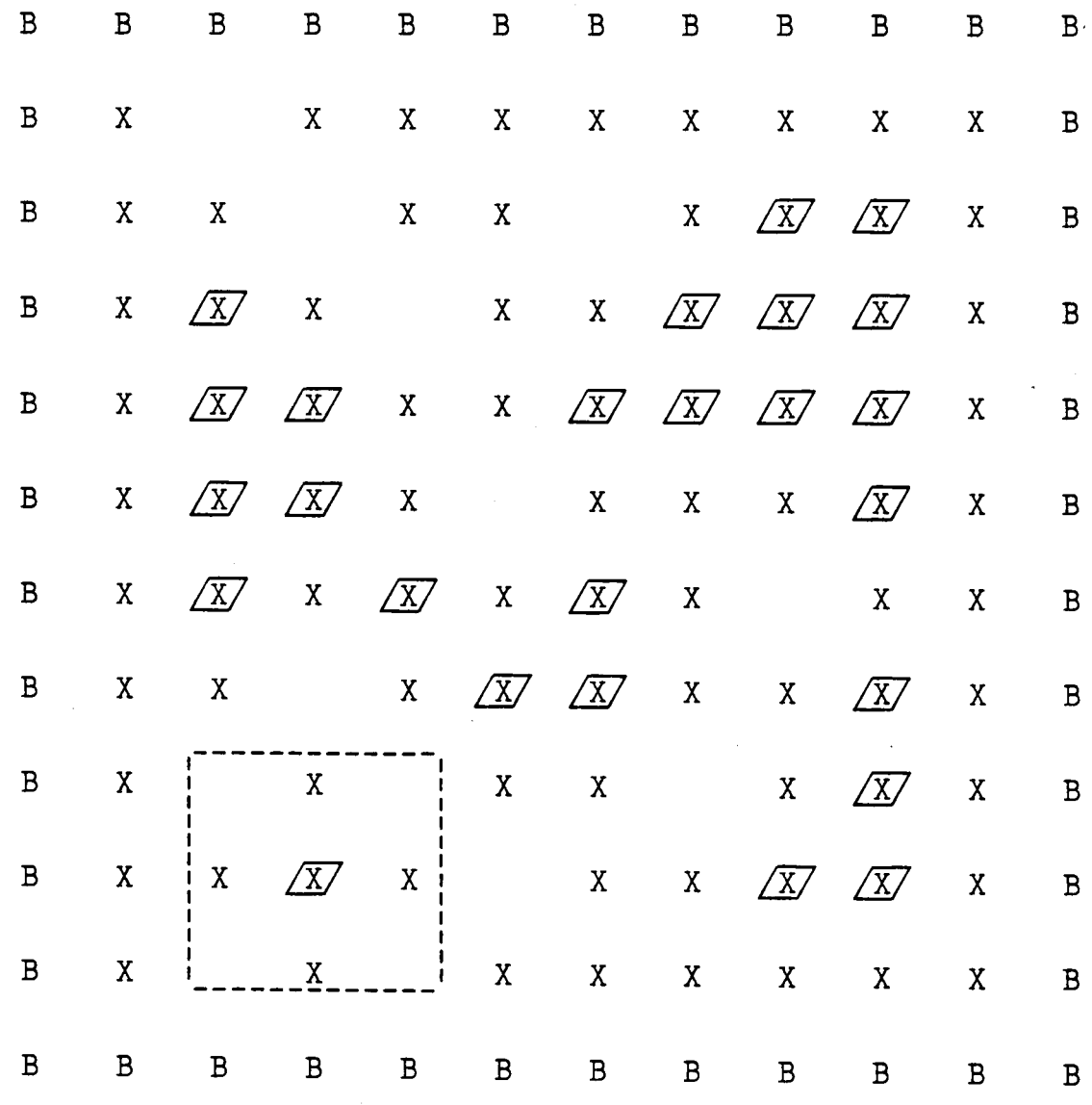


Figure 1. Location of sample trees on one half-acre split plot in the Species-Spacing Comparison Study where each tree is positioned at a 4.57 × 4.57 meter (15 × 15 foot) spacing.

B = border tree

X = surviving tree

X = sample tree

= full configuration

measured except height (see Results, p. 58). Trees grown at wider spacings were larger than trees grown at closer spacings in both white and Virginia pine. Results indicate that intertree competition is effectively occurring among fifteen-year-old pine trees growing at spacings of 3.66 x 3.66 meters (12 x 12 feet) or less.

An earlier investigation (at age 10) of the same plantation did not produce significant differences in measured characteristics between trees grown at the 3.66 x 3.66 meter (12 x 12 feet) spacing and trees grown at the 4.57 x 4.57 meter (15 x 15 feet) spacing (Thor et al., 1979). The change between the ten-year and 15-year measurements reflects the increased area of competitive interaction surrounding each tree with increasing plantation age. It is possible that this area of influence may now extend far enough to affect trees in the 4.57 x 4.57 meter (15 x 15 feet) spacing at age 15, however, since wider spacings were not available, this could not be verified statistically. To avoid excluding possible intertree interaction that might be occurring, each tree analyzed in the main investigation was assumed to be centered in a circular shaped area of competition with a radius of 4.57 meters (15 feet).

Determining the number of effective competitors with any given tree in the main-study plantations was straightforward once the size of the area of intertree interaction was established. Any neighboring tree that grew within the area of competitive influence with a given test tree was considered to be an effective competitor. Since both the white pine and the Virginia pine study plantations were established on uniform

1.22 x 2.44 meter (4 x 8 feet) spacings, each individual tree within those areas had the same potential number of effective competitors. Actual numbers of effective competitors varied from tree to tree as a result of mortality and proximity to the edge of the plantation. A diagrammatic example of the spatial relationships determining the potential effective competitors of a hypothesized test tree is shown in Figure 2. As is evident, a test tree may be competing with as many as 20 neighboring trees.

Results of the spacing study indicated that trees at closer spacings were smaller in most dimensions than trees planted at wider spacings (Thor et al., 1979). This can be interpreted as a response to increasing competition. The intensity of competition is a function of spacing, and its effect decreases as spacing increases (Sakai and Mukaide, 1967). Stated another way, competition is inversely related to growing space (Gerrard, 1969).

To facilitate quantifying the varying intensities of competitive interaction which a given tree encounters with its neighbors, the area of competitive influence surrounding each sample tree was divided into concentric, competitive-influence zones of isointensity (Figure 3). For a given test tree, all neighboring trees occupying the same zone of competitive influence occurred at the same effective spacing and were assumed to interact with the test tree at the same level of intensity. Trees occupying different zones differed in their effective spacing in relation to the test tree and were assumed to interact with the test tree at different intensities. Trees in zones farther from the test

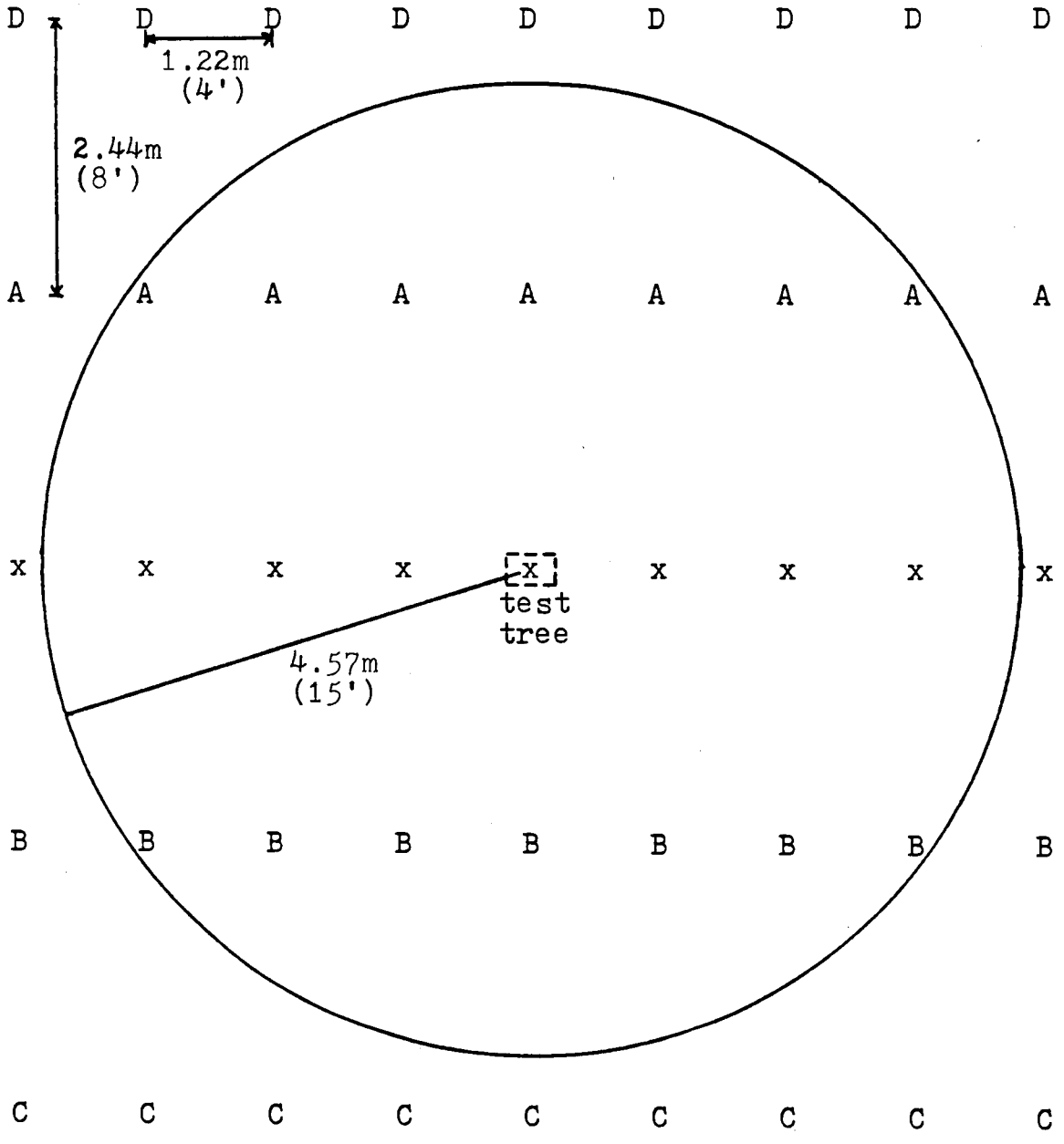


Figure 2. Schematic layout of portion of progeny plantation. Letters represent tree positions and family designations. The circle encloses the area of competitive influence for the test tree.

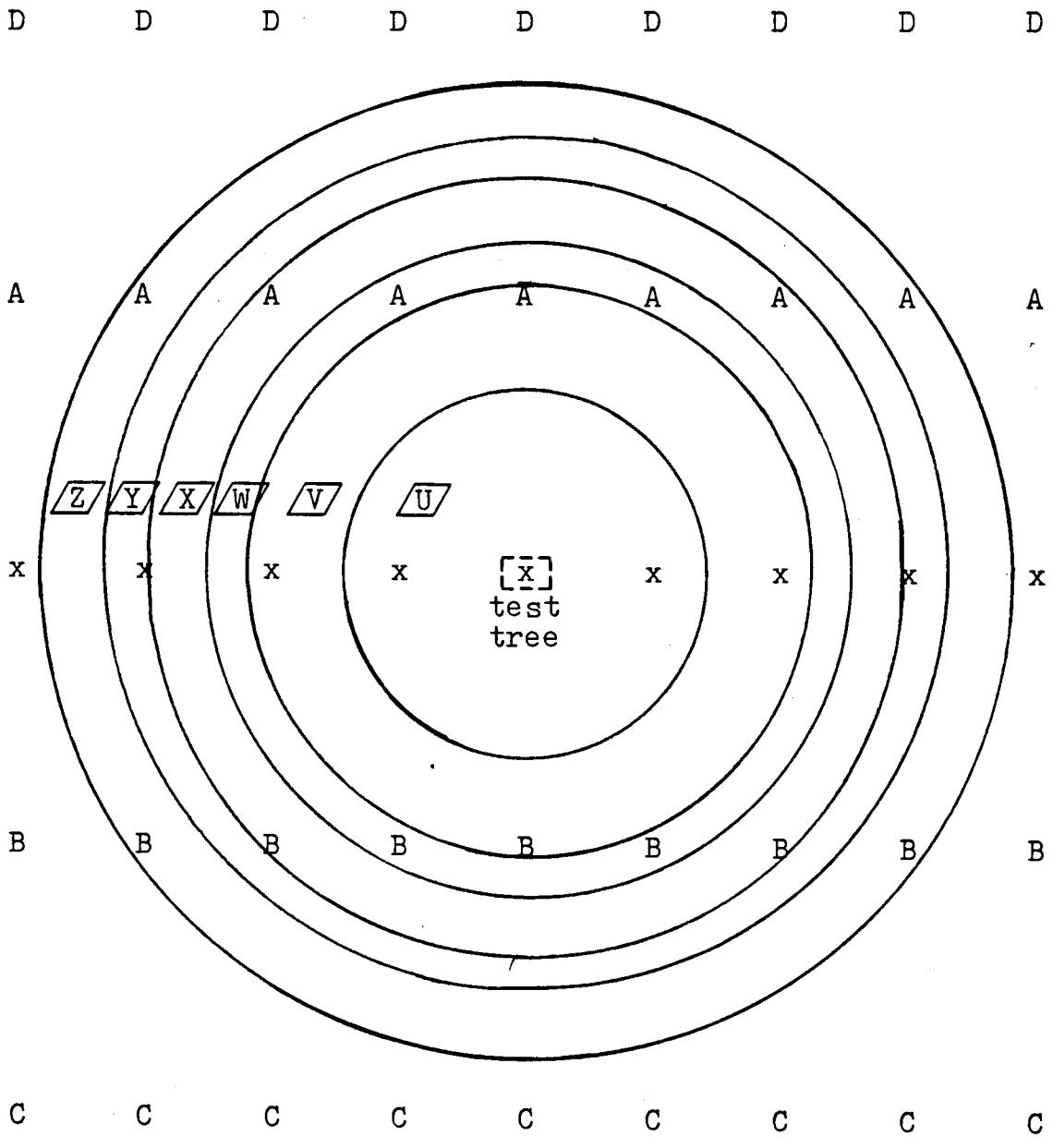


Figure 3. Competitive-influence zones.

U = zone for trees on a 1.22 × 1.22 meter (4 × 4') effective spacing

V = zone for trees on a 2.44 x 2.44 meter (8 × 8') effective spacing

W = zone for trees on a 2.72 × 2.72 meter (8.94 × 8.94') effective spacing

X = zone for trees on a 3.45 × 3.45 meter (11.31 × 11.31') effective spacing

Y = zone for trees on a 3.66 × 3.66 meter (12 × 12') effective spacing

Z = zone for trees on a 4.40 × 4.40 meter (14.42 × 14.42') effective spacing in relation to the test tree

tree were assumed to compete with the test tree at a lower level than trees occupying closer zones.

To obtain estimates of the average intensity level of each competitive-influence zone, a series of regression analyses of the spacing study data was performed. Each characteristic measured was examined as a function of spacing and the equations of the best fitting regression line were determined using the least-squares method. The linear regression of DBH on spacing derived for white pine is presented as an example (Figure 4). Both linear and quadratic regression models were used.

$$Y = a + bX \qquad \text{(Linear Regression Model)}$$

$$Y = a + bX + b'X^2 \qquad \text{(Quadratic Regression Model)}$$

where

X = independent variable = spacing,

Y = dependent variable = characteristic measured,

a = intercept of vertical axis,

b = regression coefficient of linear term = slope in linear model, and

b' = regression coefficient of quadratic term.

For the purposes of this study, only the linear form of regression models will be considered. The quadratic and higher-powered regression models have certain mathematical properties which limit their usefulness in some applications of the methodology presented here, whereas, the

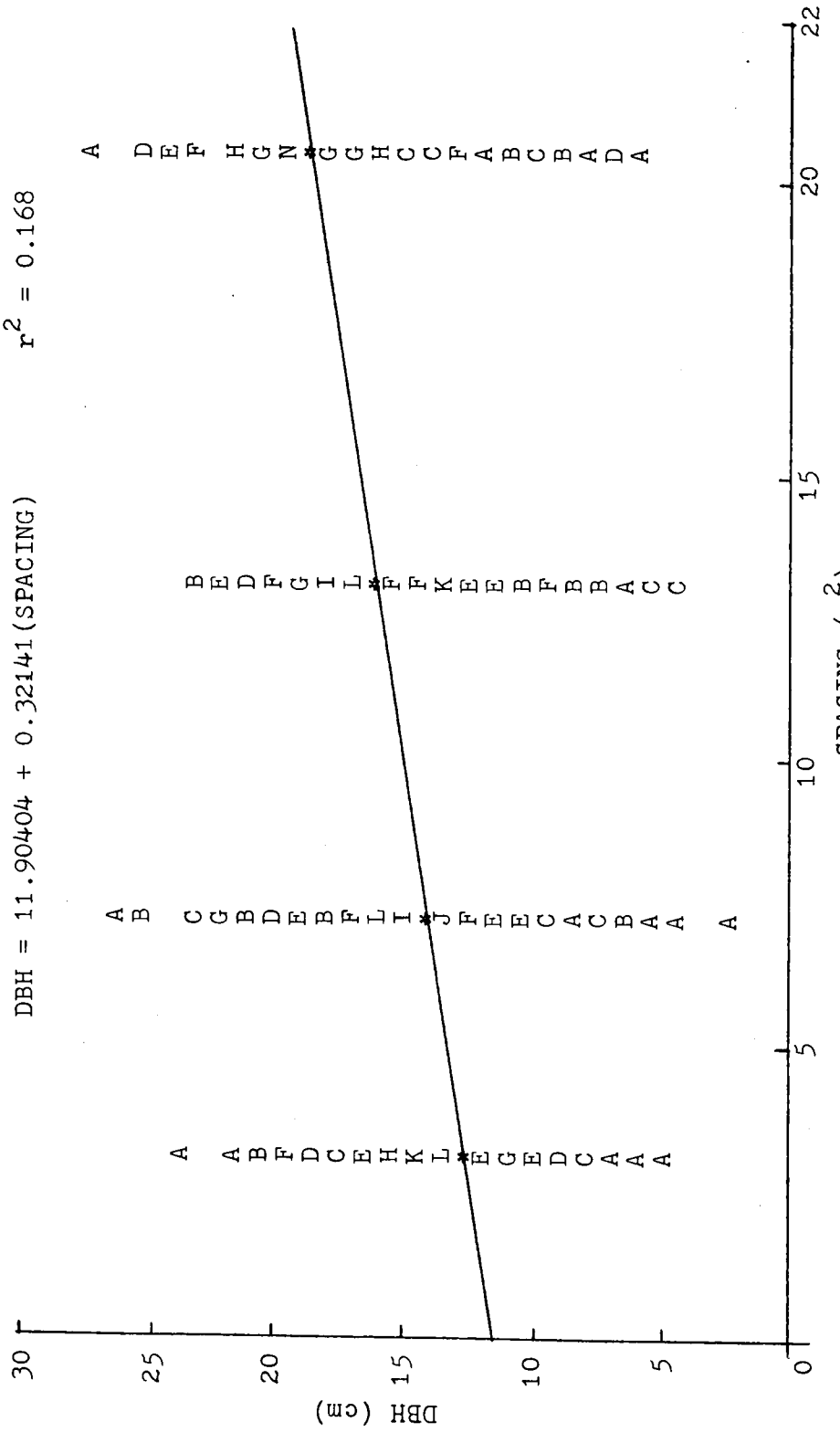


Figure 4. Regression of DBH on spacing in white pine (spacing study data).

A = 1 obs., B = 2 obs., etc.
* = predicted values

linear regression models were found to be applicable in all cases. Aside from this, linear models were highly correlated with quadratic models in all cases, and results derived using one type of model as a basis did not differ significantly from results obtained using the other type of model. For a more detailed discussion of quadratic models, refer to Appendix A.

All characteristics measured (except height in Virginia pine) were found to be positively related to spacing. Since competitive influence among trees expresses itself in an inverse fashion in relation to growing space, a regression of the competitive influence on each measured characteristic was derived using the equation

$$Y' = a + b(Xmax - X)$$
$$= a' - bX$$

where

Y' = competitive influence on a measured characteristic,

X = spacing,

$Xmax$ = maximum spacing encountered or 20.9 square meters (225 sq. ft.) per tree,

a = Y intercept ($X = 0$),

b = slope, and

a' = $a + b(Xmax)$ = Y' intercept ($X = 0$).

Over the range of spacings measured, the slope of the regression of dimension on spacing was inverted and a new vertical axis intercept

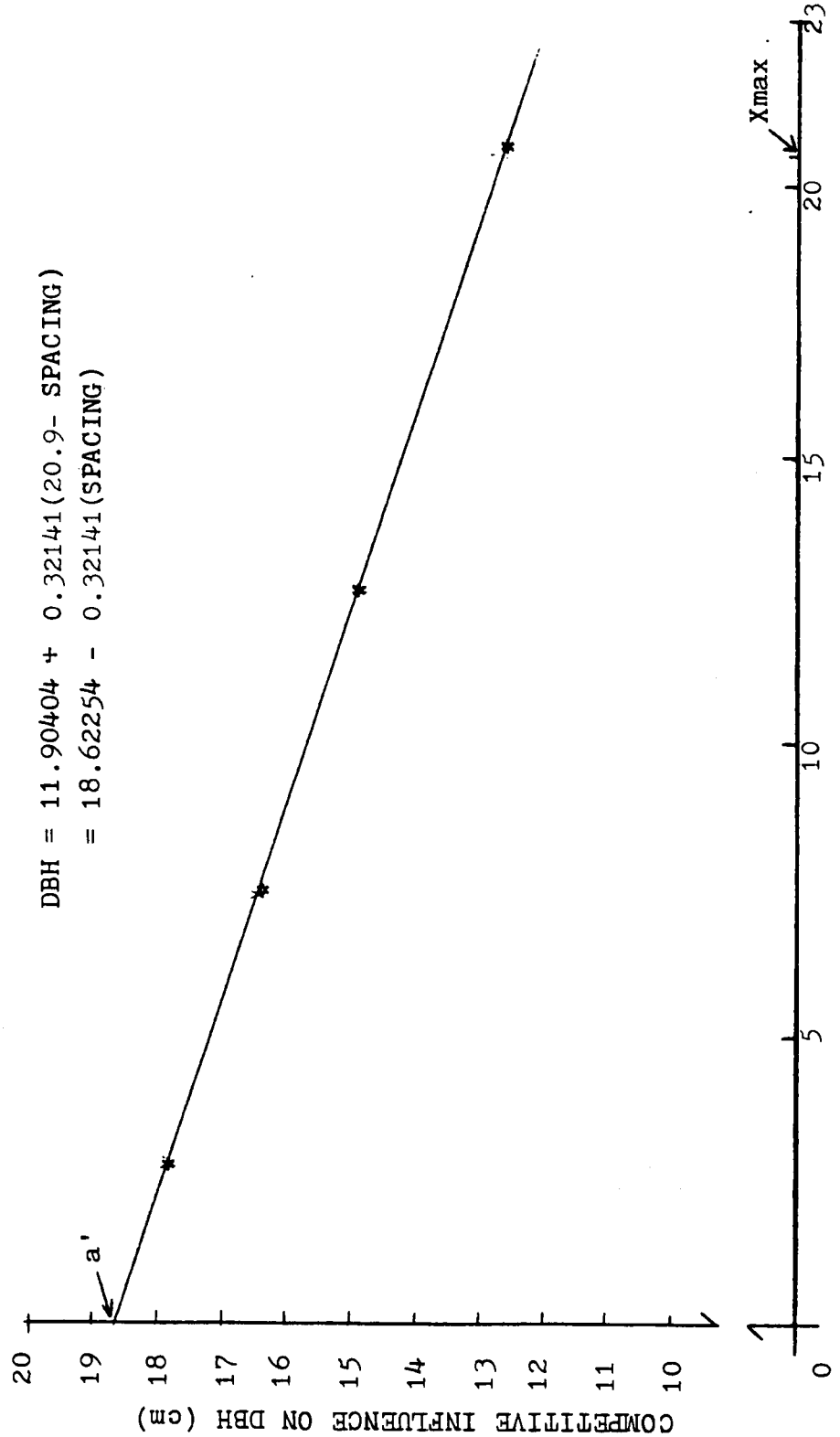


Figure 5. Regression of competitive influence on DBH of white pine on spacing.

(a' = Y' intercept) was formed (Figure 5). The new Y' intercept (a') represented the point (X = 0) at which maximum competitive influence occurred. By reassigning a value of unity to the vertical axis at the point of the Y' intercept (a'), a new scale of relative competitive influence was derived. Any point on this new scale below the intercept and above the origin represents some fraction of competitive influence which ranged from zero to one (Figure 6).

The relative intensity of competition for each competitive influence zone surrounding individual trees in the Virginia pine and white pine heritability study plantations was then predicted from the reverse regressions. In this manner a distinct set of relative competitive-intensity coefficients was derived for each measured characteristic. Individual trees in each competitive-influence zone were assumed to interact with the test tree at these defined intensity levels plus or minus any absolute deviation resulting from individually expressed competitive abilities. In other words, trees at a given effective spacing were assumed to interact according to their own individual competitive abilities, but at a mean relative intensity defined by that spacing.

Evaluating Competitive Ability

Two different methods of estimating competitive abilities were used in the main part of this study. Both make use to some extent of information derived in the preliminary study.

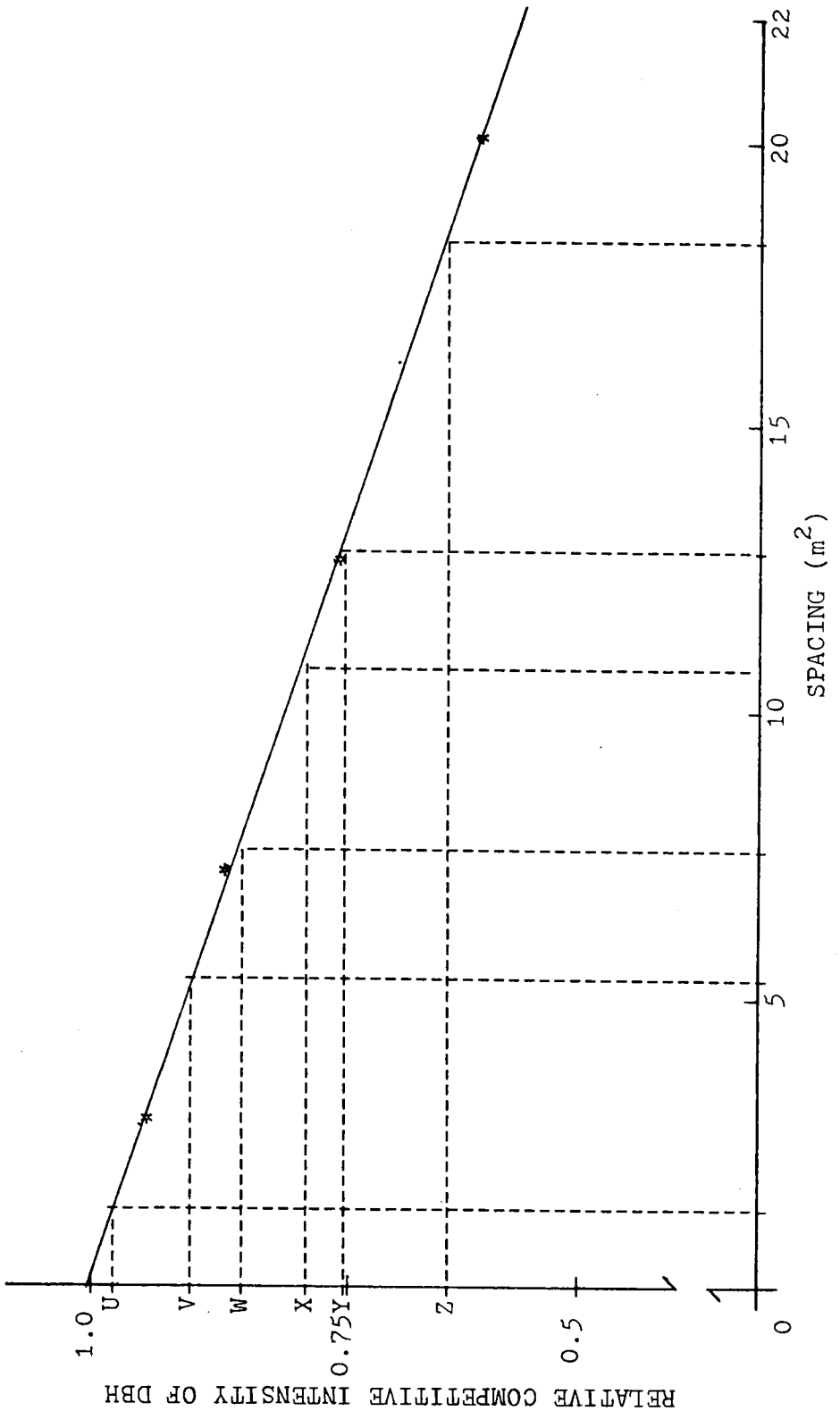


Figure 6. Regression of relative competitive intensity on spacing in white pine (based on DBH).

Letters U through Z represent relative competitive-intensity coefficients derived for the competitive influence zones in Figure 3, p. 25.

Dimension-Difference Index

Sakai and Mukaide (1967) asserted that the sum of competitive effects on a given tree is equal to the sum of the differences in competitive ability between that tree and each other tree with which it effectively competes. This essentially implies that deviations from the situation in which all trees are equal competitors are expressable as differences in competitive abilities among trees. Thus, for any given tree, the competitive response is the additive effects of interaction between itself and each of its effective competitors. This can be expressed algebraically in the following equation based on the diagram presented in Figure 7.

$$
\begin{aligned}
A_{i,j} = {} & (c_{i,j} - c_{i-1,j-3}) + (c_{i,j} - c_{i-1,j-2}) + (c_{i,j} - c_{i-1,j-1}) \\
& + (c_{i,j} - c_{i-1,j}) + (c_{i,j} - c_{i-1,j+1}) + (c_{i,j} - c_{i-1,j+2}) \\
& + (c_{i,j} - c_{i-1,j+3}) + (c_{i,j} - c_{i,j-3}) + (c_{i,j} - c_{i,j-2}) \\
& + (c_{i,j} - c_{i,j-1}) + (c_{i,j} - c_{i,j+1}) + (c_{i,j} - c_{i,j+2}) \\
& + (c_{i,j} - c_{i,j+3}) + (c_{i,j} - c_{i+1,j-3}) + (c_{i,j} - c_{i+1,j-2}) \\
& + (c_{i,j} - c_{i+1,j-1}) + (c_{i,j} - c_{i+1,j}) + (c_{i,j} - c_{i+1,j+1}) \\
& + (c_{i,j} - c_{i+1,j+2}) + (c_{i,j} - c_{i+1,j+3}) \qquad (1)
\end{aligned}
$$

where

$A_{i,j}$ = sum of competitive effects on tree (i,j), and

$C_{i,j}$ = competitive ability of tree (i,j).

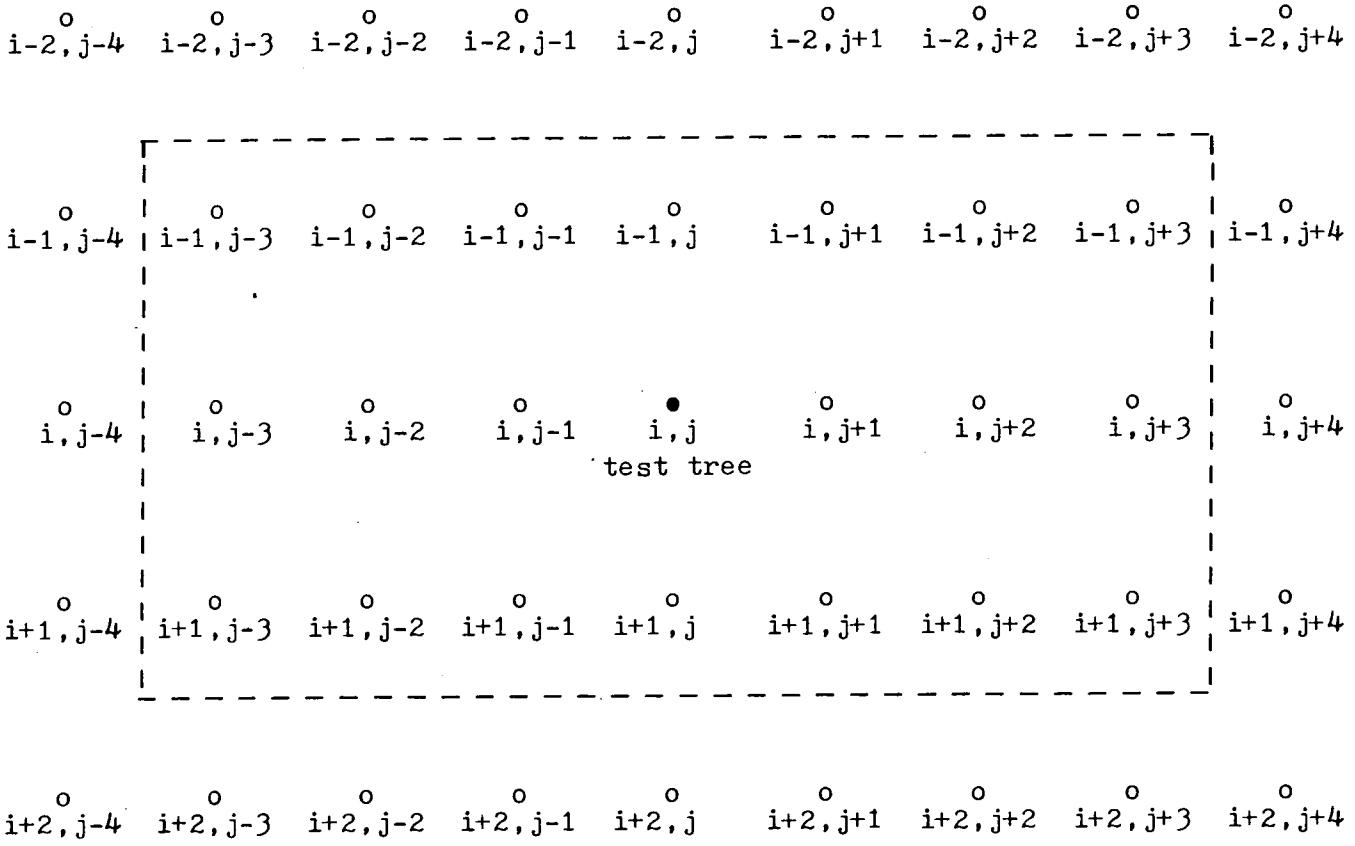


Figure 7. Position of trees in a plantation.

i = row position of test tree

j = column position of test tree

encloses effective competitors of test tree

It is then possible to approximate the sum of the competitive effects for any given tree by simply substituting for competitive ability in the above equation a measured characteristic that is sensitive to competition. For example, substituting DBH for competitive ability, equation (1) may be rewritten as follows.

$$
\begin{aligned}
A_{i,j} = {} & (d_{i,j} - d_{i-1,j-3}) + (d_{i,j} - d_{i-1,j-2}) + (d_{i,j} - d_{i-1,j-1}) \\
& + (d_{i,j} - d_{i-1,j}) + (d_{i,j} - d_{i-1,j+1}) + (d_{i,j} - d_{i-1,j+2}) \\
& + (d_{i,j} - d_{i-1,j+3}) + (d_{i,j} - d_{i,j-3}) + (d_{i,j} - d_{i,j-2}) \\
& + (d_{i,j} - d_{i,j-1}) + (d_{i,j} - d_{i,j+1}) + (d_{i,j} - d_{i,j+2}) \\
& + (d_{i,j} - d_{i,j+3}) + (d_{i,j} - d_{i+1,j-3}) + (d_{i,j} - d_{i+1,j-2}) \\
& + (d_{i,j} - d_{i+1,j-1}) + (d_{i,j} - d_{i+1,j}) + (d_{i,j} - d_{i+1,j+1}) \\
& + (d_{i,j} - d_{i+1,j+2}) + (d_{i,j} - d_{i+1,j+3}) \qquad (2)
\end{aligned}
$$

where

$A_{i,j}$ = sum of competitive effects on tree (i,j), and

$D_{i,j}$ = DBH of tree (i,j).

Applying this procedure to plantations of the type encountered in this study required additional adjustment. Figure 8 represents the arrangement of trees depicted in Figure 2 (p. 24) and Figure 3 (p. 25) in more detail. Five families, D, A, X, B, and C, are shown in this figure with individual trees arranged in a 1.22 x 2.44 meter (4 x 8 feet) spacing. The numbers refer to individual tree positions within family row plots.

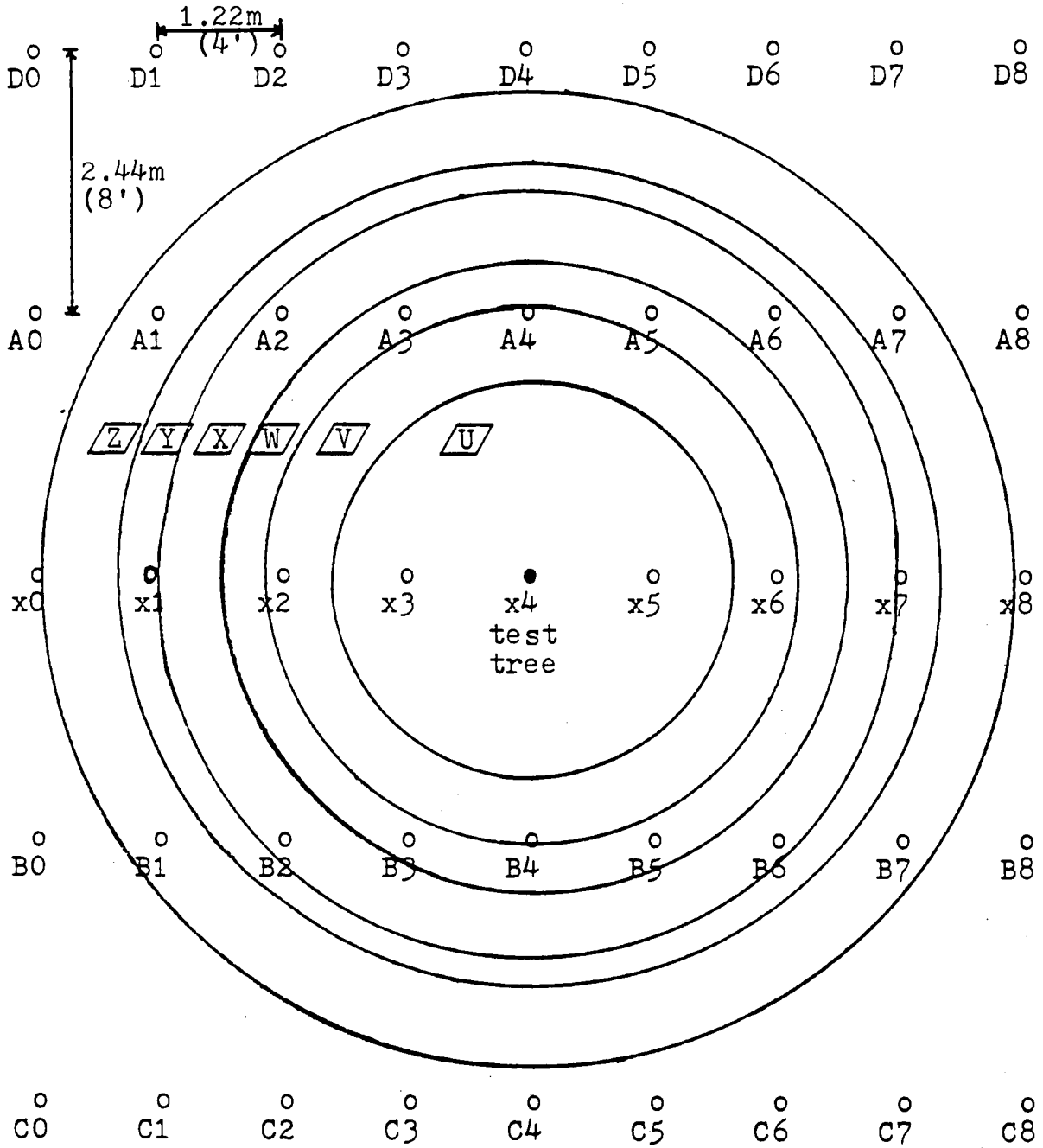


Figure 8. Position of trees in a simulated portion of a heritability study plantation.

Competitive Influence Zones are shown for test tree X4. Letters U through Z represent relative competitive-intensity coefficients associated with each zone.

Since all effective competitors were not spaced at an equal distance from the test tree, it was necessary to incorporate into the above expression some estimate of the effect of spacing on competition. This was done by including relative competitive-intensity coefficients derived from the spacing study in equation (2). Thus, based on Figure 8, a new expression of the following form was derived:

$$\begin{aligned} A_{x4} = {} & U(d_{x4} - d_{x3}) + U(d_{x4} - d_{x5}) \\ & + V(d_{x4} - d_{x2}) + V(d_{x4} - d_{x6}) + V(d_{x4} - d_{A4}) + V(d_{x4} - d_{B4}) \\ & + W(d_{x4} - d_{A3}) + W(d_{x4} - d_{A5}) + W(d_{x4} - d_{B3}) + W(d_{x4} - d_{B5}) \\ & + X(d_{x4} - d_{A2}) + X(d_{x4} - d_{A6}) + X(d_{x4} - d_{B2}) + X(d_{x4} - d_{B6}) \\ & + Y(d_{x4} - d_{X1}) + Y(d_{x4} - d_{X7}) \\ & + Z(d_{x4} - d_{A1}) + Z(d_{x4} - d_{A7}) + Z(d_{x4} - d_{B1}) + Z(d_{x4} - d_{B7}) \end{aligned}$$

or

$$\begin{aligned} A_{x4} = {} & U(2d_{x4} - d_{x3} - d_{x5}) \\ & + V(4d_{x4} - d_{x2} - d_{x6} - d_{A4} - d_{B4}) \\ & + W(4d_{x4} - d_{A3} - d_{A5} - d_{B3} - d_{B5}) \\ & + X(4d_{x4} - d_{A2} - d_{A6} - d_{B2} - d_{B6}) \\ & + Y(2d_{x4} - d_{x1} - d_{x7}) \\ & + Z(4d_{x4} - d_{A1} - d_{A7} - d_{B1} - d_{B7}) \end{aligned} \qquad (3)$$

where

A_{x4} = sum of competitive effects on tree x4,

d_{x4} = DBH of tree x4,

U = relative competitive-intensity coefficient of trees on 1.22 x 1.22 meter (4 x 4 feet) effective spacing,

V = relative competitive-intensity coefficient of trees on 2.44 x 2.44 meter (8 x 8 feet) effective spacing,

W = relative competitive-intensity coefficient of trees on 2.72 x 2.72 meter (8.94 x 8.94 feet) effective spacing,

X = relative competitive-intensity coefficient of trees on 3.45 x 3.45 meter (11.31 x 11.31 feet) effective spacing,

Y = relative competitive-intensity coefficient of trees on 3.66 x 3.66 meter (12 x 12 feet) effective spacing, and

Z = relative competitive-intensity coefficient of trees on 4.40 x 4.40 meter (14.42 x 14.42 feet) effective spacing.

The linear distances between trees used to compute effective spacings W, X, and Z were derived from Figure 8 using the Pythagorean theorem.

In the computation of sums of competitive effects, whenever a dead or missing effective competitor was encountered, its potential influence on the test tree under consideration was ignored. For example, if trees A4 and X2 were missing and tree B5 was dead (Figure 8) at the time of measurement, the sum of competitive effects on tree X4 would have been calculated as follows.

$$A_{x4} = U(2d_{x4} - d_{x3} - d_{x5}) + V(2d_{x4} - d_{x6} - d_{B4}) + W(3d_{x4} - d_{A3} - d_{A5} - d_{B3}) + X(4d_{x4} - d_{A2} - d_{A6} - d_{B2} - d_{B6}) + Y(2d_{x4} - d_{x1} - d_{x7}) + Z(4d_{x4} - d_{A1} - d_{A7} - d_{B1} - d_{B7})$$

From the sums of competitive effects, mean competitive effects were computed for each sampled tree.

$$\overline{A_{x4}} = \frac{A_{x4}}{N} \qquad (4)$$

where

$\overline{A_{x4}}$ = competitive fitness of tree x4 (based on DBH),

A_{x4} = sum of competitive effects on tree x4, and

N = number of surviving effective competitors of tree x4.

These mean competitive-effect values were used in the main analyses as measures of the competitive fitness or ability of the sampled trees.

The calculated $\overline{A_{ij}}$ value for a tree could be positive, negative, or zero. Thus, it exhibited an immediate indication of a tree's competitive fitness relative to its existing neighbors. This value was assumed to express the deviation of a given sample tree from the situation in which it and each of its neighbors are equal competitors. Subtracting this value from the measured characteristic value produced a

new value indicative of that tree's performance in the situation in which no competition is expressed.

$$D^*_{x4} = D_{x4} - \overline{A_{x4}} \tag{5}$$

where

D_{x4} = DBH of tree x4,

$\overline{A_{x4}}$ = competitive fitness of tree x4 (based on DBH), and

D^*_{x4} = DBH of tree x4 with no expressed competition (Dimension-Difference Index).

Distance-Ratio Index

Since intertree competition should express a functional relationship between tree size and effective growing space, it can be represented in units of either or both of these parameters. The distance-ratio index makes use of spacing by assuming that competitive fitness is reflected by the effective growing space utilized by a tree relative to its neighbors. To estimate the effective growing space utilized, the point of equal competitive influence between a given test tree and each of its competitors was determined and then the distances from the test tree to all such points were averaged to obtain a mean distance. This mean distance was assumed to represent the radius of a circular area of effective growing space surrounding the test tree. Mathematical derivation of this is shown below using DBH once again as the measured characteristic of interest.

$$P_j = \frac{d_o}{d_o + d_i} (D) \qquad (6)$$

where

P_j = point of equal competitive influence between test tree (o) and neighboring tree (i) expressed as a linear distance from the test tree (o),

d_o = DBH of test tree (o),

d_i = DBH of neighboring tree (i), and

D = distance between the two trees.

This formula is identical to that used by Pelz (1978) in calculating the area of the polygon which represents the area potentially available (APA) to a tree growing in a stand. Here, however, instead of a polygon, a circular area of effective growing space utilized, similar to the competition circles defined by Gerrard (1969), was derived for each tree in the following manner. First, equation (6) was expanded to include all interactions of neighboring trees with a given test tree.

$$R_o = \Sigma P_j \qquad \text{(general form)}$$

For test tree x4 in Figure 8 (p. 35), the expanded equation was:

$$R_{x4} = \frac{d_{x4}}{d_{x4} + d_{x3}} (1.22) + \frac{d_{x4}}{d_{x4} + d_{x5}} (1.22) + \frac{d_{x4}}{d_{x4} + d_{x2}} (2.44)$$

$$+ \frac{d_{x4}}{d_{x4} + d_{x6}} (2.44) + \frac{d_{x4}}{d_{x4} + d_{A4}} (2.44) + \frac{d_{x4}}{d_{x4} + d_{B4}} (2.44)$$

$$+ \frac{d_{x4}}{d_{x4} + d_{A3}} (2.72) + \frac{d_{x4}}{d_{x4} + d_{A5}} (2.72) + \frac{d_{x4}}{d_{x4} + d_{B3}} (2.72)$$

$$+ \frac{d_{x4}}{d_{x4} + d_{B5}} (2.72) + \frac{d_{x4}}{d_{x4} + d_{A2}} (3.45) + \frac{d_{x4}}{d_{x4} + d_{A6}} (3.45)$$

$$+ \frac{d_{x4}}{d_{x4} + d_{B2}} (3.45) \quad \frac{d_{x4}}{d_{x4} + d_{B6}} (3.45) + \frac{d_{x4}}{d_{x4} + d_{x1}} (3.66)$$

$$+ \frac{d_{x4}}{d_{x4} + d_{x7}} (3.66) \quad \frac{d_{x4}}{d_{x4} + d_{A1}} (4.40) + \frac{d_{x4}}{d_{x4} + d_{A7}} (4.40)$$

$$+ \frac{d_{x4}}{d_{x4} + d_{B1}} (4.40) \quad \frac{d_{x4}}{d_{x4} + d_{B7}} (4.40) \qquad (7)$$

Then a mean value was determined,

$$\overline{R_{x4}} = \frac{R_{x4}}{N} \qquad (8)$$

where

$\overline{R_{x4}}$ = radius of area of effective growing space utilized by tree x4,

R_{x4} = sum of distances to the point of equal competitive influence between the test tree (x4) and each effective competitor, and

N = number of effective competitors (20 in this case) of a given test tree (x4).

Missing or dead trees were treated in the same manner as described for the Dimension-Difference Index, and the number of neighboring trees to be included was once again determined from the spacing-study data. A circular area of effective growing space utilized was then computed for each sample tree as follows:

$$GS_o = \pi(\overline{R_o})^2 \qquad \text{(general form)} \tag{9}$$

or

$$GS_{x4} = \pi(\overline{R_{x4}})^2 \qquad \text{(for test tree x4)}$$

where

GS_{x4} = effective growing space utilized by tree x4.

To make the Distance-Ratio Index comparable to the Dimension-Difference Index for analytical purposes, the characteristic measured was regressed on growing space for all sampled trees. For example, using DBH of white pine, the linear regression of DBH on effective growing space utilized was derived (Figure 9).

The deviations of predicted values of measured characteristics from their overall means as determined by these regressions were taken to represent estimates of competitive fitness. A least-squares adjustment based on these regressions was then performed to obtain estimates of tree performance with no expressed competition as follows:

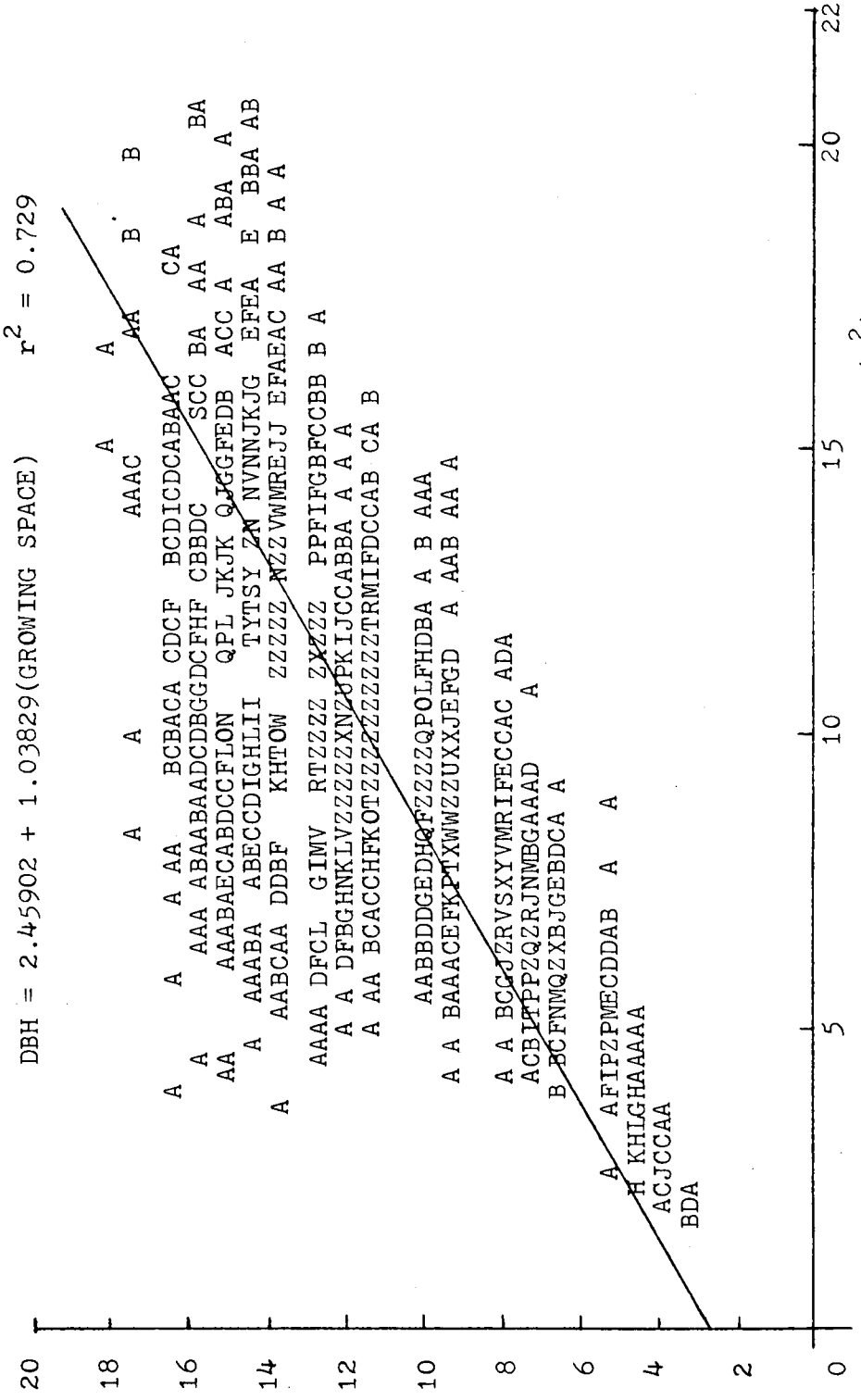


Figure 9. Regression of DBH on effective growing space utilized for white pine.

A = 1 obs., B = 2 obs., etc.

$$D^{**}_{x4} = D_{x4} - (\hat{D}_{x4} - \overline{D_i}) \quad (10)$$

where

D^{**}_{x4} = DBH of tree x4 with no expressed competition (Distance-Ratio Index),

D_{x4} = DBH of tree x4,

$\hat{D}_{x4}$ = predicted value of DBH for tree x4 from $\overline{R_{x4}}$ based upon linear regression of DBH on effective growing space utilized, and

$\overline{D_i}$ = mean DBH of all sampled trees.

Sampling

Every tree, including all trees spaced within 4.57 meters (15 feet) of the plantation edges, in the white pine heritability study was measured for all study characteristics. In the Virginia pine plantation, severe mechanical damage had been sustained in recent thinning efforts. Only four of the ten replications which had not been thinned were deemed suitable for analysis. Every tree in each of these four replications, including border trees spaced within 4.57 meters (15 feet) of the edges of the replication blocks, was measured for all study characteristics. Measurements were collected in the spring and early summer of 1981 when the white pine trees were 11 years of old and the Virginia pine trees were 14 years old.

Values for competitive fitness were computed for all trees using both the Dimension-Difference Index and the Distance-Ratio Index methods. Thus, each tree had five associated variables for each

measured characteristic; the measured value, two competitive-fitness estimates expressed in terms of that characteristic, and two estimates of that characteristic with no competition expressed.

In order to adhere to the implicit assumptions dictated by the Analysis of Variance (ANOVA) procedure, sampling of trees within the plantations to be evaluated was required. Specifically, the assumption of statistically independent observations was violated in the analysis of derived competitive-fitness estimates if no prior sampling was performed. Therefore, a sampling scheme was devised to select trees according to the following criteria in the Virginia pine and white pine plantations.

1. Every family plot in every replication was considered (border trees were excluded).

2. If a family plot (originally containing ten trees) had more than four surviving trees at the time of measurement, a sample of four of these was randomly selected for inclusion in statistical analyses.

3. If a family plot contained exactly four trees, this family plot was included in the analyses.

4. If a family plot contained fewer than four trees, this family plot was omitted from further consideration.

As a result of mortality, this scheme resulted in a random sample of slightly less than 40 percent of the entire white pine plantation and the four usable replications of Virginia pine. Unbalanced samples of 1,820 trees in the Virginia pine and 4,196 trees in the white pine, each representing 128 families, were selected.

Statistical Analyses

The primary instrument utilized in the analysis of intertree competition is the ANOVA model presented in Table 3. This univariate model separates the total variance of a measured characteristic into individual source components representative of the genetic and environmental influences operating within the study plantation. The environmental contribution to the total variance is estimated by the replications source and the genetic contributions are estimated by the stands and families-within-stand sources. Estimates of interactions between genetic and environmental factors are provided by the replications x stands and replications x families-within-stands sources; the within plot source of variation provides an error term useful in testing the contributions of the other source components.

Each of the five variables associated with each of the seven characteristics measured in both the white pine and Virginia pine plantations were analyzed in univariate fashion using the ANOVA model described above. From these, determinations were made as to whether competitive fitness exhibited a large enough response to be detected in the genetic sources of variation. The hypotheses tested in these analyses expressed as questions were as follows.

1. Do tree dimensions, including deviational responses due to intertree competition, differ among stands and/or among families within stand?

Table 3. Model for Analysis of Variance in Progeny Plantations

Source of variation	df	Expected mean squares
Replications	R-1	$\sigma^2_W + W\sigma^2_{RXF(S)} + WF\sigma^2_{RXS} + WSF\sigma^2_R$
Stands	S-1	$\sigma^2_W + W\sigma^2_{RXF(S)} + WR\sigma^2_{F(S)} + WF\sigma^2_{RXS} + WRF\sigma^2_S$
Replications x stands	(R-1)(S-1)	$\sigma^2_W + W\sigma^2_{RXF(S)} + WF\sigma^2_{RXS}$
Families in stands	(F-1)S	$\sigma^2_W + W\sigma^2_{RXF(S)} + WR\sigma^2_{F(S)}$
Replications x families in stands	(R-1)(F-1)S	$\sigma^2_W + W\sigma^2_{RXF(S)}$
Within plot	(W-1)RFS	σ^2_W

R = number of replications.

S = number of stands.

F = number of families within stands.

W = number of trees per plot.

σ^2_W = within plot variance component.

$\sigma^2_{RXF(S)}$ = component of variance due to interaction of replications with families within stands.

$\sigma^2_{F(S)}$ = component of variance among families within stands.

σ^2_{RXS} = component of variance due to interaction of replications with stands.

σ^2_S = component of variance among stands.

σ^2_R = component of variance among replications.

2. Does expressed competitive fitness (estimated by either the Dimension-Difference Index or the Distance-Ratio Index) differ among stands and/or among families within stand?
3. Do tree dimensions adjusted for competition (by either the Dimension-Difference Index or the Distance-Ratio Index) differ among stands and/or among families within stand?

Estimates of the variance components, the percentage of total variance made up by each component, and narrow-sense heritability also were computed. Narrow-sense heritability of each variable was estimated according to the following half-sib progeny formula presented by Evans (1971).

$$h^2 = \frac{4S^2_{f(S)}}{S^2_{f(S)} + S^2_{rxf(S)} + S^2_w} \qquad (11)$$

where

h^2 = narrow-sense heritability estimated from half-sib progeny,

$S^2_{f(S)}$ = estimated variance due to among-family differences,

$S^2_{rxf(S)}$ = estimated variance due to interactions among families and replications, and

S^2_w = estimated variance within family row plots.

Expected gains in the next generation also were computed for each variable by two methods assuming a selection intensity of 25 percent at both the individual and family levels. The equation for computing gains from single-tree selection alone is given below (Wright, 1976).

$$G_A = \sigma i h^2$$

where

G_A = expected gain from single-tree selection,

σ = the standard deviation of the population,

i = selection intensity expressed in standard deviations, and

h^2 = estimated narrow-sense heritability.

Gains from combined single tree and family selection were computed according to the following formula reported by Namkoong et al. (1965).

$$G_B = i_A \frac{\sigma^2_{F(S)}}{\sigma_1} + i_B \frac{3\sigma^2_{F(S)}}{\sigma_2}$$

where

G_B = expected gain from combined single tree and family selection,

i_A = family selection intensity,

i_B = within-family selection intensity,

$$\sigma_1^2 = \frac{\sigma^2_W}{nR} + \frac{\sigma^2_{RXF(S)}}{R} + \sigma^2_{F(S)} \text{ ,}$$

$$\sigma_2^2 = \sigma^2_W + \sigma^2_{RXF(S)} \text{ ,}$$

n = number of individuals within a plot, and

R, σ^2_W, $\sigma^2_{F(S)}$, and $\sigma^2_{RXF(S)}$ are as defined (Table 3).

Multivariate comparisons were then made among combinations of variables associated with each measured characteristic. These comparisons provided answers to two questions:

1. Do the results determined by univariate analyses of measured tree dimensions change significantly when these dimensions are adjusted for intertree competitive influences?
2. Does the Dimension-Difference Index differ from the Distance-Ratio Index in the determination of estimated intertree competitive influence?

Three different analytical procedures were used to test statistical hypotheses relating to the above questions.

1. Pearson Product-Moment Correlations. Of interest here was the degree of association exhibited by members of pairs of variables. For example, does the DBH in white pine grown under competition correlate highly with estimates of DBH of the same trees adjusted for competition? Similarly, does the competitive fitness of these same trees expressed as deviations in DBH and computed by the Dimension-Difference Index correlate highly with estimates of competitive fitness computed by the Distance-Ratio Index?

2. Multiple Regressions. When two variables of interest whose means have been centered on zero are regressed against a third variable with which each is highly correlated, it is possible to determine the relative contributions of each to the total variance expressed. Stated another way, the addition of a second independent variable to a regression model may or may not significantly alter the position of the best fitting regression line due to the additional variance contributed. The relative contributions of each independent variable to the variance expressed in such regressions may be determined by examining the Type IV

Sums of Squares of deviations. Regression models of the following type were examined in these comparisons.

$$Y = a + b_1X_1 + b_2X_2$$

where

Y = dependent variable,

a = Y intercept,

X_1 and X_2 = independent variables, and

b_1 and b_2 = regression coefficients associated with X_1 and X_2.

Table 4 contains the variables substituted for X_1, X_2 and Y in making the desired comparisons.

Tests of slope differences were made to compare the linear regressions derived from the spacing study data and those derived from the progeny plantations using the Distance-Ratio Index method. The methodology used was that for subhypothesis testing of slope difference in covariance analysis (ANCOVA). The linear model assumed was:

$$Y_{ijk} = \mu + A_i + B_j + (AB)_{ij} + \varepsilon_{ijk}$$

where

Y_{ijk} = size of the kth tree exposed to the ith level of treatment A and the jth level of treatment B,

μ = mean of dimension measured,

A_i = spacing level (i = 1, 2, ..., n),

Table 4. Variables Compared in Multiple Regressions to Test if Variances Are Altered by Removal of Competitve Effects or by the Type of Index Used to Determine These Effects

Y	X_1	X_2
$D\text{-}COMP_2$	DBH	$D\text{-}WOUT_1$
$H\text{-}COMP_2$	HEIGHT	$H\text{-}WOUT_1$
$C\text{-}COMP_2$	CROWN	$C\text{-}WOUT_1$
$B\text{-}COMP_2$	BA	$B\text{-}WOUT_1$
$CA\text{-}COMP_2$	CA	$CA\text{-}WOUT_1$
$V\text{-}COMP_2$	VOLUME	$V\text{-}WOUT_1$
$T\text{-}COMP_2$	TREESIZE	$T\text{-}WOUT_1$
$D\text{-}COMP_1$	DBH	$D\text{-}WOUT_2$
$H\text{-}COMP_1$	HEIGHT	$H\text{-}WOUT_2$
$C\text{-}COMP_1$	CROWN	$C\text{-}WOUT_2$
$B\text{-}COMP_1$	BA	$B\text{-}WOUT_2$
$CA\text{-}COMP_1$	CA	$CA\text{-}WOUT_2$
$V\text{-}COMP_1$	VOLUME	$V\text{-}WOUT_2$
$T\text{-}COMP_1$	TREESIZE	$T\text{-}WOUT_2$
TREESIZE	$D\text{-}COMP_1$	$D\text{-}COMP_2$
TREESIZE	$H\text{-}COMP_1$	$H\text{-}COMP_2$
TREESIZE	$C\text{-}COMP_1$	$C\text{-}COMP_2$
TREESIZE	$B\text{-}COMP_1$	$B\text{-}COMP_2$
TREESIZE	$CA\text{-}COMP_1$	$CA\text{-}COMP_2$
TREESIZE	$V\text{-}COMP_1$	$V\text{-}COMP_2$
TREESIZE	$T\text{-}COMP_1$	$T\text{-}COMP_2$

Table 4 (continued)

Y	X_1	X_2
TREESIZE	$D\text{-}WOUT_1$	$D\text{-}WOUT_2$
TREESIZE	$H\text{-}WOUT_1$	$H\text{-}WOUT_2$
TREESIZE	$C\text{-}WOUT_1$	$C\text{-}WOUT_2$
TREESIZE	$B\text{-}WOUT_1$	$B\text{-}WOUT_2$
TREESIZE	$CA\text{-}WOUT_1$	$CA\text{-}WOUT_2$
TREESIZE	$V\text{-}WOUT_1$	$V\text{-}WOUT_2$
TREESIZE	$T\text{-}WOUT_1$	$T\text{-}WOUT_2$

CROWN = crown diameter.

BA = basal area.

CA = crown area.

TREESIZE = derived factor.

D-COMP = competitive fitness based on DBH.

H-COMP = competitive fitness based on height.

C-COMP = competitive fitness based on crown diameter.

B-COMP = competitive fitness based on basal area.

CA-COMP = competitive fitness based on crown area.

V-COMP = competitive fitness based on volume.

T-COMP = competitive fitness based on TREESIZE.

D-WOUT = DBH without competition.

H-WOUT = height without competition.

C-WOUT = crown diameter without competition.

B-WOUT = basal area without competition.

CA-WOUT = crown area without competition.

V-WOUT = volume without competition.

T-WOUT = TREESIZE without competition.

Subscript 1 = Dimension-Difference Index.

Subscript 2 = Distance-Ratio Index.

B_j = plantation classification [(1) progeny test or (2) spacing study],

$(AB)_{ij}$ = interaction of spacing and plantation, and

ε_{ijk} = random error associated with the kth tree.

Of interest here was the relative contribution of interaction. If it was significant, the slopes of the regressions of dimension on spacing differed between the two plantations. Such differences, when they occurred, provided additional evidence that competitive-fitness estimates derived from the two different indices differed.

3. Spearman Rank Correlations. Perhaps most important to the tree breeder is some indication of how important intertree competition is to the expressed distribution of variance components since this distribution is of ultimate importance in estimation of heritabilities. In this study, components of variance of each characteristic measured were ranked in descending order according to size. Spearman rank correlation was then used to determine whether or not association existed between members of pairs of variables. Ranked variance component distributions of tree dimensions with and without competitive interactions were compared as were those of competitive-fitness estimates derived by the two indices.

Evaluation should include the effects of competition on the distributions of means by stand and by family-within-stand classifications. Spearman rank correlations between members of pairs of variables were therefore computed to determine if association was evident between

distributions of means by stand and family classifications when these were ranked according to size. The comparisons of interest were again the distributions associated with variables including and excluding competitional deviations and between distributions of competitive-fitness variables derived by the two indices.

CHAPTER IV

RESULTS

Preliminary Study

A preliminary investigation of white pine and Virginia pine growing in a Species-Spacing Comparison Study was performed to determine the levels of competitive influence likely to be encountered by trees growing in the progeny test plantations evaluated in the main study. A key to symbols used as abbreviations for the measured and derived characteristics in the tabulation of results is provided for reference (page xi).

Coefficients of correlation between members of pairs of characteristics measured on trees in the spacing study plantation were calculated (Table 5). Similar relationships were evident in both species. Height showed the least amount of association with the other characteristics considered. Groupings of high relationship were evident among the characteristics of DBH, BA, and volume. The derived factor, TREESIZE, was highly correlated with all characteristics except height in both species and volume in Virginia pine.

With the exception of height in Virginia pine, all characteristics were significantly greater in magnitude for trees planted at the widest spacing of 20.9 square meters (225 sq. ft.) than for trees at all other closer spacings (Table 6), and were positively related to spacing (Table 7). In white pine, tree height was the least sensitive of the

Table 5. Coefficients of Correlation of Characteristics Measured and Derived in the Spacing Study

			Virginia Pine (N = 312)				
DBH	1.000						
HEIGHT	0.469	1.000					
CROWN	0.771	0.221	1.000				
BA		0.447	0.766	1.000			
CA	0.752	0.217		0.760	1.000		
VOLUME	0.951	0.623	0.714	0.968	0.713	1.000	
TREESIZE	0.812	0.650	0.963	0.820	0.960	0.725	1.000
	DBH	HEIGHT	CROWN	BA	CA	VOLUME	TREESIZE
			White Pine (N = 400)				
DBH	1.000						
HEIGHT	0.744	1.000					
CROWN	0.870	0.577	1.000				
BA		0.692	0.863	1.000			
CA	0.844	0.541		0.865	1.000		
VOLUME	0.953	0.755	0.830	0.983	0.843	1.000	
TREESIZE	0.975	0.765	0.928	0.976	0.920	0.970	1.000
	DBH	HEIGHT	CROWN	BA	CA	VOLUME	TREESIZE

Table 6. Means by Spacing and Results of Duncan's New Multiple Range Test (alpha = .05) for Characteristics in the Spacing Study

Spacing (m^2)	Spacing (sq. ft.)	N	DBH (cm)	HEIGHT (m)	CROWN (m)	BA (m^2)	CA (m^2)	VOLUME (m^3)
				Virginia Pine				
3.34	(36)	84	11.87A[a]	8.92A	3.11A	0.012A	8.17A	0.043A
7.53	(81)	98	14.20B	8.90A	4.15B	0.017B	14.08B	0.061B
13.38	(144)	71	16.86C	8.85A	4.94C	0.023C	19.82C	0.084C
20.90	(225)	59	17.97D	8.81A	5.73D	0.026D	21.14D	0.095D
				White Pine				
3.34	(36)	100	12.72A	9.20A	2.67A	0.014A	6.03A	0.070A
7.53	(81)	100	14.93B	9.30A	3.56B	0.019B	10.85B	0.095B
13.38	(144)	100	15.73B	9.33A	4.17C	0.021B	14.52C	0.106B
20.90	(225)	100	18.75C	9.86B	4.95D	0.030C	20.14D	0.155C

[a]Values with the same postscripted letter are not significantly different at the 0.05 level.

Table 7. Linear Regression Equations, Tests of Significance of Intercepts and Slope Coefficients, and Correlation Coefficients in Regressions of Measured and Derived Characteristics on Spacing in the Spacing Study Plantation

Equation	T for Ho: Intercept=0	T for Ho: Slope=0	r^2
	Virginia Pine (N = 312)		
DBH (cm) = 11.2463 + 0.3552 (SPACING (m^2))	35.47**	13.45**	0.368
HEIGHT (m) = 8.9449 - 0.0065 (SPACING (m^2))	67.38**	-0.60	0.001
CROWN (m) = 2.8495 + 0.1464 (SPACING (m^2))	30.24**	18.60**	0.527
BA (m^2) = 0.0098 + 0.00086 (SPACING (m^2))	13.70**	14.20**	0.394
CA (m^2) = 5.6822 + 1.0129 (SPACING (m^2))	9.03**	19.31**	0.546
VOLUME (m^3) = 0.0366 + 0.0032 (SPACING (m^2))	11.37**	11.26**	0.290
TREESIZE = 1.2885 + 0.1259 (SPACING (m^2))	19.00**	22.24**	0.614

Table 7 (continued)

Equation	T for Ho: Intercept=0	T for Ho: Slope=0	r^2
	White Pine (N = 400)		
DBH (cm) = 11.9040 + 0.3214 (SPACING (m^2))	25.41**	8.97**	0.168
HEIGHT (m) = 9.0409 + 0.0334 (SPACING (m^2))	52.81**	2.56*	0.016
CROWN (m) = 2.4298 + 0.1249 (SPACING (m^2))	24.61**	16.53**	0.407
BA (m^2) = 0.0117 + 0.00086 (SPACING (m^2))	10.28**	9.59**	0.187
CA (m^2) = 4.1087 + 0.7772 (SPACING (m^2))	6.62**	16.36**	0.402
VOLUME (m^3) = 0.0551 + 0.0043 (SPACING (m^2))	8.11**	8.80**	0.162
TREESIZE = 0.8273 + 0.0732 (SPACING (m^2))	9.53**	11.04**	0.234

*Significant at 0.05 level.

**Significant at 0.01 level.

characteristics analyzed to changes in spacing levels, yet it was evidently influenced by spacing to a significant degree.

The relative competitive-intensity coefficients, derived for each characteristic in both pine species (Table 8), represented the relative decrease in competitive influence which an average tree encounters with its neighbors as the effective spacing of these trees increases.

Main Study

The main focus of this investigation concerned the analysis of intertree competition and its effects on evaluation of stand and family performance in the White Pine and Virginia Pine Heritability Study plantations. Correlation coefficients were derived between members of pairs of characteristics measured and derived for all sampled trees (Table 9). Each species was analyzed separately.

Patterns of relationships similar to those found for each species in the Species-Spacing Comparison Study were observed. In both species, height generally showed the least amount of association with the other characteristics measured. Groupings of high relationship among DBH, BA, and volume were observed. With the exception of height in both species, TREESIZE correlated highly with all other characteristics.

Although statistical tests of comparison were not performed, overall means of all dimensional characteristics of both species appeared to be of greater magnitude in the spacing study than in the progeny tests (Table 10). This was, for the most part, due to age differences between plantations. Trees in the spacing study were

Table 8. Relative Competitive-Intensity Coefficients[a] of Seven Characteristics

m	SPACING (ft^2)	DBH	HEIGHT	CROWN	BA	CA	VOLUME	TREESIZE
				Virginia Pine				
0	(0)	1.000	1.000	1.000	1.000	1.000	1.000	1.000
1.49	(16)	0.972	1.000	0.963	0.954	0.944	0.954	0.952
5.95	(64)	0.887	1.000	0.853	0.816	0.776	0.816	0.809
7.43	(80)	0.859	1.000	0.816	0.770	0.720	0.770	0.761
11.89	(128)	0.774	1.000	0.705	0.632	0.551	0.631	0.618
13.38	(144)	0.745	1.000	0.669	0.586	0.495	0.585	0.570
19.32	(208)	0.632	1.000	0.521	0.401	0.271	0.401	0.379
				White Pine				
0	(0)	1.000	1.000	1.000	1.000	1.000	1.000	1.000
1.49	(16)	0.974	0.995	0.963	0.957	0.943	0.956	0.954
5.95	(64)	0.897	0.980	0.853	0.828	0.773	0.824	0.815
7.43	(80)	0.872	0.975	0.816	0.785	0.716	0.780	0.769
11.89	(128)	0.795	0.959	0.705	0.655	0.546	0.647	0.631
13.38	(144)	0.769	0.954	0.669	0.612	0.489	0.603	0.585
19.32	(208)	0.666	0.934	0.521	0.440	0.262	0.427	0.400

[a]These values represent the relative decrease in competitive influence which an average tree encounters with its neighbors as the effective spacing of these trees increases.

Table 9. Coefficients of Correlation of Characteristics Measured and Derived in the Heritability Study Plantations

			Virginia Pine (N = 1820)				
DBH	1.000						
HEIGHT	0.269	1.000					
CROWN	0.820	0.628	1.000				
BA		0.619	0.807	1.000			
CA	0.825	0.620		0.825	1.000		
VOLUME	0.973	0.711	0.810	0.988	0.833	1.000	
TREESIZE	0.964	0.708	0.924	0.966	0.935	0.972	1.000
	DBH	HEIGHT	CROWN	BA	CA	VOLUME	TREESIZE
			White Pine (N = 4196)				
DBH	1.000						
HEIGHT	0.723	1.000					
CROWN	0.813	0.739	1.000				
BA		0.680	0.768	1.000			
CA	0.797	0.716		0.780	1.000		
VOLUME	0.938	0.788	0.769	0.967	0.795	1.000	
TREESIZE	0.958	0.817	0.909	0.952	0.915	0.961	1.000
	DBH	HEIGHT	CROWN	BA	CA	VOLUME	TREESIZE

Table 10. Means of Measured Characteristics

	A	B	C	D
DBH (cm)	14.891	11.304	15.533	10.437
HEIGHT (m)	8.877	7.983	9.419	6.173
CROWN (m)	4.347	4.086	3.839	3.799
BA (m^2)	0.018	0.010	0.021	0.009
CA (m^2)	16.075	13.867	12.882	12.402
VOLUME (m^3)	0.068	0.034	0.107	0.032

A = Virginia Pine in Spacing Study (N = 312).

B = Virginia Pine Heritability Study (N = 1820).

C = White Pine in Spacing Study (N = 400).

D = White Pine Heritability Study (N = 4196).

fifteen years old at the time of measurement, while the Virginia pine and white pine heritability studies were fourteen and eleven years old, respectively.

All characteristics in both white and Virginia pine displayed significant positive relationships with effective growing space utilized as computed by the Distance-Ratio Index method (Table 11). Deviations of predicted values on these regression lines from the overall means represented Distance-Ratio Index competitive fitness estimates for trees analyzed.

Significant differences at the .01 level were found among stands in all characteristics in both species (Tables 12 and 13). Similarly, when competitional deviations computed by either the Dimension-Difference Index (DDI) or the Distance-Ratio Index (DRI) were adjusted for, there were significant differences (α = .01) among stands in all characteristics.

In Virginia pine (Table 12), DDI and DRI competitive-fitness values based on DBH, basal area, volume and TREESIZE differed among stands at the .01 significance level. DDI competitive-fitness values based on crown diameter and crown area also differed among stands at the .01 level in Virginia pine, whereas, DRI competitive fitness based on crown area differed at the .05 level, and no significant difference among stands was observed in DRI competitive fitness based on crown diameter. Both DDI and DRI competitive-fitness values based on height in Virginia pine were found to significantly differ among stands (.05 level).

Table 11. Linear Regression Equations, Tests of Significance of Intercepts and Slope Coefficients, and Correlation Coefficients in Regressions of Characteristics on Effective Growing Space Utilized

Equation	T for Ho: Intercept=0	T for Ho: Slope=0	r^2
Virginia Pine Heritability Study (N = 1820)			
DBH (cm) = 3.9075 + 0.9795 (SPACING (m^2))	30.29**	59.26**	0.658
HEIGHT (m) = 5.4686 + 0.3348 (SPACING (m^2))	58.01**	27.00**	0.286
CROWN (m) = 1.3091 + 0.3649 (SPACING (m^2))	27.91**	61.65**	0.676
BA (m^2) = 0.0016 + 0.0011 (SPACING (m^2))	12.35**	77.10**	0.765
CA (m^2) = 2.0747 + 1.4876 (SPACING (m^2))	11.85**	74.15**	0.751
VOLUME (m^3) = 0.0034 + 0.0043 (SPACING (m^2))	7.81**	77.40**	0.767
TREESIZE = 0.2224 + 0.1173 (SPACING (m^2))	5.53**	40.39**	0.472

Table 11 (continued)

Equation	T for Ho: Intercept=0	T for Ho: Slope=0	r^2
White Pine Heritability Study (N = 4196)			
DBH (cm) = 2.4590 + 1.0383 (SPACING (m^2))	30.82**	106.10**	0.728
HEIGHT (m) = 1.9524 + 0.5630 (SPACING (m^2))	32.53**	72.54**	0.556
CROWN (m) = 0.9572 + 0.3692 (SPACING (m^2))	31.93**	100.28**	0.705
BA (m^2) = 0.0009 + 0.0011 (SPACING (m^2))	10.30**	111.63**	0.748
CA (m^2) = 1.6399 + 1.3218 (SPACING (m^2))	14.01**	103.03**	0.716
VOLUME (m^3) = 0.0012 + 0.0032 (SPACING (m^2))	3.61**	104.26**	0.721
TREESIZE = 0.4594 + 0.0958 (SPACING (m^2))	17.70**	52.90**	0.400

**Significant at 0.01 level.

Table 12. Mean Squares and Degrees of Freedom in Analysis of Variance of Virginia Pine Characteristics

	Source					
	R	S	RXS	F(S)	RXF(S)	W
	df = 3	df = 11	df = 33	df = 116	df = 291	df = 1365
DBH	48.619**	27.301**	6.980	6.716	0.000	5.461
$D\text{-}COMP_1$	1.107	12.617**	3.215	3.665	0.000	4.189
$D\text{-}COMP_2$	9.208	7.666**	3.683	3.716	0.000	3.759
$D\text{-}WOUT_1$	58.618**	5.287**	2.333**	1.876**	0.234	0.266
$D\text{-}WOUT_2$	73.692**	12.986**	4.792**	3.876**	0.263	1.297
HEIGHT	14.228**	1.914**	0.730*	0.920**	0.046	0.433
$H\text{-}COMP_1$	0.101	1.104*	0.535	0.626	0.000	0.507
$H\text{-}COMP_2$	0.798**	0.265*	0.185	0.201**	0.005	0.145
$H\text{-}WOUT_1$	12.601**	0.339**	0.279**	0.255**	0.042**	0.027
$H\text{-}WOUT_2$	15.339**	2.041**	0.678**	0.669**	0.054	0.272
CROWN	1.190	3.707**	1.328*	1.250**	0.045	0.868
$C\text{-}COMP_1$	0.122	1.581**	0.496	0.584	0.000	0.566
$C\text{-}COMP_2$	1.653*	0.930	0.682	0.729	0.012	0.626
$C\text{-}WOUT_1$	1.046**	0.729**	0.540**	0.386**	0.060	0.064
$C\text{-}WOUT_2$	0.136	1.813**	1.015**	0.671**	0.068	0.196
BA $(x10^{-4})$	1.733**	0.945**	0.252	0.221	0.000	0.184
$B\text{-}COMP_1$ $(x10^{-4})$	0.033	0.300**	0.079	0.084	0.000	0.102
$B\text{-}COMP_2$ $(x10^{-4})$	0.200	0.364**	0.130	0.057	0.000	0.015

Table 12 (continued)

	Source					
	R	S	RXS	F(S)	RXF(S)	W
	df = 3	df = 11	df = 33	df = 116	df = 291	df = 1365
B-WOUT$_1$ (x10^{-4})	2.033**	0.255**	0.091**	0.029**	0.008	0.018
B-WOUT$_2$ (x10^{-4})	2.333**	0.282**	0.133**	0.038**	0.008	0.027
CA	93.946**	156.733**	61.980**	50.849**	1.874	35.251
CA-COMP$_1$	2.165	41.800**	13.917	15.474	0.000	15.847
CA-COMP$_2$	47.118	56.898*	30.608	33.875	0.294	28.636
CA-WOUT$_1$	95.244**	45.881**	28.024**	18.601**	2.502	5.156
CA-WOUT$_2$	21.370**	48.193**	38.648**	22.784**	2.585	5.484
VOLUME (x10^{-3})	3.523**	1.360**	0.376	0.129	0.000	0.258
V-COMP$_1$ (x10^{-3})	0.030	0.418**	0.117	0.496**	0.093	0.043
V-COMP$_2$ (x10^{-3})	0.273	0.521**	0.182	2.136**	0.000	0.215
V-WOUT$_1$ (x10^{-3})	3.837**	0.381**	0.141**	0.042**	0.011	0.025
V-WOUT$_2$ (x10^{-3})	3.943**	0.382**	0.192**	0.485**	0.011	0.038
TREESIZE	1.699**	1.226**	0.358	0.317*	0.000	0.250
T-COMP$_1$	2.313**	0.614**	0.271**	0.206**	0.010	0.136
T-COMP$_2$	3.030**	0.580**	0.344**	0.274**	0.030	0.073
T-WOUT$_1$	0.984**	0.211**	0.110**	0.092**	0.008	0.028
T-WOUT$_2$	2.604**	0.446**	0.282**	0.263**	0.018	0.105

Table 12 (continued)

*Significant at 0.05 level.

**Significant at 0.01 level.

R = Replications.

S = Stands.

F(S) = Families within Stand.

W = Within Plot.

RXS = Replication-by-Stand interaction.

RXF(S) = Replication-by-Families-within-Stand interaction.

Table 13. Mean Squares and Degrees of Freedom in Analysis of Variance of White Pine Characteristics

	Source					
	R	S	RXS	F(S)	RXF(S)	W
	df = 9	df = 12	df = 108	df = 115	df = 804	df = 3147
DBH	163.79**	327.16**	10.46	29.71**	0.27	8.55
$D\text{-}COMP_1$	3.33	142.27**	8.83*	16.11**	0.08	6.84
$D\text{-}COMP_2$	3.35	123.34**	9.53**	16.62**	0.32	6.93
$D\text{-}WOUT_1$	157.24**	41.65**	2.08**	4.65**	0.47**	0.37
$D\text{-}WOUT_2$	206.92**	63.97**	2.75**	6.46**	0.62	1.43
HEIGHT	97.02**	77.90**	2.65**	6.84**	0.20	1.16
$H\text{-}COMP_1$	1.59	38.32**	2.50**	4.85**	0.11	1.24
$H\text{-}COMP_2$	0.98	17.07**	1.57**	3.10**	0.09	0.92
$H\text{-}WOUT_1$	89.77**	7.73**	0.90**	1.09**	0.20**	0.07
$H\text{-}WOUT_2$	95.14**	26.13**	1.07**	1.97**	0.21	0.33
CROWN	31.37**	32.80**	1.39*	3.49**	0.08	1.02
$C\text{-}COMP_1$	0.69	11.56**	0.88*	1.53**	0.02	0.66
$C\text{-}COMP_2$	0.76	12.41**	1.18**	1.83**	0.06	0.82
$C\text{-}WOUT_1$	32.25**	5.71**	0.36**	0.72**	0.07	0.07
$C\text{-}WOUT_2$	34.87**	6.59**	0.44**	0.80**	0.09	0.18
BA $(x10^{-5})$	45.22**	75.17**	2.66	7.17**	0.07	2.24
$B\text{-}COMP_1$ $(x10^{-5})$	0.78	48.42**	2.97	5.44**	0.04	2.39
$B\text{-}COMP_2$ $(x10^{-5})$	0.67	35.75**	2.57**	4.57**	0.09	1.81

Table 13 (continued)

	Source					
	R	S	RXS	F(S)	RXF(S)	W
	df = 9	df = 12	df = 108	df = 115	df = 804	df = 3147
B-WOUT$_1$ (x10^{-5})	44.11**	4.00**	0.60**	0.87**	0.13**	0.08
B-WOUT$_2$ (x10^{-5})	53.56**	10.42**	0.80**	1.40**	0.16	0.34
CA	1033.33**	914.88**	45.50**	104.05**	2.68	31.03
CA-COMP$_1$	9.40	203.51**	18.28*	28.62**	0.34	13.74
CA-COMP$_2$	22.37	425.46**	40.61**	60.59**	2.40	24.49
CA-WOUT$_1$	1044.57**	262.00**	14.12**	31.56**	2.20	4.49
CA-WOUT$_2$	1186.80**	131.88**	14.67**	21.58**	2.78	5.13
VOLUME (x10^{-4})	98.22**	135.63**	4.50*	12.24**	0.14	3.58
V-COMP$_1$ (x10^{-4})	0.68	39.11**	2.61*	4.69**	0.02	2.08
V-COMP$_2$ (x10^{-4})	1.09	63.08**	4.24**	8.04**	0.19	2.80
V-WOUT$_1$ (x10^{-4})	96.07**	30.28**	0.97**	2.72**	0.18	0.31
V-WOUT$_2$ (x10^{-4})	106.77**	19.26**	1.59**	2.52**	0.25	0.65
TREESIZE	8.25**	14.55**	0.46*	1.31**	0.02	0.35
T-COMP$_1$	4.62**	4.18**	0.37**	0.61**	0.03	0.20
T-COMP$_2$	9.53**	1.41**	0.42**	0.42**	0.06	0.08
T-WOUT$_1$	6.32**	3.37**	0.13**	0.27**	0.02	0.03
T-WOUT$_2$	13.46**	7.34**	0.40**	0.73**	0.03	0.17

Table 13 (continued)

*Significant at 0.05 level.

**Significant at 0.01 level.

R = Replications.

S = Stands.

F(S) = Families within Stand.

W = Within Plot.

RXS = Replication-by-Stand interaction.

RXF(S) = Replication-by-Families-within-Stand interaction.

In white pine (Table 13), all DDI and DRI competitive-fitness values for all characteristics exhibited significant differences among stands (.01 level). Means by stand and by family within stand were computed for both white pine and Virginia pine (Appendix C).

Differences significant at the .01 level among families within stands were observed in height, crown diameter, and crown area in Virginia pine (Table 12) and in all characteristics in white pine (Table 13). TREESIZE in Virginia pine (Table 12) differed among families at the .05 level of significance, but the characteristics of DBH, basal area, and volume displayed no significant family differences. DDI and DRI competitive-fitness values based on volume and TREESIZE and DRI competitive fitness based on height differed among families at the .01 level in Virginia pine. No other differences among families in competitive-fitness estimates in Virginia pine were observed.

In white pine (Table 13), all competitive-fitness estimates (DDI and DRI) based on characteristics measured differed significantly ($\alpha = .01$) among families within stands. When competitional deviations computed by the DDI and DRI methods were adjusted for, significant differences ($\alpha = .01$) among families within stands remained in all characteristics in both species.

The majority of the variances observed in all of the characteristics in both the white pine and Virginia pine resulted from within-plot differences (Tables 14 and 15). Little or no variance was contributed by the replication-by-stand interaction source in any of the characteristics in either species.

Table 14. Variance Components and Percentage Contribution of Variance in Measured and Derived Characteristics of Virginia Pine

	Source											
	R	%	S	%	RXS	%	F(S)	%	RXF(S)	%	W	%
DBH	0.11453	2	0.12174	2	0.04964	1	0.18091	3	0.00000	0	5.46099	92
$D\text{-}COMP_1$	0.00000	0	0.06500	2	0.00000	0	0.04064	1	0.00000	0	4.81929	97
$D\text{-}COMP_2$	0.00800	0	0.03266	1	0.00000	0	0.00000	0	0.00000	0	3.75928	99
$D\text{-}WOUT_1$	0.12872	16	0.01699	2	0.01846	2	0.02990	4	0.33061	42	0.26565	34
$D\text{-}WOUT_2$	0.14936	7	0.03884	2	0.01312	1	0.09297	5	0.37568	19	1.31633	66
HEIGHT	0.03393	6	0.00707	1	0.00000	0	0.01333	2	0.06822	13	0.43283	78
$H\text{-}COMP_1$	0.00000	0	0.00368	1	0.00000	0	0.00921	2	0.00000	0	0.50684	97
$H\text{-}COMP_2$	0.00116	1	0.00056	0	0.00000	0	0.00121	1	0.00817	5	0.14521	93
$H\text{-}WOUT_1$	0.03088	26	0.00057	0	0.00000	0	0.00000	0	0.05869	50	0.02669	23
$H\text{-}WOUT_2$	0.03593	9	0.00760	2	0.00000	0	0.00594	1	0.07919	20	0.27164	68
CROWN	0.00031	0	0.01609	2	0.00142	0	0.01205	1	0.06336	7	0.86752	90
$C\text{-}COMP_1$	0.00000	0	0.00777	1	0.00000	0	0.00591	1	0.00000	0	0.56609	98
$C\text{-}COMP_2$	0.00168	0	0.00385	1	0.00000	0	0.00200	0	0.01682	3	0.62616	96
$C\text{-}WOUT_1$	0.00136	1	0.00135	1	0.00320	2	0.00008	0	0.08452	55	0.06362	41
$C\text{-}WOUT_2$	0.00000	0	0.00298	1	0.00653	2	0.00685	2	0.10016	32	0.19576	63
BA ($x10^{-6}$)	0.40	2	0.41	2	0.20	1	0.56	3	0.00	0	18.36	92
$B\text{-}COMP_1$ ($x10^{-6}$)	0.00	0	0.15	1	0.00	0	0.06	1	0.00	0	10.21	98
$B\text{-}COMP_2$ ($x10^{-6}$)	0.00	0	0.17	1	0.00	0	0.06	0	0.00	0	14.97	99
$B\text{-}WOUT_1$ ($x10^{-6}$)	0.45	13	0.09	2	0.08	2	0.16	4	1.03	29	1.78	50

Table 14 (continued)

	Source											
	R	%	S	%	RXS	%	F(S)	%	RXF(S)	%	W	%
B-WOUT$_2$ (x10^{-6})	0.47	10	0.07	2	0.06	1	0.18	4	1.19	26	2.65	57
CA	0.09504	0	0.62275	2	0.22598	1	0.48004	1	2.66432	7	35.25129	89
CA-COMP$_1$	0.00000	0	0.19808	1	0.00000	0	0.13237	1	0.00000	0	15.84658	98
CA-COMP$_2$	0.02467	0	0.25432	1	0.00000	0	0.22257	1	0.41650	1	28.63548	97
CA-WOUT$_1$	0.15974	2	0.11529	1	0.17291	2	0.02758	3	3.53741	36	5.15612	56
CA-WOUT$_2$	0.00000	0	0.00425	0	0.34673	4	0.20917	2	3.75532	38	5.48436	56
VOLUME (x10^{-6})	8.18	3	5.88	2	2.77	1	7.76	3	0.00	0	258.30	91
V-COMP$_1$ (x10^{-6})	0.00	0	2.07	1	0.00	0	1.11	1	0.00	0	144.38	98
V-COMP$_2$ (x10^{-6})	0.00	0	2.58	1	0.00	0	1.55	1	0.00	0	214.47	98
V-WOUT$_1$ (x10^{-6})	8.88	17	1.32	2	1.33	3	2.16	4	15.12	28	24.70	46
V-WOUT$_2$ (x10^{-6})	8.42	13	0.94	1	1.19	2	1.73	3	16.15	24	37.73	57
TREESIZE	0.00357	1	0.00544	2	0.00191	1	0.00650	3	0.0000	0	0.24986	93
T-COMP$_1$	0.00421	3	0.00218	1	0.00073	0	0.00225	2	0.01412	9	0.13553	85
T-COMP$_2$	0.00494	4	0.00116	1	0.00049	0	0.00199	2	0.04442	35	0.07361	58
T-WOUT$_1$	0.00146	3	0.00064	1	0.00047	1	0.00069	2	0.01236	29	0.02759	64
T-WOUT$_2$	0.00407	3	0.00106	1	0.00053	0	0.00156	1	0.02807	20	0.10540	75

R = Replications. S = Stands. F(S) = Families within Stand. W = Within Plot.

RXS = Replication-by-Stand interaction.

RXF(S) = Replication-by-Families-within-Stand interaction.

Table 15. Variance Components and Percentage Contribution of Variance in Measured and Derived Characteristics of White Pine

	Source											
	R	%	S	%	RXS	%	F(S)	%	RXF(S)	%	W	%
DBH	0.46668	4	1.18313	11	0.00000	0	0.46319	4	0.51048	5	8.54751	76
$D\text{-}COMP_1$	0.00000	0	0.49882	6	0.03973	1	0.19409	3	0.18150	2	6.83673	88
$D\text{-}COMP_2$	0.00000	0	0.41630	5	0.03567	1	0.15890	2	0.49248	6	6.93251	86
$D\text{-}WOUT_1$	0.44762	28	0.15245	9	0.00000	0	0.04356	3	0.59679	37	0.36887	23
$D\text{-}WOUT_2$	0.61119	19	0.25963	8	0.00000	0	0.06052	2	0.77234	25	1.43031	46
HEIGHT	0.26265	12	0.26302	13	0.02774	1	0.11788	6	0.27460	13	1.15723	55
$H\text{-}COMP_1$	0.00000	0	0.13653	8	0.02177	1	0.07633	5	0.15831	10	1.24410	76
$H\text{-}COMP_2$	0.00126	0	0.05623	5	0.01040	1	0.04145	4	0.12014	10	0.91864	80
$H\text{-}WOUT_1$	0.23705	41	0.02124	3	0.00000	0	0.00000	0	0.24939	43	0.07442	13
$H\text{-}WOUT_2$	0.25734	27	0.08877	9	0.00000	0	0.01594	2	0.25873	27	0.32914	35
CROWN	0.07935	6	0.09944	7	0.00000	0	0.04964	4	0.12509	9	1.02192	74
$C\text{-}COMP_1$	0.00000	0	0.03876	5	0.00271	1	0.01562	2	0.03839	5	0.64932	87
$C\text{-}COMP_2$	0.00060	0	0.03878	4	0.00221	0	0.01255	2	0.08934	9	0.81745	85
$C\text{-}WOUT_1$	0.08193	30	0.01393	5	0.00000	0	0.00749	3	0.09399	35	0.07286	27
$C\text{-}WOUT_2$	0.09077	22	0.01868	4	0.00000	0	0.00584	1	0.11938	29	0.18264	44
BA ($\times 10^{-5}$)	0.132	5	0.268	9	0.000	0	0.119	4	0.116	4	2.243	78
$B\text{-}COMP_1$ ($\times 10^{-5}$)	0.000	0	0.166	6	0.010	0	0.069	3	0.064	2	2.391	89
$B\text{-}COMP_2$ ($\times 10^{-5}$)	0.000	0	0.122	6	0.011	1	0.048	2	0.137	6	1.812	85
$B\text{-}WOUT_1$ ($\times 10^{-5}$)	0.124	32	0.014	4	0.000	0	0.003	1	0.161	42	0.082	21

Table 15 (continued)

	Source											
	R	%	S	%	RXS	%	F(S)	%	RXF(S)	%	W	%
$B\text{-}WOUT_2$ $(x10^{-5})$	0.158	21	0.041	6	0.000	0	0.011	2	0.189	25	0.345	46
CA	2.64833	6	2.74139	7	0.06715	0	1.55669	4	3.80058	9	31.02853	74
$CA\text{-}COMP_1$	0.00000	0	0.68008	4	0.08471	1	0.28772	2	0.53757	3	13.73798	90
$CA\text{-}COMP_2$	0.00000	0	1.38588	5	0.15175	0	0.47503	2	3.25176	11	24.49027	82
$CA\text{-}WOUT_1$	2.67231	24	0.68343	6	0.00000	0	0.45479	4	2.95192	26	4.48784	40
$CA\text{-}WOUT_2$	3.09631	25	0.31037	3	0.00000	0	0.11308	1	3.53573	29	5.12939	42
VOLUME $(x10^{-5})$	2.763	6	4.726	10	0.000	0	2.211	5	2.015	4	35.844	75
$V\text{-}COMP_1$ $(x10^{-5})$	0.000	0	1.334	6	0.123	0	0.637	3	0.379	2	20.787	89
$V\text{-}COMP_2$ $(x10^{-5})$	0.000	0	2.174	6	0.187	1	0.970	3	2.673	8	28.030	82
$V\text{-}WOUT_1$ $(x10^{-5})$	2.636	28	1.060	11	0.000	0	0.425	4	2.314	24	3.116	33
$V\text{-}WOUT_2$ $(x10^{-5})$	3.023	22	0.690	5	0.000	0	0.211	2	3.090	23	6.528	48
TREESIZE	0.02207	5	0.04937	10	0.00000	0	0.02226	5	0.02584	5	0.35369	75
$T\text{-}COMP_1$	0.01256	5	0.01411	5	0.00082	0	0.00641	3	0.04169	15	0.19588	72
$T\text{-}COMP_2$	0.02626	14	0.00465	2	0.00245	1	0.00095	1	0.07895	42	0.07662	40
$T\text{-}WOUT_1$	0.01612	19	0.01046	12	0.00087	1	0.00364	4	0.02152	25	0.03430	39
$T\text{-}WOUT_2$	0.03463	12	0.02179	8	0.00329	1	0.00932	3	0.04720	17	0.16906	59

R = Replications. S = Stands. F(S) = Families within Stand. W = Within Plot.

RXS = Replication-by-Stand interaction.

RXF(S) = Replication-by-Families-within-Stand interaction.

The variances of competitive-fitness estimates computed by both the DDI and DRI methods were composed almost entirely of within-plot variations in Virginia pine (Table 14) and in the majority of within-plot variations in white pine (Table 15). Minor contributions to the total variances of competition estimates were made by stands, families-within-stand, and replication-by-families-within-stand components in white pine. When competitional deviations derived by the DDI and DRI methods were adjusted for, the percentage contributions of within-plot sources to total variances expressed in all characteristics were reduced in both species. This reduction was, in most cases, accompanied by increases in contributions by replications and replication-by-families-within-stand interaction components.

Low estimates of narrow-sense heritability of all characteristics were observed (Tables 16 and 17), ranging from 0.05 (crown area in Virginia pine) to 0.30 (height in white pine). In general, estimates of heritability of characteristics in white pine (Table 17) were of greater magnitude than those in Virginia pine (Table 16).

Estimates of heritability of competitive-fitness were also very small in both Virginia pine (Table 16) and white pine (Table 17). For most characteristics, competitive-fitness estimates derived by the DRI method appeared to have lower heritabilities than those derived using the DDI approach.

When competitional deviations were adjusted for, estimates of heritability both increased or decreased depending on the characteristic. This unpredictability of the effects of competition on heritability was

Table 16. Estimates of Narrow-Sense Heritability of Characteristics of Virginia Pine

DBH	$D\text{-}COMP_1$	$D\text{-}COMP_2$	$D\text{-}WOUT_1$	$D\text{-}WOUT_2$
0.128	0.038	0.000	0.191	0.208
HEIGHT	$H\text{-}COMP_1$	$H\text{-}COMP_2$	$H\text{-}WOUT_1$	$H\text{-}WOUT_2$
0.103	0.071	0.031	0.000	0.067
CROWN	$C\text{-}COMP_1$	$C\text{-}COMP_2$	$C\text{-}WOUT_1$	$C\text{-}WOUT_2$
0.051	0.041	0.012	0.002	0.091
BA	$B\text{-}COMP_1$	$B\text{-}COMP_2$	$B\text{-}WOUT_1$	$B\text{-}WOUT_2$
0.118	0.023	0.016	0.215	0.179
CA	$CA\text{-}COMP_1$	$CA\text{-}COMP_2$	$CA\text{-}WOUT_1$	$CA\text{-}WOUT_2$
0.050	0.033	0.030	0.013	0.088
VOLUME	$V\text{-}COMP_1$	$V\text{-}COMP_2$	$V\text{-}WOUT_1$	$V\text{-}WOUT_2$
0.117	0.031	0.029	0.206	0.124
TREESIZE	$T\text{-}COMP_1$	$T\text{-}COMP_2$	$T\text{-}WOUT_1$	$T\text{-}WOUT_2$
0.101	0.059	0.066	0.068	0.063

Table 17. Estimates of Narrow-Sense Heritability of Characteristics of White Pine

DBH	$D\text{-}COMP_1$	$D\text{-}COMP_2$	$D\text{-}WOUT_1$	$D\text{-}WOUT_2$
0.195	0.108	0.084	0.172	0.107
HEIGHT	$H\text{-}COMP_1$	$H\text{-}COMP_2$	$H\text{-}WOUT_1$	$H\text{-}WOUT_2$
0.304	0.206	0.153	0.000	0.106
CROWN	$C\text{-}COMP_1$	$C\text{-}COMP_2$	$C\text{-}WOUT_1$	$C\text{-}WOUT_2$
0.166	0.088	0.055	0.172	0.076
BA	$B\text{-}COMP_1$	$B\text{-}COMP_2$	$B\text{-}WOUT_1$	$B\text{-}WOUT_2$
0.192	0.109	0.096	0.049	0.081
CA	$CA\text{-}COMP_1$	$CA\text{-}COMP_2$	$CA\text{-}WOUT_1$	$CA\text{-}WOUT_2$
0.171	0.079	0.067	0.230	0.052
VOLUME	$V\text{-}COMP_1$	$V\text{-}COMP_2$	$V\text{-}WOUT_1$	$V\text{-}WOUT_2$
0.221	0.117	0.123	0.297	0.086
TREESIZE	$T\text{-}COMP_1$	$T\text{-}COMP_2$	$T\text{-}WOUT_1$	$T\text{-}WOUT_2$
0.222	0.105	0.024	0.245	0.165

evident in both species, and appeared to be characteristic of both methods (DDI and DRI). No consistency of differences between DDI and DRI competition effects on heritabilities was observed over the range of characteristics measured.

Anticipated gains due to selection for superior competitors were small but measurable in most characteristics of both species (Tables 18 and 19). Gains derived when competitional deviations were adjusted for were in all cases smaller than gains derived under competition. Competition apparently acted to increase variation in most tree dimensions measured. Removing competition reduced the selection differential, resulting in decreased gains, regardless of whether heritabilities were increased or decreased.

Using Pearson product-moment correlations, characteristics adjusted for competition by the DDI and DRI methods were compared to characteristics as originally measured (Table 20). Comparisons between DDI and DRI competitive-fitness values and between characteristics adjusted for DDI and DRI competition also were made (Table 21). In both species and for all comparisons, a significant amount of association was observed. Although correlation coefficients as low as .290 (between height and $H\text{-}WOUT_1$ in Virginia pine) were found, relationships were undoubtedly real because the samples were quite large. High correlations between DDI and DRI competitive-fitness values were observed (Table 21), especially in white pine, indicating a high degree of association among individual observations of competitive fitness as computed by the DDI and DRI methods.

Table 18. Anticipated Gains in Characteristics of Virginia Pine at Age Fourteen, by Two Selection Schemes

	A	%	B	%
		(cm)		
DBH	0.555	5	0.344	3
$D\text{-}COMP_1$	0.153	1	0.089	1
$D\text{-}COMP_2$	0.000	0	0.000	0
$D\text{-}WOUT_1$	0.229	2	0.113	1
$D\text{-}WOUT_2$	0.453	4	0.274	2
		(m)		
HEIGHT	0.129	2	0.078	1
$H\text{-}COMP_1$	0.097	1	0.058	1
$H\text{-}COMP_2$	0.023	0	0.014	0
$H\text{-}WOUT_1$	0.000	0	0.000	0
$H\text{-}WOUT_2$	0.068	1	0.040	1
CROWN	0.091	2	0.055	1
$C\text{-}COMP_1$	0.061	1	0.035	1
$C\text{-}COMP_2$	0.019	0	0.011	0
$C\text{-}WOUT_1$	0.001	0	0.001	0
$C\text{-}WOUT_2$	0.081	2	0.046	1
		(m^2)		
BA ($x10^{-3}$)	0.944	9	0.582	6
$B\text{-}COMP_1$ ($x10^{-3}$)	0.147	1	0.085	1
$B\text{-}COMP_2$ ($x10^{-3}$)	0.123	1	0.071	1
$B\text{-}WOUT_1$ ($x10^{-3}$)	0.582	6	0.330	3
$B\text{-}WOUT_2$ ($x10^{-3}$)	0.575	6	0.335	3
CA	0.571	4	0.341	2
$CA\text{-}COMP_1$	0.258	2	0.142	1
$CA\text{-}COMP_2$	0.318	2	0.185	1
$CA\text{-}WOUT_1$	0.061	0	0.034	0
$CA\text{-}WOUT_2$	0.434	3	0.237	2

Table 18 (continued)

	A	%	B	%
			(m^3)	
VOLUME ($x10^{-2}$)	0.349	10	0.216	6
$V\text{-}COMP_1$ ($x10^{-2}$)	0.072	2	0.043	1
$V\text{-}COMP_2$ ($x10^{-2}$)	0.083	2	0.049	1
$V\text{-}WOUT_1$ ($x10^{-2}$)	0.209	6	0.118	3
$V\text{-}WOUT_2$ ($x10^{-2}$)	0.151	4	0.088	3
TREESIZE	0.095	5	0.058	3
$T\text{-}COMP_1$	0.042	2	0.025	1
$T\text{-}COMP_2$	0.037	2	0.021	1
$T\text{-}WOUT_1$	0.023	1	0.013	1
$T\text{-}WOUT_2$	0.029	2	0.024	1

A = Combined Family and Single Tree Selection.

B = Single Tree Selection.

Table 19. Anticipated Gains in Characteristics of White Pine at Age Eleven, by Two Selection Schemes

	A	%	B	%
		(cm)		
DBH	1.155	11	0.656	6
$D\text{-}COMP_1$	0.613	6	0.325	3
$D\text{-}COMP_2$	0.497	5	0.254	2
$D\text{-}WOUT_1$	0.302	3	0.120	1
$D\text{-}WOUT_2$	0.308	3	0.147	1
		(m)		
HEIGHT	0.665	11	0.381	6
$H\text{-}COMP_1$	0.472	8	0.264	4
$H\text{-}COMP_2$	0.313	5	0.169	3
$H\text{-}WOUT_1$	0.000	0	0.000	0
$H\text{-}WOUT_2$	0.154	2	0.070	1
CROWN	0.353	9	0.193	5
$C\text{-}COMP_1$	0.159	4	0.082	2
$C\text{-}COMP_2$	0.116	3	0.057	2
$C\text{-}WOUT_1$	0.126	3	0.053	1
$C\text{-}WOUT_2$	0.082	2	0.037	1
		(m^2)		
BA ($x10^{-2}$)	0.185	21	0.105	12
$B\text{-}COMP_1$ ($x10^{-2}$)	0.116	13	0.061	7
$B\text{-}COMP_2$ ($x10^{-2}$)	0.091	10	0.047	5
$B\text{-}WOUT_1$ ($x10^{-2}$)	0.014	2	0.005	1
$B\text{-}WOUT_2$ ($x10^{-2}$)	0.037	4	0.017	2
CA	1.997	16	1.095	9
$CA\text{-}COMP_1$	0.663	5	0.337	3
$CA\text{-}COMP_2$	0.771	6	0.381	3
$CA\text{-}WOUT_1$	1.138	9	0.560	5
$CA\text{-}WOUT_2$	0.301	2	0.135	1

Table 19 (continued)

	A	%	B	%
		(m^3)		
VOLUME ($x10^{-2}$)	0.834	26	0.481	15
$V\text{-}COMP_1$ ($x10^{-2}$)	0.363	11	0.194	6
$V\text{-}COMP_2$ ($x10^{-2}$)	0.444	14	0.237	7
$V\text{-}WOUT_1$ ($x10^{-2}$)	0.387	12	0.191	6
$V\text{-}WOUT_2$ ($x10^{-2}$)	0.167	5	0.080	3
TREESIZE	0.264	15	0.152	9
$T\text{-}COMP_1$	0.105	6	0.053	3
$T\text{-}COMP_2$	0.019	1	0.008	0
$T\text{-}WOUT_1$	0.104	6	0.052	3
$T\text{-}WOUT_2$	0.148	8	0.078	4

A = Combined Family and Single Tree Selection.

B = Single Tree Selection.

Table 20. Pearson Product-Moment Correlations of Characteristics Adjusted for Competition with the DDI and DRI and the Seven Original Characteristics

	$WOUT_1$	(PROB > |R|)	$WOUT_2$	(PROB > |R|)
		Virginia Pine (N = 1820)		
DBH	0.597	(0.0001)	0.584	(0.0001)
HEIGHT	0.290	(0.0001)	0.845	(0.0001)
CROWN	0.721	(0.0001)	0.569	(0.0001)
BA	0.798	(0.0001)	0.484	(0.0001)
CA	0.869	(0.0001)	0.499	(0.0001)
VOLUME	0.797	(0.0001)	0.483	(0.0001)
TREESIZE	0.704	(0.0001)	0.726	(0.0001)
		White Pine (N = 4196)		
DBH	0.588	(0.0001)	0.521	(0.0001)
HEIGHT	0.462	(0.0001)	0.666	(0.0001)
CROWN	0.731	(0.0001)	0.542	(0.0001)
BA	0.797	(0.0001)	0.502	(0.0001)
CA	0.872	(0.0001)	0.532	(0.0001)
VOLUME	0.796	(0.0001)	0.528	(0.0001)
TREESIZE	0.711	(0.0001)	0.774	(0.0001)

$WOUT_1$ = same variables adjusted for competition by the DDI method.

$WOUT_2$ = same variables adjusted for competition by the DRI method.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

Table 21. Pearson Product-Moment Correlations of DDI and DRI Competitive Fitness Estimates and Characteristics Adjusted for Competition with the DDI and DRI

	$-COMP_2$	(PROB > |R|)	$-WOUT_2$	(PROB > |R|)
		Virginia Pine (N = 1820)		
$D-COMP_1$	0.854	(0.0001)		
$H-COMP_1$	0.584	(0.0001)		
$C-COMP_1$	0.867	(0.0001)		
$B-COMP_1$	0.914	(0.0001)		
$CA-COMP_1$	0.903	(0.0001)		
$V-COMP_1$	0.914	(0.0001)		
$T-COMP_1$	0.862	(0.0001)		
$D-WOUT_1$			0.647	(0.0001)
$H-WOUT_1$			0.388	(0.0001)
$C-WOUT_1$			0.689	(0.0001)
$B-WOUT_1$			0.681	(0.0001)
$CA-WOUT_1$			0.663	(0.0001)
$V-WOUT_1$			0.682	(0.0001)
$T-WOUT_1$			0.916	(0.0001)
		White Pine (N = 4196)		
$D-COMP_1$	0.923	(0.0001)		
$H-COMP_1$	0.879	(0.0001)		
$C-COMP_1$	0.917	(0.0001)		
$B-COMP_1$	0.939	(0.0001)		
$CA-COMP_1$	0.915	(0.0001)		
$V-COMP_1$	0.915	(0.0001)		
$T-COMP_1$	0.850	(0.0001)		
$D-WOUT_1$			0.774	(0.0001)
$H-WOUT_1$			0.770	(0.0001)
$C-WOUT_1$			0.783	(0.0001)

Table 21 (continued)

	$-COMP_2$	(PROB > |R|)	$-WOUT_2$	(PROB > |R|)
$B-WOUT_1$			0.740	(0.0001)
$CA-WOUT_1$			0.735	(0.0001)
$V-WOUT_1$			0.751	(0.0001)
$T-WOUT_1$			0.941	(0.0001)

$-COMP_2$ = competitive fitness based on the DRI method.

$-WOUT_2$ = measured characteristics adjusted for competition by the DRI method.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

Multiple regression comparisons of characteristic variables in Virginia pine (Table 22) and white pine (Table 23) were interpreted by examining the Type IV sums of squares. Type IV sums of squares of deviations from the mean represented the contributions of each independent variable in terms of variance, or the contribution of each independent variable after other independent variables considered were already included in the regression model. With the means of all variables centered on zero, a significant Type IV sum of squares of an independent variable in a multiple regression with two independent variables indicated that the variance contributed by the first independent variable (already included) was altered when this second independent variable was added to the model. A significant Type IV sum of squares, therefore, provided evidence that the variances of the two independent variables included in a multiple regression model differed.

In Virginia pine (Table 22), when each characteristic adjusted for DDI or DRI competition was compared to the same characteristics as originally measured, the variances were found to differ significantly. When DDI and DRI competitive-fitness estimates were compared, the variances based on all characteristics, except DBH and crown diameter, also differed significantly in Virginia pine. All comparisons between each characteristic adjusted for DDI and DRI competition in Virginia pine revealed significant differences in variances.

In white pine (Table 23), all comparisons made resulted in significant variance differences, except for the comparison of crown diameter adjusted for DDI competition with crown diameter adjusted for

Table 22. Multiple-Regression Comparisons[a] of Characteristic Variables in Virginia Pine

Dependent variable	Independent variables	Type IV SS[b]	F value	R^2
$D\text{-}COMP_2$	DBH	4491.2558	4431.88**	0.730
	$D\text{-}WOUT_1$	488.5546	482.10**	
$H\text{-}COMP_2$	HEIGHT	95.3337	929.95**	0.341
	$H\text{-}WOUT_1$	15.7369	153.51**	
$C\text{-}COMP_2$	CROWN	700.7987	4386.99**	0.754
	$C\text{-}WOUT_1$	91.5683	573.22**	
$B\text{-}COMP_2$	BA	0.0148	6233.10**	0.838
	$B\text{-}WOUT_1$	0.0020	825.56**	
$CA\text{-}COMP_2$	CA	23438.1282	4474.44**	0.822
	$CA\text{-}WOUT_1$	3815.4762	728.39**	
$V\text{-}COMP_2$	VOLUME	0.2128	6349.14**	0.840
	$V\text{-}WOUT_1$	0.0282	842.60**	
$T\text{-}COMP_2$	TREESIZE	189.3979	9156.73**	0.834
	$T\text{-}WOUT_1$	82.4316	3985.28**	
$D\text{-}COMP_1$	DBH	5276.1292	13718.68**	0.903
	$D\text{-}WOUT_2$	185.4114	482.10**	
$H\text{-}COMP_1$	HEIGHT	317.1291	3511.41**	0.823
	$H\text{-}WOUT_2$	13.8640	153.51**	
$C\text{-}COMP_1$	CROWN	765.3806	13695.81**	0.899
	$C\text{-}WOUT_2$	32.1182	573.22**	
$B\text{-}COMP_1$	BA	0.0146	16889.78**	0.910
	$B\text{-}WOUT_2$	0.0007	825.56**	
$CA\text{-}COMP_1$	CA	23007.1981	14413.74**	0.897
	$CA\text{-}WOUT_2$	1162.6572	728.39**	
$V\text{-}COMP_1$	VOLUME	0.2079	16305.81**	0.906
	$V\text{-}WOUT_2$	0.0107	842.60**	
$T\text{-}COMP_1$	TREESIZE	212.9307	31466.59**	0.957
	$T\text{-}WOUT_2$	26.9679	3985.28**	

Table 22 (continued)

Dependent variable	Independent variables	Type IV SS[b]	F value	R^2
TREESIZE	$D\text{-}COMP_1$	100.8343	2181.65**	0.825
	$D\text{-}COMP_2^1$	0.1481	3.20	
TREESIZE	$H\text{-}COMP_1$	128.9445	945.50**	0.485
	$H\text{-}COMP_2^1$	2.7917	20.47**	
TREESIZE	$C\text{-}COMP_1$	86.4555	1443.44**	0.773
	$C\text{-}COMP_2^1$	0.1221	2.04	
TREESIZE	$B\text{-}COMP_1$	43.9672	944.84**	0.824
	$B\text{-}COMP_2^1$	2.4837	53.37**	
TREESIZE	$CA\text{-}COMP_1$	46.9288	823.66**	0.784
	$CA\text{-}COMP_2^1$	2.6257	46.08**	
TREESIZE	$V\text{-}COMP_1$	36.0663	841.35**	0.838
	$V\text{-}COMP_2^1$	5.1775	120.78**	
TREESIZE	$T\text{-}COMP_1$	211.5795	9113.75**	0.912
	$T\text{-}COMP_2^1$	23.7088	1021.25**	
TREESIZE	$D\text{-}WOUT_1$	33.4327	204.16**	0.382
	$D\text{-}WOUT_2^1$	31.5268	192.53**	
TREESIZE	$H\text{-}WOUT_1$	9.3128	51.18**	0.313
	$H\text{-}WOUT_2^1$	147.6232	811.33**	
TREESIZE	$C\text{-}WOUT_1$	71.6963	457.47**	0.408
	$C\text{-}WOUT_2^1$	5.1279	32.72**	
TREESIZE	$B\text{-}WOUT_1$	188.5248	1742.18**	0.591
	$B\text{-}WOUT_2^1$	4.6770	43.22**	
TREESIZE	$CA\text{-}WOUT_1$	216.0768	2247.40**	0.637
	$CA\text{-}WOUT_2^1$	6.8125	70.86**	
TREESIZE	$V\text{-}WOUT_1$	200.2389	1882.78**	0.598
	$V\text{-}WOUT_2^1$	7.8300	76.62**	
TREESIZE	$T\text{-}WOUT_1$	4.4984	36.62**	0.536
	$T\text{-}WOUT_2^1$	19.8451	161.55**	

Table 22 (continued)

**Significant at 0.01 level.

[a]Comparisons were of characteristic variables including and excluding competition, between DDI and DRI competitive fitness estimates, and of characteristics adjusted for competition with the DDI and DRI.

[b]A significant Type IV SS indicates the variances of the two independent variables considered in a multiple regression differ.

Table 23. Multiple-Regression Comparisons[a] of Characteristic Variables in White Pine

Dependent variable	Independent variables	Type IV SS[b]	F value	R^2
$D\text{-}COMP_2$	DBH	27040.1938	23017.64**	0.853
	$D\text{-}WOUT_1$	4177.1075	3555.71**	
$H\text{-}COMP_2$	HEIGHT	3684.7507	14201.94**	0.773
	$H\text{-}WOUT_1$	1038.7591	4003.63**	
$C\text{-}COMP_2$	CROWN	2836.6919	18355.76**	0.838
	$C\text{-}WOUT_1$	537.6435	3479.00**	
$B\text{-}COMP_2$	BA	0.0767	31123.02**	0.883
	$B\text{-}WOUT_1$	0.0120	4875.00**	
$CA\text{-}COMP_2$	CA	63869.8941	13248.93**	0.837
	$CA\text{-}WOUT_1$	15003.7313	3112.32**	
$V\text{-}COMP_2$	VOLUME	0.8736	15870.99**	0.837
	$V\text{-}WOUT_1$	0.1638	2976.28**	
$T\text{-}COMP_2$	TREESIZE	675.8006	26446.25**	0.863
	$T\text{-}WOUT_1$	362.8865	14200.92**	
$D\text{-}COMP_1$	DBH	27519.2487	51342.06**	0.930
	$D\text{-}WOUT_2$	1905.8553	3555.71**	
$H\text{-}COMP_1$	HEIGHT	5261.9212	23706.53**	0.863
	$H\text{-}WOUT_2$	888.6498	4003.63**	
$C\text{-}COMP_1$	CROWN	2644.4550	40690.82**	0.913
	$C\text{-}WOUT_2$	266.7295	3488.74**	
$B\text{-}COMP_1$	BA	0.0993	62927.70**	0.941
	$B\text{-}WOUT_2$	0.0077	4875.00**	
$CA\text{-}COMP_1$	CA	53534.1632	36143.15**	0.902
	$CA\text{-}WOUT_2$	4627.6672	3124.33	
$V\text{-}COMP_1$	VOLUME	0.8113	41662.70**	0.915
	$V\text{-}WOUT_2$	0.0580	2976.28**	
$T\text{-}COMP_1$	TREESIZE	814.5566	85512.11**	0.964
	$T\text{-}WOUT_2$	135.2727	14200.92**	

Table 23 (continued)

Dependent variable	Independent variables	Type IV SS[b]	F value	R^2
TREESIZE	$D\text{-}COMP_1$	268.7746	3153.79**	0.817
	$D\text{-}COMP_2$	1.2729	14.94**	
TREESIZE	$H\text{-}COMP_1$	250.4323	1499.34**	0.642
	$H\text{-}COMP_2$	1.4517	8.69**	
TREESIZE	$C\text{-}COMP_1$	268.8255	2187.51**	0.736
	$C\text{-}COMP_2$	1.6956	13.80**	
TREESIZE	$B\text{-}COMP_1$	153.4138	1715.46**	0.808
	$B\text{-}COMP_2$	1.7795	19.90**	
TREESIZE	$CA\text{-}COMP_1$	176.1240	1473.39**	0.743
	$CA\text{-}COMP_2$	5.2139	43.61**	
TREESIZE	$V\text{-}COMP_1$	125.0947	1437.99**	0.813
	$V\text{-}COMP_2$	27.3418	314.30**	
TREESIZE	$T\text{-}COMP_1$	1024.7591	28765.57**	0.923
	$T\text{-}COMP_2$	154.5827	4339.22**	
TREESIZE	$D\text{-}WOUT_1$	132.1957	407.83**	0.305
	$D\text{-}WOUT_2$	22.7555	70.20**	
TREESIZE	$H\text{-}WOUT_1$	72.8430	199.19**	0.216
	$H\text{-}WOUT_2$	343.3757	938.95**	
TREESIZE	$C\text{-}WOUT_1$	319.7413	1122.72**	0.389
	$C\text{-}WOUT_2$	0.8215	2.88	
TREESIZE	$B\text{-}WOUT_1$	43.5372	116.81**	0.201
	$B\text{-}WOUT_2$	305.7835	820.40**	
TREESIZE	$CA\text{-}WOUT_1$	855.1309	4865.98**	0.623
	$CA\text{-}WOUT_2$	72.8439	414.51**	
TREESIZE	$V\text{-}WOUT_1$	851.3760	4766.18**	0.617
	$V\text{-}WOUT_2$	89.3998	500.48**	
TREESIZE	$T\text{-}WOUT_1$	5.8325	31.44**	0.602
	$T\text{-}WOUT_2$	191.1448	1030.45**	

Table 23 (continued)

**Significant at 0.01 level.

[a]Comparisons were of characteristic variables including and excluding competition, between DDI and DRI competitive fitness estimates, and of characteristics adjusted for competition with the DDI and DRI.

[b]A significant Type IV SS indicates the variances of the two independent variables considered in a multiple regression differ.

DRI competition. These results indicated that intertree competition was influencing the variances of tree dimensions in sample populations derived from both the White Pine and Virginia Pine Heritability Study plantations. In addition, differences in variance between DDI- and DRI-derived values were evident for most characteristics, suggesting that these two indices were not alike in what they estimate.

For each characteristic in both species, the slope of the dimension-on-spacing regression from the spacing study (subsequently used in the DDI method) was compared to the slope of the regression of dimension on effective growing space utilized computed by the DRI method (Tables 24 and 25). This comparison was incorporated into the spacing-by-plantation interaction term in each analysis so that a significant contribution of such interaction indicated a difference between slopes. Except for TREESIZE in Virginia pine, all slope comparisons were found to be significant. Differences observed between DDI- and DRI-derived slopes of tree dimension-on-growing space regression in all characteristics, except TREESIZE in Virginia pine, provided further evidence that the two indices differed in what they estimated.

Spearman rank correlation comparisons between variance component distributions for characteristics adjusted for competition and those for characteristics as originally measured were made (Table 26). In Virginia pine, only the comparisons involving the characteristics of height and crown diameter adjusted for DRI competition to unadjusted height and crown diameter, respectively, exhibited significant amounts

Table 24. Slope Comparisons[a] in Virginia Pine

Dependent variable	Independent variables	Type I SS	F value	R^2
DBH	SPACING*PLANTATION	1746.9899	603.83**	0.656
HEIGHT	SPACING*PLANTATION	243.7504	445.17**	0.298
CROWN	SPACING*PLANTATION	244.9897	654.97**	0.646
BA	SPACING*PLANTATION	0.6919×10^{-3}	68.54**	0.709
CA	SPACING*PLANTATION	1821.4937	138.06**	0.705
VOLUME	SPACING*PLANTATION	0.6785×10^{-2}	37.38**	0.670
TREESIZE	SPACING*PLANTATION	0.4469	2.55	0.606

**Significant at 0.01 level.

[a]Comparisons were between the slopes of regressions of dimension on spacing from the Spacing Study data and slopes of regressions of dimension on effective growing space utilized (DRI) from the Virginia Pine Heritability Study data.

Table 25. Slope Comparisons[a] in White Pine

Dependent variable	Independent variables	Type I SS	F value	R^2
DBH	SPACING*PLANTATION	5735.1925	1231.05**	0.676
HEIGHT	SPACING*PLANTATION	2270.2294	2081.07**	0.633
CROWN	SPACING*PLANTATION	651.9603	1445.63**	0.674
BA	SPACING*PLANTATION	0.6444×10^{-3}	36.10**	0.646
CA	SPACING*PLANTATION	4184.0598	294.22**	0.675
VOLUME	SPACING*PLANTATION	0.1342×10^{-1}	25.47**	0.613
TREESIZE	SPACING*PLANTATION	7.2374	22.46**	0.373

**Significant at 0.01 level.

[a]Comparisons were between the slopes of regressions of dimension on spacing from the Spacing Study data and slopes of regressions of dimension on effective growing space utilized (DRI) from the White Pine Heritability Study data.

Table 26. Spearman Rank Correlations of Variance Component Distributions of Characteristics Adjusted for Competition with the DDI and DRI and the Seven Original Characteristics

	$WOUT_1$	(PROB > |R|)	$WOUT_2$	(PROB > |R|)
		Virginia Pine (N = 6)		
DBH	-0.143	(0.7872)	0.257	(0.6228)
HEIGHT	0.725	(0.1032)	0.943	(0.0048)
CROWN	0.486	(0.3287)	0.829	(0.0416)
BA	0.257	(0.6228)	0.257	(0.6228)
CA	0.543	(0.2657)	0.771	(0.0724)
VOLUME	0.371	(0.4685)	0.371	(0.4685)
TREESIZE	0.257	(0.6228)	0.257	(0.6228)
		White Pine (N = 6)		
DBH	0.543	(0.2657)	0.829	(0.0416)
HEIGHT	0.696	(0.1248)	0.943	(0.0048)
CROWN	0.714	(0.1108)	0.943	(0.0048)
BA	0.257	(0.8228)	0.600	(0.2080)
CA	0.943	(0.0048)	0.943	(0.0048)
VOLUME	0.714	(0.1108)	0.600	(0.2080)
TREESIZE	0.714	(0.1108)	0.714	(0.1108)

$WOUT_1$ = same variables adjusted for competition by the DDI method.

$WOUT_2$ = same variables adjusted for competition by the DRI method.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

of association. In white pine, this association was also significant. In addition, crown area adjusted for DDI and DRI competition each compared to crown area as originally measured showed significant degrees of relationship in white pine. The variance component distributions of most characteristics in both species, however, were significantly altered upon adjustment for competition-influenced variance, suggesting that heritability estimates derived from selected variance components also would differ significantly upon adjustment for competition.

Variance component distributions of DDI- and DRI-derived estimates were compared also using Spearman rank correlations (Table 27). In Virginia pine, competitive-fitness variance component distributions differed significantly in the characteristics of DBH, height, crown diameter, and crown area, according to the method of derivation used. However, upon adjustment for competitional variance, only crown characteristics differed between the DDI and DRI methods. In white pine, a significant relationship was observed between variance component distributions derived for DDI estimates and those derived for DRI estimates in all characteristics measured. This indicated that, with a few exceptions such as crown characteristics in Virginia pine, the heritabilities of DDI competition estimates and those of characteristics adjusted for DDI competition were not significantly different from heritabilities of estimates and competition-free characteristics derived using the DRI approach.

When stand means were ranked and compared, no significant differences in these distributions were observed between characteristics

Table 27. Spearman Rank Correlations of Variance Component Distributions of DDI and DRI Competitive Fitness Estimates and of Characteristics Adjusted for Competition with the DDI and DRI

	$-COMP_2$	(PROB > |R|)	$-WOUT_2$	(PROB > |R|)
		Virginia Pine (N = 6)		
$D-COMP_1$	0.742	(0.0913)		
$H-COMP_1$	0.516	(0.2946)		
$C-COMP_1$	0.638	(0.1733)		
$B-COMP_1$	1.000	(0.0000)		
$CA-COMP_1$	0.638	(0.1733)		
$V-COMP_1$	1.000	(0.0000)		
$T-COMP_1$	1.000	(0.0000)		
$D-WOUT_1$			0.886	(0.0188)
$H-WOUT_1$			0.812	(0.0499)
$C-WOUT_1$			0.543	(0.2657)
$B-WOUT_1$			1.000	(0.0000)
$CA-WOUT_1$			0.771	(0.0724)
$V-WOUT_1$			1.000	(0.0000)
$T-WOUT_1$			1.000	(0.0000)
		White Pine (N = 6)		
$D-COMP_1$	0.829	(0.0416)		
$H-COMP_1$	1.000	(0.0000)		
$C-COMP_1$	0.943	(0.0048)		
$B-COMP_1$	0.829	(0.0416)		
$CA-COMP_1$	0.943	(0.0048)		
$V-COMP_1$	0.829	(0.0416)		
$T-COMP_1$	0.829	(0.0416)		
$D-WOUT_1$			0.829	(0.0416)
$H-WOUT_1$			0.812	(0.0499)
$C-WOUT_1$			0.829	(0.0416)

Table 27 (continued)

	$-COMP_2$ (PROB > |R|)	$-WOUT_2$	(PROB > |R|)
$B-WOUT_1$		0.829	(0.0416)
$CA-WOUT_1$		1.000	(0.0000)
$V-WOUT_1$		0.943	(0.0048)
$T-WOUT_1$		1.000	(0.0000)

$-COMP_2$ = competitive fitness based on the DRI method.

$-WOUT_2$ = measured characteristics adjusted for competition by the DRI method.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

as originally measured and the same characteristics adjusted for competition (Table 28). Similarly, with the exception of height in Virginia pine, no differences in distributions of stand means of competition estimates and of characteristics adjusted for competition were observed between the DDI and DRI methods (Table 29).

When family means were ranked and compared, no significant differences were found (Tables 30 and 31). Intertree competition apparently had little or no effect on the ranking of stand or family means. Furthermore, the DDI method of deriving competition estimates did not appear to differ significantly from the DRI method in its effect on the rankings of stand and family means.

Table 28. Spearman Rank Correlations of Distributions of Stand Means of Characteristics Adjusted for Competition with the DDI and DRI and Those for the Seven Original Characteristics

	$WOUT_1$	(PROB > |R|)	$WOUT_2$	(PROB > |R|)
		Virginia Pine (N = 12)		
DBH	0.851	(0.0004)	0.907	(0.0001)
HEIGHT	0.606	(0.0368)	0.911	(0.0001)
CROWN	0.853	(0.0004)	0.881	(0.0002)
BA	0.860	(0.0003)	0.846	(0.0005)
CA	0.944	(0.0001)	0.783	(0.0026)
VOLUME	0.853	(0.0004)	0.818	(0.0011)
TREESIZE	0.818	(0.0011)	0.783	(0.0026)
		White Pine (N = 13)		
DBH	0.961	(0.0001)	0.929	(0.0001)
HEIGHT	0.929	(0.0001)	0.972	(0.0001)
CROWN	0.890	(0.0001)	0.868	(0.0001)
BA	0.835	(0.0004)	0.874	(0.0001)
CA	0.978	(0.0001)	0.786	(0.0015)
VOLUME	0.956	(0.0001)	0.863	(0.0001)
TREESIZE	0.984	(0.0001)	0.973	(0.0001)

$WOUT_1$ = same variables adjusted for competition by the DDI method.

$WOUT_2$ = same variables adjusted for competition by the DRI method.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

Table 29. Spearman Rank Correlations of Distributions of Stand Means of DDI and DRI Competitive Fitness Estimates and of Characteristics Adjusted for Competition with the DDI and DRI

	$-COMP_2$	(PROB > |R|)	$-WOUT_2$	(PROB > |R|)
		Virginia Pine (N = 12)		
$D-COMP_1$	0.832	(0.0008)		
$H-COMP_1$	0.315	(0.3191)		
$C-COMP_1$	0.825	(0.0010)		
$B-COMP_1$	0.909	(0.0001)		
$CA-COMP_1$	0.895	(0.0001)		
$V-COMP_1$	0.944	(0.0001)		
$T-COMP_1$	0.944	(0.0001)		
$D-WOUT_1$			0.874	(0.0002)
$H-WOUT_1$			0.517	(0.0849)
$C-WOUT_1$			0.881	(0.0002)
$B-WOUT_1$			0.923	(0.0001)
$CA-WOUT_1$			0.867	(0.0003)
$V-WOUT_1$			0.909	(0.0001)
$T-WOUT_1$			0.958	(0.0001)
		White Pine (N = 13		
$D-COMP_1$	0.951	(0.0001)		
$H-COMP_1$	0.951	(0.0001)		
$C-COMP_1$	0.912	(0.0001)		
$B-COMP_1$	0.961	(0.0001)		
$CA-COMP_1$	0.967	(0.0001)		
$V-COMP_1$	0.951	(0.0001)		
$T-COMP_1$	0.934	(0.0001)		
$D-WOUT_1$			0.956	(0.0001)
$H-WOUT_1$			0.951	(0.0001)
$C-WOUT_1$			0.951	(0.0001)

Table 29 (continued)

	$-COMP_2$	(PROB > |R|)	$-WOUT_2$	(PROB > |R|)
$B-WOUT_1$			0.956	(0.0001)
$CA-WOUT_1$			0.852	(0.0002)
$V-WOUT_1$			0.907	(0.0001)
$T-WOUT_1$			0.956	(0.0001)

$-COMP_2$ = competitive fitness based on the DRI method.

$-WOUT_2$ = measured characteristics adjusted for competition by the DRI method.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

Table 30. Spearman Rank Correlations of Distributions of Family Means of Characteristics Adjusted for Competition with the DDI and DRI and Those for the Seven Original Characteristics

	$WOUT_1$	(PROB > |R|)	$WOUT_2$	(PROB > |R|)
		Virginia Pine (N = 128)		
DBH	0.701	(0.0001)	0.705	(0.0001)
HEIGHT	0.560	(0.0001)	0.866	(0.0001)
CROWN	0.752	(0.0001)	0.659	(0.0001)
BA	0.827	(0.0001)	0.628	(0.0001)
CA	0.876	(0.0001)	0.590	(0.0001)
VOLUME	0.822	(0.0001)	0.631	(0.0001)
TREESIZE	0.586	(0.0001)	0.523	(0.0001)
		White Pine (N = 128)		
DBH	0.894	(0.0001)	0.836	(0.0001)
HEIGHT	0.703	(0.0001)	0.883	(0.0001)
CROWN	0.880	(0.0001)	0.816	(0.0001)
BA	0.670	(0.0001)	0.778	(0.0001)
CA	0.949	(0.0001)	0.766	(0.0001)
VOLUME	0.933	(0.0001)	0.759	(0.0001)
TREESIZE	0.898	(0.0001)	0.888	(0.0001)

$WOUT_1$ = same variables adjusted for competition by the DDI method.

$WOUT_2$ = same variables adjusted for competition by the DRI method.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

Table 31. Spearman Rank Correlations of Distributions of Family Means of DDI and DRI Competitive Fitness Estimates and of Characteristics Adjusted for Competition with the DDI and DRI

	$-COMP_2$	(PROB > |R|)	$-WOUT_2$	(PROB > |R|)
		Virginia Pine (N = 128)		
$D-COMP_1$	0.757	(0.0001)		
$H-COMP_1$	0.485	(0.0001)		
$C-COMP_1$	0.833	(0.0001)		
$B-COMP_1$	0.882	(0.0001)		
$CA-COMP_1$	0.904	(0.0001)		
$V-COMP_1$	0.893	(0.0001)		
$T-COMP_1$	0.884	(0.0001)		
$D-WOUT_1$			0.773	(0.0001)
$H-WOUT_1$			0.555	(0.0001)
$C-WOUT_1$			0.828	(0.0001)
$B-WOUT_1$			0.826	(0.0001)
$CA-WOUT_1$			0.822	(0.0001)
$V-WOUT_1$			0.833	(0.9350)
$T-WOUT_1$			0.935	(0.0001)
		White Pine (N = 128)		
$D-COMP_1$	0.943	(0.0001)		
$H-COMP_1$	0.916	(0.0001)		
$C-COMP_1$	0.938	(0.0001)		
$B-COMP_1$	0.969	(0.0001)		
$CA-COMP_1$	0.962	(0.0001)		
$V-COMP_1$	0.968	(0.0001)		
$T-COMP_1$	0.894	(0.0001)		
$D-WOUT_1$			0.940	(0.0001)
$H-WOUT_1$			0.859	(0.0001)
$C-WOUT_1$			0.896	(0.0001)

Table 31 (continued)

	$-COMP_2$	(PROB > |R|)	$-WOUT_2$	(PROB > |R|)
$B-WOUT_1$			0.912	(0.0001)
$CA-WOUT_1$			0.872	(0.0001)
$V-WOUT_1$			0.892	(0.0001)
$T-WOUT_1$			0.974	(0.0001)

$-COMP_2$ = competitive fitness based on the DRI method.

$-WOUT_2$ = measured characteristics adjusted for competition by the DRI method.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

CHAPTER V

DISCUSSION

The assumption was made that intertree competition could be analyzed in progeny test plantations at a single time by partitioning the expressed variance into components which were either competitively influenced or noncompetitively influenced. What was estimated then, was neither pure competition nor the direct effects of competition. Rather, it was the portion of the total variation observed that was assumed to have been under the influence of intertree competition at the time of measurement. Competitively influenced variance was taken to represent the combined competitive ability responses of individuals or of groups in the plantations measured. Noncompetitively influenced variance, on the other hand, represented the combined responses of individuals or of groups expected under no expressed competition.

All of the characteristics measured appeared to be influenced by competition. Height was least sensitive to spacing in the spacing study, and this was reflected in the range of relative competitive-intensity coefficients (Table 8, p. 62) derived and used in the DDI method. Height did, however, appear significantly related to effective growing space utilized in each species, by the DRI approach (Table 11, p. 66), but the strength of relationship, as indicated by $\underline{r}^2$ values, was least among those of the measured characteristics. Since relationships of dimension and growing space were the basis for estimating

competition in each of the indices developed, it is concluded that height was least influenced by intertree competition.

Crown characteristics (crown diameter and crown area) were among the characteristics most sensitive to growing space (Tables 7 and 11, pp. 59 and 66). Crown characteristics, however, are probably useful only if they are correlated with bole dimensions such as DBH, BA, and volume. In both white pine and Virginia pine, low heritability estimates were observed in crown diameter, crown area, and competition estimates based on these characteristics in comparison to other characteristics measured. Although crown characteristics were found to be responsive to competitive influences, very little of this appeared to be associated with genetic potential. Little attention, therefore, should be paid to breeding of these characteristics for competitive advantage or otherwise.

DBH, BA, and volume appear to be the most important characteristics to consider when analyzing competition. Not only are these the most useful dimensions to fiber and lumber producers, they also are influenced significantly by competition and are highly heritable characteristics as compared to other tree dimensions. In both white pine and Virginia pine, relatively high estimates of heritability of competitive fitness estimates based on these characteristics were obtained, indicating that selecting for superior competitors in these traits is a feasible way to add to future gains.

A statistical factor, TREESIZE, was derived for each species and introduced into the competition analyses as a variable representing the

combined influences of all measured characteristics. It was anticipated that competition might be better represented by a variable representative of several measured dimensions than by characteristics considered individually. Although high positive correlations between TREESIZE and the characteristics of DBH, BA, and volume were found in both species, TREESIZE was found not to be as useful as single characteristics in representing competition. Relationships of TREESIZE and growing space (Tables 7 and 11) showed considerable lack of fit in both white and Virginia pine, as indicated by low $\underline{r}^2$ values.

Similar analytical responses were observed between TREESIZE and the characteristics of DBH, BA, and volume, but estimates of heritability of each of these differed. The estimates of heritability of TREESIZE in Virginia pine both with and without adjustment for competition, appeared consistently smaller than the estimates of heritability of DBH, BA and volume. The reverse was observed with respect to estimates of heritability of competitive-fitness estimates based on these characteristics. In white pine, estimates of heritability of DBH, BA, volume variables in relation to those of TREESIZE variables exhibited trends opposite to those observed in Virginia pine. The tree-size factor may be confounded by differential responses of individual characteristics to competition.

Comparison of the DDI and DRI methods in several of the analyses performed suggested that these two indices were not alike in what they estimated. An important question still to be answered, therefore, is: Which index is better? The DRI appears to be the more appropriate of

the two for at least two reasons. First, the DDI method relies on regression data collected from the Species-Spacing Comparison Study, a plantation that was distinct from the two progeny plantations which were actually evaluated for competitive influence. Genetic and environmental sources of variation which were not a part of the progeny plantations evaluated might have been introduced by this approach. As Sakai and Hatakeyama (1963) pointed out, the validity of analyses that assume equal environmental variances between two separate plantations may be questionable. A second reason is the age differences between plantations. In using the DDI approach, spacing relationships observed in the 15-year-old spacing study were assumed to be operating in the 14-year-old Virginia pine plantation and the 11-year-old white pine plantation. Recent findings such as those reported by Tauer (1975) suggest that competitive influences may change dramatically over time.

Besides these major difficulties, the dimension-on-spacing regressions used to compute relative competitive-intensity coefficients in the DDI method showed considerable lack of fit. Since only four spacings were represented in the spacing study, only four predicted values were computed for each dimension from which a regression was estimated (Figure 4, p. 27). For each characteristic in each species, therefore, a low $\underline{r}^2$ value was calculated, even though sample sizes of up to 400 trees were analyzed (Table 7). With such low $\underline{r}^2$ values, it is difficult to place much confidence in the competitive-intensity values derived, even as descriptive statistics for the spacing study plantation alone.

The DRI approach was developed after the difficulties associated with the DDI method became apparent. This index was considered to be an improvement since all variation accounted for was internal to the sample of trees being analyzed. One particularly noticeable area of improvement was the high $\underline{r}^2$ values obtained for regressions of dimension on effective growing space utilized (Table 11).

The DRI method offers a practical means of evaluating intertree competition in plantations of any age, particularly to tree breeders who don't have spacing study plantations which are necessary for use of the DDI approach. It is believed that with slight modification the methodology of the DRI approach can be made applicable to other species and progeny test situations, including those of hardwoods, for a reasonably efficient qualitative and quantitative evaluation of intertree competition.

Information needed before the DRI method can be employed, however, is the appropriate area to include in the zone of competitive influence that surrounds each test tree. In the current study, this determination was made subjectively based on information gathered from the Species-Spacing Study plantation. It may be that regression of dimension on effective growing space utilized (as in Figure 9, p. 43) could be used statistically to place limits on the area of competitive influence. Hypothetically, as trees planted at greater and greater spacings are included, the regression of dimension on effective growing space utilized should level off to zero slope in the region of largest effective growing spaces. In such cases, where a curvilinear response

is observed, only the portion of the curve expressing a significant positive slope should be included in the area of effective competitive influence.

The results of univariate analyses of variance for characteristics measured were probably influenced to some extent by sample size, particularly with respect to the detection of family differences in the Virginia pine. In the Virginia pine plantation, only four replications were measured. Within each of these four replications only four trees out of each family were sampled. Thus, comparisons among families within stands for each characteristic pitted groupings that were composed of a maximum of 16 observations (in some cases fewer) against one another. It is doubtful that these samples were large enough to detect family differences at the level of precision assumed for each characteristic during measurement. Family differences in DBH, BA, and volume and in competitive-fitness estimates based on DBH and BA might have been detected in Virginia pine had the sample size been larger.

Restricting interpretation to the results obtained with the DRI approach and the commercially important traits of DBH, BA, and volume, differences among stands were found in all characteristics as originally measured and upon adjustment for competition in both species. Competitive-fitness estimates based on all characteristics in both species also differed significantly among stands. Family differences were observed in white pine in all characteristics, both with and without adjustment for competition, and in competitive-fitness estimates based on all characteristics measured. In Virginia pine, family differences were

significant in all characteristics when adjusted for competition, but were not significant in unadjusted DBH, BA, and volume. Competitive-fitness estimates based on volume also exhibited significant differences among families. Failure to find family differences in Virginia pine was probably the result of small sample size rather than genuine responses of the characteristics themselves.

Results of the multiple regression (Tables 22 and 23, pp. 91 and 94), covariance slope comparison (Tables 24 and 25, pp. 98 and 99), and Spearman rank correlation of variance components (Table 26, p. 100) analyses of the characteristics of DBH, BA, and volume in both white pine and Virginia pine indicated significant differences between each of these characteristics and the same characteristics adjusted for DRI-derived competitional deviations. Each of these analyses in some manner compared variances of characteristics measured or distributions of variance components of characteristics. Thus, it appears safe to conclude that competition had a significant impact on the observed variances in DBH, BA, and volume.

Spearman rank correlations (Tables 28 and 30, pp. 105 and 108) showed that the distributions of stand and family means of DBH, BA, and volume in both species were relatively unaffected by competitive influences operating within the plantations. These observed effects of the influences of competition on means and variances are in agreement with the findings of Simmonds (1962) and Trenbath (1974).

Since the rankings of stand and family means were relatively unaffected by competition, it appears that selection performed at these

levels is a relatively safe practice in both white pine and Virginia pine at these stages in their development. What probably is not safe without considering competition is selection at the individual-tree level. A major portion of the variance estimated to be competitively influenced was in the within-family-plot category, caused by variation among individual trees. This component of variance appears to be an important contributor to derived estimates of heritability which are used to determine estimates of gain from selection.

Both inflations and deflations were observed in white pine and Virginia pine heritability estimates computed for important tree characteristics upon adjustment for competition-influenced variance. Competition might therefore be responsible for over- or underestimation of genetic gains in these characteristics. This observation agrees with conclusions of Hamblin and Rosielle (1978) from work with barley.

It is postulated that for a given characteristic (for example DBH), heritability of the measured value (h^2_{DBH}) and heritability of the characteristic adjusted for competition (h^2_{D-WOUT}) are nested, the smaller value within and contributing to the larger value. Thus, if the heritability for original DBH was larger than the heritability for DBH adjusted for competition, the former estimate would include the latter. In the converse situation (i.e., $h^2_{DBH} < h^2_{D-WOUT}$), h^2_{D-WOUT} would include h^2_{DBH}. This relationship among heritability estimates provides room for improvement in realized gains by maximizing the heritability estimate within its competitional allowance (i.e., $|h^2_{DBH} - h^2_{D-WOUT}|$).

By selecting individual trees within superior families which are superior performers under the influence of encountered competition and which excel also when competitional variance is adjusted for, it appears reasonable that the improvement realized will include gains resulting from genetic makeup plus advantages expressed by competitive fitness. This is postulated under the assumption that offspring of superior competitors in a random planting will perform similarly in a new random planting or in plantings of mixtures of each other. Thus, by accounting for competition, it might be possible to maximize heritability within its competitive allowance, and improve realized gains.

For example, possible gains realized in the next generation at the same age from mass selection when conventional estimation techniques are used and when competitional variance is considered were estimated (Table 32). In this example, the individual selection gain formula ($G = i\sigma h^2$) was used for simplicity. Conventional GAIN represents the estimated gain computed using h^2, where h^2 is the heritability estimate derived by conventional methodology. This estimated gain includes any competitional variance that is occurring within the plantation. GAIN-MIN represents the minimum probable gain realized in the next generation if competitional variance is ignored. The formula $G_{min} = i\sigma h^2_{min}$ was used to compute GAIN-MIN, where h^2_{min} represents the smaller of h^2 and h^2_{WOUT}. GAIN-MAX represents the maximum probable gain realized in the next generation if trees selected are superior both under current competitional stresses and when variance is adjusted for competition. Here, $G_{max} = i\sigma h^2_{max}$ was the formula used to compute

Table 32. Conventional Gains, Minimum Gains if Competition Is Ignored, and Maximum Gains if Competition Is Taken into Account from Single Tree (Mass) Selection[a]

	Conventional Gain	%	GAIN-MIN	%	GAIN-MAX	%
			Virginia Pine (Fourteen Growing Seasons)			
DBH (cm)	0.344	3	0.344	3	0.559	5
HEIGHT (m)	0.078	1	0.051	1	0.078	1
CROWN (m)	0.055	1	0.055	1	0.097	2
BA ($m^2 \times 10^{-3}$)	0.582	6	0.582	6	0.882	9
CA (m^2)	0.341	2	0.341	2	0.601	4
VOLUME ($m^3 \times 10^{-2}$)	0.216	6	0.216	6	0.229	6
			White Pine (Eleven Growing Seasons)			
DBH (cm)	0.656	6	0.360	3	0.656	6
HEIGHT (m)	0.381	6	0.131	1	0.381	6
CROWN (m)	0.193	5	0.088	2	0.193	5
BA ($m^2 \times 10^{-2}$)	0.105	12	0.044	5	0.105	12
CA (m^2)	1.095	9	0.333	3	1.095	9
VOLUME ($m^3 \times 10^{-2}$)	0.481	15	0.187	6	0.481	15

[a]Selection intensity is 25%.

GAIN-MAX, where h^2_{max} represents the larger of h^2 and h^2_{WOUT}. The h^2_{WOUT} used was that derived from trees adjusted for DRI-derived competition. The σ used in each formula was the square root of the conventional error mean square (EMS) which includes competitional variance. The selection intensity (i) was again 25% or 1.15 units of standard deviation.

A selection scheme which considers trees on the basis of performance exhibited under competition and also when competitional variance is adjusted for should maximize the gain realized in the succeeding generation. The reason for this is that trees so selected respond to both heritability estimates (with and without competition) at the selection intensity chosen and the larger of the two heritability estimates can be used. If half-sib offspring of these trees were planted in a new stand of similar environment, and underwent similar exposure to competition, performance should be at least as good at the same age of measurement as estimated by conventional gains and better in some cases.

By relying on conventional estimates, there is the danger of promising more than will be realized in the case of inflated heritability estimates when not selecting for competitive fitness simultaneously. On the other hand, when conventional estimates of heritability are diminished by competition, it may be possible to add significantly to gains realized by selecting trees which appear most resistant to competitive pressures.

This study makes no attempt to determine when selection for mature characteristics should be made in progeny plantations. Franklin (1979)

considered this problem and suggested that selection based on mature characteristics in forest trees should be delayed until at least half of the rotation age. This conclusion resulted from observations of the behavior of additive-genetic and environmental variance components, phenotypic variance, and heritability estimates over the rotation cycle in four North American conifer species. The responses of variance components and heritability estimates were heavily influenced by intertree competition during the phase of stand development when selection for mature characteristics was considered optimum. Perhaps analytical techniques which take into consideration the influences of intertree competition in progeny plantations can be used to move the optimum period of selection to an earlier age.

A real understanding of how intertree competition is affecting individual-tree, stand and family performance in progeny test plantations cannot be gained from a single static analysis. Competition is a dynamic process which is undoubtedly responsible for continual changes in expressed characteristics in plantations throughout the rotation period. As such, it should be carefully monitored through all stages of stand development, from establishment to maturity. This study provides techniques and methodology which can be applied to plantations not originally designed to monitor competitive interactions. Perhaps future study plantations will be established under designs that are more amenable to competition evaluation. Increased understanding of competition, how it changes over time, and how it affects progeny performance

in tree improvement plantations will make possible improved heritability estimates and, consequently, improve the accuracy of predicted gains.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The influences of intertree competition in open-pollinated progeny plantations of Virginia pine and white pine were determined as dimensional-spatial relationships among individually sampled trees and their effectively competing neighbors. Two separate indices of competitive fitness were developed, the Dimension-Difference Index (DDI) and the Distance-Ratio Index (DRI). Competitive interactions were evaluated in each species in terms of six measured characteristics and a statistically derived tree size factor.

On the basis of the results obtained in this investigation, the following conclusions were reached:

1. The DRI appeared to be better than the DDI in estimating competitive influences occurring among individually sampled trees, stands and families in open-pollinated progeny plantations of both Virginia and white pine. The DRI was not dependent on information gathered from a conveniently nearby spacing test, of same species and age, which was required in application of the DDI. Methodology employed in the DRI appears to be applicable to forest tree improvement plantations of species and ages other than those studied here.

2. Three of the characteristics measured were found to be important when considering the influences of competition in tree improvement plantations: diameter at breast height, basal area, and

volume. These three traits, in addition to being significantly influenced by competition, were observed to be among the most highly heritable of the characteristics measured.

3. The tree-size factors derived based on all measured characteristics were not as useful as measured characteristics individually for representing tree performance under the influence of competition.

4. The overall variances and distributions of variance components were significantly influenced by intertree competition. The majority of variance attributable to competitive interaction in each case was located in the component of within-plot variances. Upon adjustment for competition, variance within plots was reduced, and this was accompanied by increased percentage contribution to the total variance by replications and replications x families-within-stand-interaction sources.

5. The rankings of stand and family means and values of overall means, themselves, were relatively unchanged by adjusting for competitional variance.

6. Estimates of heritability in the narrow sense were both inflated and deflated by competition, suggesting that projected gain estimates based on these might be influenced to a significant degree.

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APPENDIXES

APPENDIX A

QUADRATIC REGRESSION MODELS

QUADRATIC REGRESSION MODELS

The dimension-on-spacing regressions used to determine effective competitors and effective interaction levels of those competitors with sampled test trees were derived in both linear and quadratic form. The quadratic equations of regression of measured and derived characteristics on spacing in Virginia pine (Table A-1) and white pine (Table A-2) were computed from the spacing study data. Quadratic regressions of dimensions on effective growing space utilized (computed by the DRI method) for Virginia pine (Table A-3) and white pine (Table A-4) also were derived.

For several of the characteristics in both species, the best-fit quadratic forms of regression equations computed were found to be unusable for one of two reasons. In the first situation, the contribution of the regression coefficient of the quadratic term in the equation derived was not significantly different from zero. The equation derived for BA (Table A-3) provides an example of this situation. Here, there was essentially nothing gained over the linear regression model by the addition of a quadratic term. The second situation was discovered in attempting to make use of these regressions for the computation of competitive-fitness values. When the regressions were reversed to estimate competitive interaction, the best-fit relationships of some variables with spacing were found to be not always decreasing over the range of spacings considered (Figures A-1 and A-2). This second situation was considered to be untenable to the assumptions concerning competition (Sakai and Mukaide, 1967; Gerrard, 1969). Any

Table A-1. Equations of Quadratic Regression of Measured and Derived Characteristics on Spacing, Parameter Tests and Correlation Coefficients in Virginia Pine from the Spacing Study Data (N = 312)

Parameter	T for Ho:Parameter=0	R^2
DBH (cm) = 9.3391 + 0.8008(SPACING (m^2)) - 0.0022(SPACING^2 (m^2))		
INTERCEPT	15.68**	0.396
SPACING	6.59**	
SPACING^2	-3.75**	
HEIGHT (m) = 8.9371 - 0.0054(SPACING (m^2)) - 0.0000065(SPACING^2 (m^2))		
INTERCEPT	35.04**	0.001
SPACING	-0.09	
SPACING^2	-0.04	
CROWN (m) = 2.2803 + 0.2788(SPACING (m^2)) - 0.00054(SPACING^2 (m^2))		
INTERCEPT	12.88**	0.548
SPACING	7.72**	
SPACING^2	-3.77**	
BA (m^2) = 0.0061 + 0.0022(SPACING (m^2)) - 0.0000032(SPACING^2 (m^2))		
INTERCEPT	4.54**	0.413
SPACING	6.17**	
SPACING^2	-3.18**	
CA (m^2) = 3.3979 + 1.5468(SPACING (m^2)) - 0.0022(SPACING^2 (m^2))		
INTERCEPT	2.83**	0.553
SPACING	6.32**	
SPACING^2	-2.23*	

Table A-1 (continued)

Parameter	T for Ho:Parameter=0	R^2
VOLUME (m^3) = 0.0235 + 0.0065(SPACING (m^2)) - 0.000011(SPACING^2 (m^2))		
INTERCEPT	3.83**	0.305
SPACING	4.88**	
SPACING^2	-2.52*	
TREESIZE = 1.7315 + 0.2293(SPACING (m^2)) - 0.00043(SPACING^2 (m^2))		
INTERCEPT	13.65**	0.634
SPACING	8.85**	
SPACING^2	-4.09**	

*Significant at 0.05 level.

**Significant at 0.01 level.

Table A-2. Equations of Quadratic Regression of Measured and Derived Characteristics on Spacing, Parameter Tests and Correlation Coefficients in White Pine from the Spacing Study Data (N = 400)

Parameter	T for Ho:Parameter=0	R^2
DBH (cm) = 11.9483 + 0.3111(SPACING (m^2)) + 0.000043(SPACING^2 (m^2))		
INTERCEPT	13.51**	0.168
SPACING	1.76	
SPACING^2	0.06	
HEIGHT (m) = 9.4527 - 0.0614(SPACING (m^2)) + 0.00032(SPACING^2 (m^2))		
INTERCEPT	29.33**	0.022
SPACING	-0.96	
SPACING^2	1.15	
CROWN (m) = 2.0532 + 0.2120(SPACING (m^2)) - 0.00032(SPACING^2 (m^2))		
INTERCEPT	11.09**	0.415
SPACING	5.72**	
SPACING^2	-2.40*	
BA (m^2) = 0.0125 + 0.00065(SPACING (m^2)) + 0.00000075(SPACING^2 (m^2))		
INTERCEPT	5.84**	0.188
SPACING	1.49	
SPACING^2	0.46	
CA (m^2) = 2.9120 + 1.0538(SPACING (m^2)) - 0.0011(SPACING^2 (m^2))		
INTERCEPT	2.49*	0.404
SPACING	4.50**	
SPACING^2	-1.21	

Table A-2 (continued)

Parameter	T for Ho:Parameter=0	R^2
VOLUME (m^3) = 0.0654 + 0.0022(SPACING (m^2)) + 0.0000086(SPACING^2 (m^2))		
INTERCEPT	5.11**	0.165
SPACING	0.85	
SPACING^2	0.95	
TREESIZE = 0.8310 + 0.0743(SPACING (m^2)) - 0.0000032(SPACING^2 (m^2))		
INTERCEPT	5.07**	0.234
SPACING	2.26	
SPACING^2	-0.03	

*Significant at 0.05 level.

**Significant at 0.01 level.

Table A-3. Equations of Quadratic Regression of Characteristics on Effective Growing Space Utilized (computed by the DRI method), Parameter Tests, and Correlation Coefficients in the Virginia Pine Heritability Study (N = 1820)

Parameter	T for Ho:Parameter=0	R^2
DBH (cm) = 2.6933 + 1.3067(SPACE (m^2)) - 0.0022(SPACE^2 (m^2))		
INTERCEPT	7.32**	0.662
SPACE	13.83**	
SPACE^2	-3.52**	
HEIGHT (m) = 4.4204 + 0.6211(SPACE (m^2)) - 0.0022(SPACE^2 (m^2))		
INTERCEPT	12.07**	0.289
SPACE	6.38**	
SPACE^2	-2.96**	
CROWN (m) = 0.3815 + 0.6232(SPACE (m^2)) - 0.0011(SPACE^2 (m^2))		
INTERCEPT	3.50**	0.691
SPACE	22.13**	
SPACE^2	-9.13**	
BA (m^2) = 0.0015 + 0.0011(SPACE (m^2)) - 0.000000043(SPACE^2 (m^2))		
INTERCEPT	6.27**	0.765
SPACE	19.47**	
SPACE^2	-0.13	
CA (m^2) = 0.8567 + 1.8342(SPACE (m^2)) - 0.0022(SPACE^2 (m^2))		
INTERCEPT	2.88**	0.754
SPACE	25.60**	
SPACE^2	-5.07*	

Table A-3 (continued)

Parameter	T for Ho:Parameter=0	R^2
VOLUME (m^3) = 0.0050 + 0.0032(SPACE (m^2)) - 0.0000022(SPACE^2 (m^2))		
INTERCEPT	6.23**	0.767
SPACE	18.49**	
SPACE^2	-2.29*	
TREESIZE = 0.0397 + 0.1582(SPACE (m^2)) - 0.00011(SPACE^2 (m^2))		
INTERCEPT	0.30	0.474
SPACE	8.00**	
SPACE^2	-2.06*	

*Significant at 0.05 level.

**Significant at 0.01 level.

Table A-4. Equations of Quadratic Regression of Characteristics on Effective Growing Space Utilized (computed by the DRI method), Parameter Tests, and Correlation Coefficients in the White Pine Heritability Study (N = 4196)

Parameter	T for Ho:Parameter=0	R^2
DBH (cm) = 0.1773 + 1.7147(SPACE (m^2)) - 0.0043(SPACE^2 (m^2))		
INTERCEPT	1.23	0.749
SPACE	45.91**	
SPACE^2	-18.71**	
HEIGHT (m) = -0.5564 + 1.2874(SPACE (m^2)) - 0.0043(SPACE^2 (m^2))		
INTERCEPT	-3.80**	0.590
SPACE	32.60**	
SPACE^2	-18.67**	
CROWN (m) = 0.0375 + 0.6566(SPACE (m^2)) - 0.0022(SPACE^2 (m^2))		
INTERCEPT	0.78	0.740
SPACE	51.66**	
SPACE^2	-23.52**	
BA (m^2) = 0.0002 + 0.0011(SPACE (m^2)) - 0.0000011(SPACE^2 (m^2))		
INTERCEPT	1.58	0.751
SPACE	41.46**	
SPACE^2	-7.46**	
CA (m^2) = -0.0248 + 1.8428(SPACE (m^2)) - 0.0032(SPACE^2 (m^2))		
INTERCEPT	-0.15	0.729
SPACE	46.66**	
SPACE^2	-13.90*	

Table A-4 (continued)

Parameter	T for Ho:Parameter=0	R^2
VOLUME (m^3) = 0.00008 + 0.0043(SPACE (m^2)) - 0.0000022(SPACE^2 (m^2))		
INTERCEPT	0.16	0.722
SPACE	35.89**	
SPACE^2	-3.48**	
TREESIZE = 0.3167 + 0.2217(SPACE (m^2)) - 0.00043(SPACE^2 (m^2))		
INTERCEPT	5.78**	0.434
SPACE	27.35**	
SPACE^2	-15.94**	

*Significant at 0.05 level.

**Significant at 0.01 level.

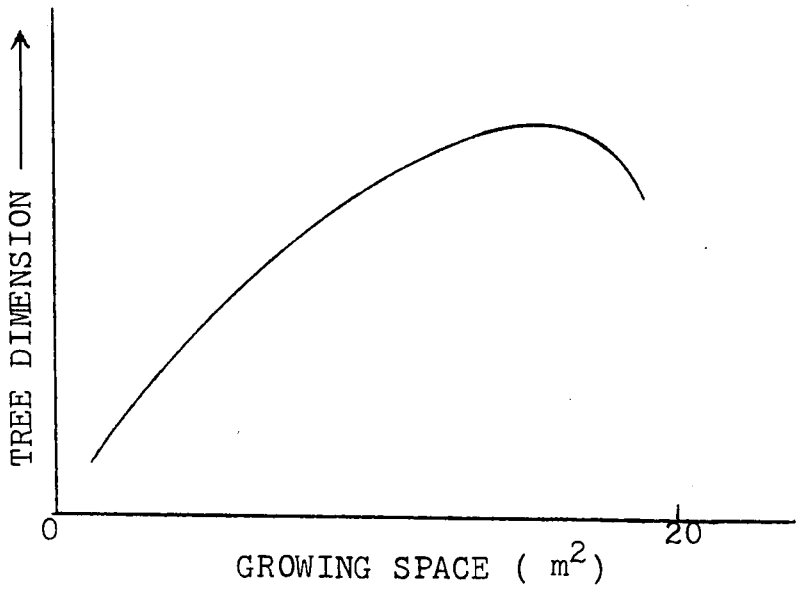


Figure A-1. One type of quadratic regression of tree dimension on growing space observed for several of the characteristics measured.

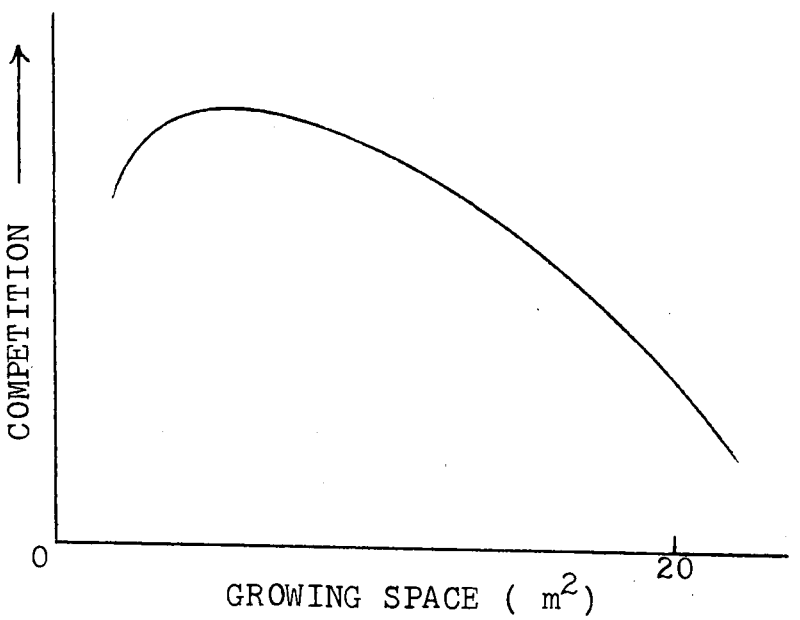


Figure A-2. The quadratic regression of competition on growing space, resulting from a reversal of Figure A-1, which shows competition as increasing with growing space over a portion of the range of growing spaces considered. The atypical nature of this response made it unusable for interpretation of competitive effects.

characteristics, therefore, which displayed such responses were omitted from further computation of competitive-fitness estimates based upon their quadratic equations.

Those characteristics which did exhibit appropriate quadratic responses to spacing were analyzed for competition in similar fashion to the way in which all characteristics were analyzed based upon their linear responses to spacing. Comparisons were made between linear- and quadratic-derived competitive-fitness values and between characteristics adjusted for linear- and quadratic-derived competitional variation.

Pearson Product-moment correlations between linear- and quadratic-derived variables in both species were computed (Table A-5), and extremely high association was evident in all comparisons made. Spearman rank correlations for linear- and quadratic-derived variance component distributions also were computed (Table A-6). Here again (with the exception of TREESIZE IN Virginia pine) near-perfect correlations were observed throughout the comparisons made indicating very little difference between linear- and quadratic derived components of variance of each characteristic and, presumably, between heritability estimates derived from these.

Multiple-regression comparisons (Tables A-7 and A-8) did show significant differences in overall variance in many of the linear- versus quadratic-derived variables. This is not surprising since linear and quadratic regressions differ in form. It is apparent that comparisons of this kind are much more sensitive to expressed differences than the other types of comparisons made. Since large sample sizes were

Table A-5. Pearson Product-Moment Correlations between Linear-Derived and Quadratic-Derived Variables of Measured Characteristics

	-QUAD
Virginia Pine (N = 1820)	
$C\text{-}COMP_1$	1.000
$B\text{-}COMP_1$	0.999
$CA\text{-}COMP_1$	1.000
$V\text{-}COMP_1$	1.000
$T\text{-}COMP_1$	1.000
$D\text{-}COMP_2$	0.998
$CA\text{-}COMP_2$	0.998
$T\text{-}COMP_2$	0.999
$C\text{-}WOUT_1$	0.993
$B\text{-}WOUT_1$	0.998
$CA\text{-}WOUT_1$	0.998
$V\text{-}WOUT_1$	0.998
$T\text{-}WOUT_1$	0.950
$D\text{-}WOUT_2$	0.997
$CA\text{-}WOUT_2$	1.000
$T\text{-}WOUT_2$	0.999
White Pine (N = 4196)	
$C\text{-}COMP_1$	1.000
$CA\text{-}COMP_2$	0.967
$T\text{-}COMP_2$	0.960
$C\text{-}WOUT_1$	0.998
$CA\text{-}WOUT_2$	1.000
$T\text{-}WOUT_2$	0.971

-QUAD = Quadratic-derived variables of the same measured characteristics.

Table A-6. Spearman Rank Correlations between Variance Component Distributions of Linear-Derived and Quadratic-Derived Variables of Measured Characteristics

	-QUAD	(PROB > |R|)
	Virginia Pine (N = 6)	
$C\text{-}COMP_1$	1.000	(0.000)
$B\text{-}COMP_1$	1.000	(0.000)
$CA\text{-}COMP_1$	1.000	(0.000)
$V\text{-}COMP_1$	1.000	(0.000)
$T\text{-}COMP_1$	1.000	(0.000)
$D\text{-}COMP_2$	0.955	(0.003)
$CA\text{-}COMP_2$	1.000	(0.000)
$T\text{-}COMP_2$	1.000	(0.000)
$C\text{-}WOUT_1$	1.000	(0.000)
$B\text{-}WOUT_1$	1.000	(0.000)
$CA\text{-}WOUT_1$	1.000	(0.000)
$V\text{-}WOUT_1$	1.000	(0.000)
$T\text{-}WOUT_1$	0.714	(0.1108)
$D\text{-}WOUT_2$	1.000	(0.000)
$CA\text{-}WOUT_2$	1.000	(0.000)
$T\text{-}WOUT_2$	1.000	(0.000)
	White Pine (N = 6)	
$C\text{-}COMP_1$	1.000	(0.000)
$CA\text{-}COMP_2$	1.000	(0.000)
$T\text{-}COMP_2$	0.943	(0.0048)
$C\text{-}WOUT_1$	1.000	(0.000)
$CA\text{-}WOUT_2$	1.000	(0.000)
$T\text{-}WOUT_2$	1.000	(0.000)

-QUAD = Quadratic-derived variables of the same measured characteristics.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

Table A-7. Multiple-Regression Comparisons of Linear- and Quadratic-Derived Variables of Characteristics Measured in Virginia Pine

Dependent variable	Independent variables	Type IV SS	F value	R^2
TREESIZE	$C\text{-}COMP_1$	0.3354	5.60*	0.773
	$C\text{-}COMP_1\text{-}Q$[a]	0.0603	1.01	
TREESIZE	$B\text{-}COMP_1$	3.0605	64.69**	0.821
	$B\text{-}COMP_1\text{-}Q$	1.0744	22.71**	
TREESIZE	$CA\text{-}COMP_1$	2.0171	34.89**	0.781
	$CA\text{-}COMP_1\text{-}Q$	1.1175	19.33**	
TREESIZE	$V\text{-}COMP_1$	1.9144	42.24**	0.828
	$V\text{-}COMP_1\text{-}Q$	0.7252	16.00**	
TREESIZE	$T\text{-}COMP_1$	0.8125	22.47**	0.863
	$T\text{-}COMP_1\text{-}Q$	0.2049	5.67*	
TREESIZE	$D\text{-}COMP_2$	1.1133	10.95**	0.616
	$D\text{-}COMP_2\text{-}Q$	0.0014	0.01	
TREESIZE	$T\text{-}COMP_2$	0.0000	0.00	0.474
	$T\text{-}COMP_2\text{-}Q$	0.5934	4.26*	
TREESIZE	$C\text{-}WOUT_1$	246.3114	5007.80**	0.814
	$C\text{-}WOUT_1\text{-}Q$	200.5258	4076.92**	
TREESIZE	$B\text{-}WOUT_1$	13.4561	136.40**	0.627
	$B\text{-}WOUT_1\text{-}Q$	22.0497	223.51**	
TREESIZE	$CA\text{-}WOUT_1$	123.6370	2758.56**	0.830
	$CA\text{-}WOUT_1\text{-}Q$	100.0715	2232.77**	
TREESIZE	$V\text{-}WOUT_1$	102.4614	1527.86**	0.754
	$V\text{-}WOUT_1\text{-}Q$	82.7079	1269.63**	
TREESIZE	$T\text{-}WOUT_1$	377.0389	98426.75**	0.985
	$T\text{-}WOUT_1\text{-}Q$	236.0926	61632.43**	
TREESIZE	$D\text{-}WOUT_2$	0.0014	0.01	0.314
	$D\text{-}WOUT_2\text{-}Q$	1.1032	6.08*	
TREESIZE	$T\text{-}WOUT_2$	0.6282	5.01*	0.527
	$T\text{-}WOUT_2\text{-}Q$	0.0005	0.00	

*Significant at 0.05 level.

**Significant at 0.01 level.

[a]Variables with suffix-Q are Quadratic-derived variables.

Table A-8. Multiple-Regression Comparisons of Linear- and Quadratic-Derived Variables of Characteristics Measured in White Pine

Dependent variable	Independent variables	Type IV SS	F value	R^2
TREESIZE	$C\text{-}COMP_1$	3.8992	31.77**	0.737
	$C\text{-}COMP_1\text{-}Q$[a]	2.3011	18.75**	
TREESIZE	$CA\text{-}COMP_2$	0.9164	5.68*	0.654
	$CA\text{-}COMP_2\text{-}Q$	0.6109	3.79	
TREESIZE	$T\text{-}COMP_2$	0.0000	0.00	0.434
	$T\text{-}COMP_2\text{-}Q$	67.0604	253.99**	
TREESIZE	$C\text{-}WOUT_1$	823.3151	7564.81**	0.766
	$C\text{-}WOUT_1\text{-}Q$	738.6047	6785.47**	
TREESIZE	$CA\text{-}WOUT_2$	0.3998	1.05	0.187
	$CA\text{-}WOUT_2\text{-}Q$	0.6112	1.61	
TREESIZE	$T\text{-}WOUT_2$	66.6621	356.75**	0.599
	$T\text{-}WOUT_2\text{-}Q$	0.0006	0.00	

*Significant at 0.05 level.

**Significant at 0.01 level.

[a]Variables with suffix-Q are Quadratic-derived variables.

used, detected differences here, although highly significant statistically, may not have a great impact on the practical interpretation of results overall. Several nonsignificant contributions also were observed indicating a definite interchangeability of linear- and quadratic-derived variables for these specific characteristics.

The distributions of stand means (Table A-9) and family means (Table A-10) were not significantly affected by the mathematical nature of the regressions used to derive competion estimates. Very high correlations were observed throughout. It is concluded, therefore, that linear-derived variables were highly substitutable for quadratic-derived variables of the same characteristic. The slight improvement of fit introduced by the use of quadratic-form regressions was overshadowed by the added complexity concurrently introduced, and this is the reason why quadratic interpretations were not included in the main presentation. There remains room for improvement in adapting quadratic and higher-powered models to the study of competitive relationships.

Table A-9. Spearman Rank Correlations between Distributions of Stand Means of Linear-Derived and Quadratic-Derived Variables of Measured Characteristics

	-QUAD	(PROB > |R|)
	Virginia Pine (N = 12)	
$C\text{-}COMP_1$	1.000	(0.000)
$B\text{-}COMP_1$	1.000	(0.000)
$CA\text{-}COMP_1$	1.000	(0.000)
$V\text{-}COMP_1$	1.000	(0.000)
$T\text{-}COMP_1$	1.000	(0.000)
$D\text{-}COMP_2$	1.000	(0.000)
$CA\text{-}COMP_2$	1.000	(0.000)
$T\text{-}COMP_2$	1.000	(0.000)
$C\text{-}WOUT_1$	1.000	(0.000)
$B\text{-}WOUT_1$	1.000	(0.000)
$CA\text{-}WOUT_1$	0.993	(0.0001)
$V\text{-}WOUT_1$	1.000	(0.000)
$T\text{-}WOUT_1$	0.993	(0.0001)
$D\text{-}WOUT_2$	0.993	(0.0001)
$CA\text{-}WOUT_2$	1.000	(0.000)
$T\text{-}WOUT_2$	0.993	(0.0001)
	White Pine (N = 13)	
$C\text{-}COMP_1$	1.000	(0.000)
$CA\text{-}COMP_2$	1.000	(0.000)
$T\text{-}COMP_2$	0.995	(0.0001)
$C\text{-}WOUT_1$	1.000	(0.000)
$CA\text{-}WOUT_2$	1.000	(0.000)
$T\text{-}WOUT_2$	0.995	(0.0001)

-QUAD = Quadratic-derived variables of the same measured characteristics.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

Table A-10. Spearman Rank Correlations between Distributions of Family Means of Linear-Derived and Quadratic-Derived Variables of Measured Characteristics

	-QUAD	(PROB > |R|)
	Virginia Pine (N = 128)	
$C\text{-}COMP_1$	1.000	(0.0001)
$B\text{-}COMP_1$	1.000	(0.0001)
$CA\text{-}COMP_1$	1.000	(0.0001)
$V\text{-}COMP_1$	1.000	(0.0001)
$T\text{-}COMP_1$	0.999	(0.0001)
$D\text{-}COMP_2$	0.997	(0.0001)
$CA\text{-}COMP_2$	1.000	(0.0000)
$T\text{-}COMP_2$	0.998	(0.0001)
$C\text{-}WOUT_1$	0.995	(0.0001)
$B\text{-}WOUT_1$	0.999	(0.0001)
$CA\text{-}WOUT_1$	0.998	(0.0001)
$V\text{-}WOUT_1$	0.998	(0.0001)
$T\text{-}WOUT_1$	0.953	(0.0001)
$D\text{-}WOUT_2$	0.998	(0.0001)
$CA\text{-}WOUT_2$	1.000	(0.0001)
$T\text{-}WOUT_2$	0.998	(0.0001)
	White Pine (N = 128)	
$C\text{-}COMP_1$	1.000	(0.0001)
$CA\text{-}COMP_2$	1.000	(0.0001)
$T\text{-}COMP_2$	0.977	(0.0001)
$C\text{-}WOUT_1$	0.999	(0.0001)
$CA\text{-}WOUT_2$	1.000	(0.0001)
$T\text{-}WOUT_2$	0.987	(0.0001)

-QUAD = Quadratic-derived variables of the same measured characteristics.

(PROB > |R|) = level of significance under Ho: no association (RHO = 0).

APPENDIX B

HERITABILITY CHANGES OVER TIME

HERITABILITY CHANGES OVER TIME

An important concern of tree improvement research has been the need to explain observed fluctuation in heritability estimates of measured traits over the rotation period in study plantations. One model recently developed (Franklin, 1979) relates levels of genetic variance to stand development on the basis of responses of four North American conifer species; Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), ponderosa pine (Pinus ponderosa Laws.), loblolly pine (Pinus taeda L.), and slash pine (Pinus elliotii Engelm.). This model is summarized (Figure B-1 and Figure B-2) for loblolly pine; however, similar trends were observed in all four conifer species examined.

The transition from the juvenile genotypic phase into the mature genotypic phase appears to coincide roughly with the intensification of intertree competition, as suggested by Namkoong and Conkle (1976). All characteristics, however, even for the same species, do not pass through this transition at the same age. For example, volume in loblolly pine (Figure B-2) reached the transition approximately 10 years later than did height (Figure B-1) in the same trees.

A summary of heritabilities estimated over time in the progeny test plantations examined in the current study was compiled (Table B-1 and Table B-2). Fluctuations in heritability estimates, similar to trends observed in other conifer species, were found. Comparison of estimates of heritability of traits adjusted for competition to conventionally

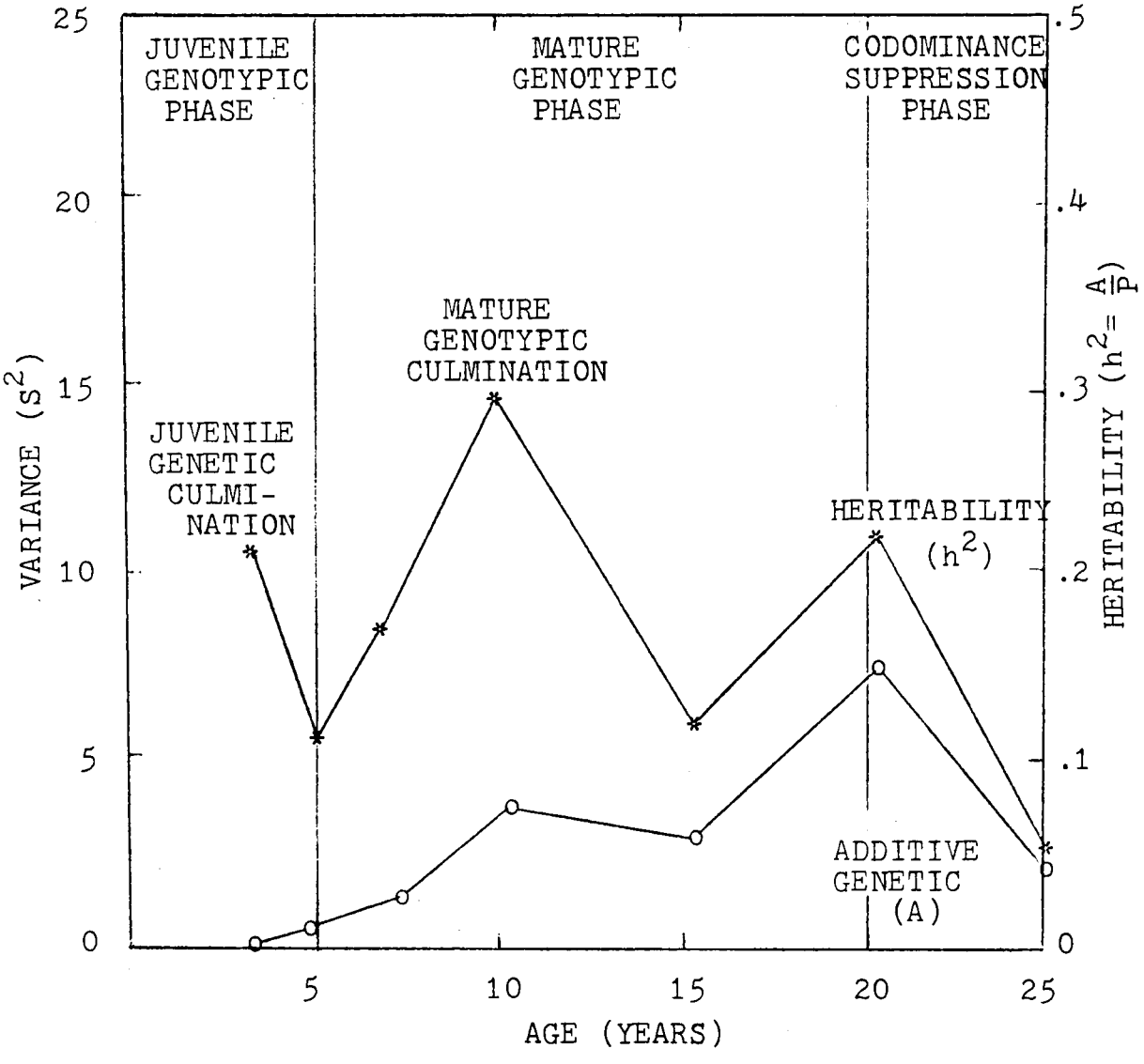


Figure B-1. Genetic phases of stand development interpreted for height in a loblolly pine family trial. Data from unpublished study NCP-45 by Trousdell (Franklin, 1979).

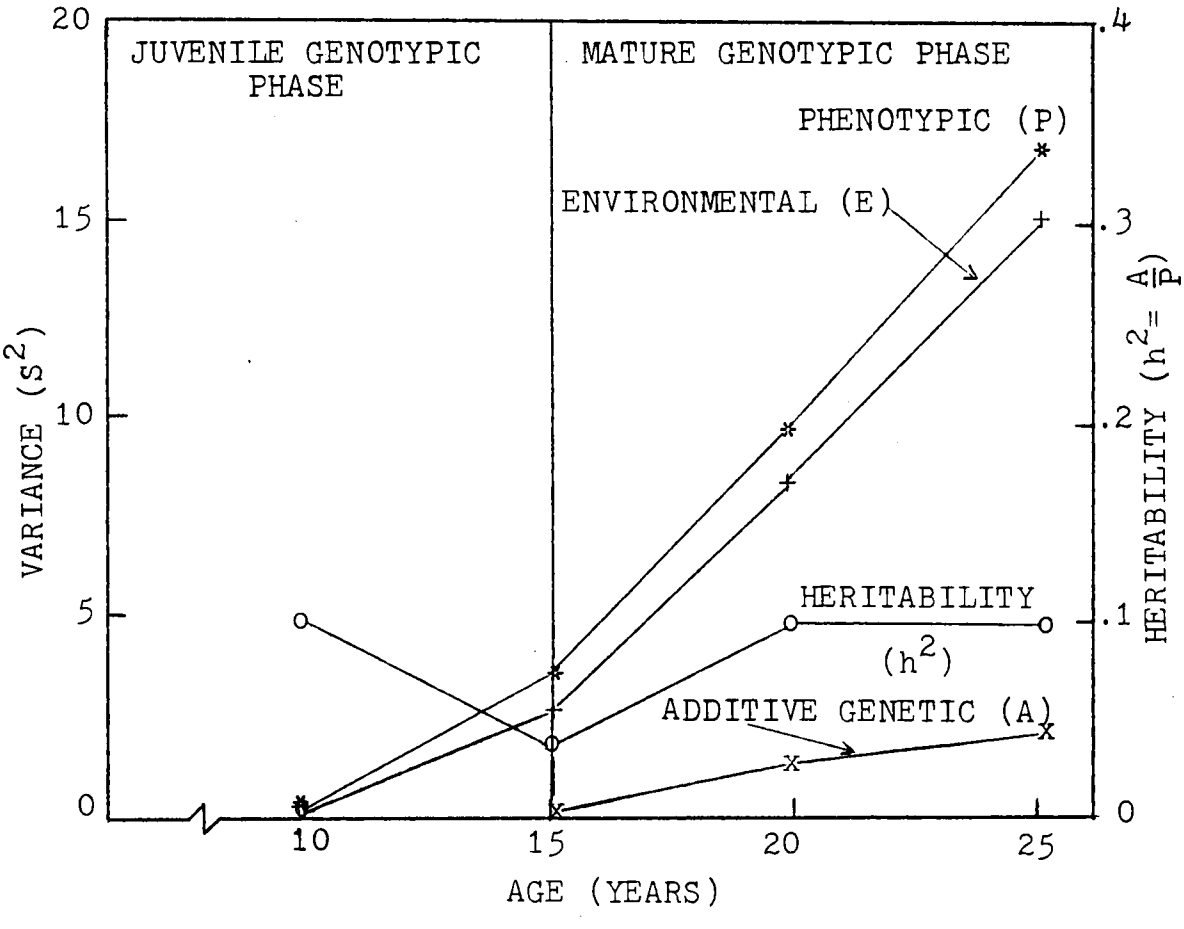


Figure B-2. Trends in variances and heritability of volume in a loblolly pine family trial through 25 years of growth. Data from unpublished study NCP-45 by Trousdell (Franklin, 1979).

Table B-1. Estimates of Narrow-Sense Heritability of Characteristics of Virginia Pine from Two-, Five-, and Fourteen-Year Measurements and of Characteristics Adjusted for DRI Competition at Age Fourteen

	Two-year[a] h^2	Five-year[b] h^2	Fourteen-year h^2	Fourteen-year[c] h^2-$WOUT_2$
Height	0.48	0.340	0.103	0.067
DBH	0.41	0.267	0.128	0.208
Branch Length	0.47	0.128	0.051[d]	0.091[d]
Volume	-	0.341	0.117	0.124

[a]Evans (1971).

[b]Rink (1974).

[c]Heritabilities of characteristics adjusted for DRI competition.

[d]Crown diameter.

Table B-2. Estimates of Narrow-Sense Heritability of Characteristics of White Pine from Eight- and Eleven-Year Measurements and of Characteristics Adjusted for DRI Competition at Age Eleven

	Eight-year[a] h^2	Eleven-year h^2	Eleven-year[b] h^2-$WOUT_2$
Height	0.370	0.304	0.106
DBH	0.296	0.195	0.107
Crown Width	0.307	0.166	0.076
Volume	0.279	0.221	0.086

[a] desBordes (1979).

[b] Heritabilities of characteristics adjusted for DRI competition.

derived estimates at the same and earlier ages provides a way of inspecting the efficacy of measuring competition in the current study.

In white pine (Table B-2), close agreement with the stand development model (Franklin, 1979) was evident. The estimates of heritability of all characteristics adjusted for competition were smaller than those derived at the same or earlier ages by conventional methods. In terms of the stand development model, the white pine plantation at age eleven may be just approaching, or already into, the mature genotypic phase for these characteristics. In effect, what was probably estimated by adjusting for competitional variance was the approximate heritability of traits at the transition age between the juvenile genotypic phase and the mature genotypic phase.

In Virginia pine (Table B-1), estimates of heritability of all characteristics, except height, were deflated by competition at age fourteen. This response is difficult to explain in terms of the stand development model (Franklin, 1979), considering that the Virginia pine plantation was older than the white pine plantation at the time of measurement. Small sample sizes might be affecting the results in this species. Another possibility is that developmental dynamics in Virginia pine differ from those observed in other conifer species. The traits in question in Virginia pine might resemble volume in loblolly pine (Figure B-2) in that they make the transition into the mature genotypic phase at a later age. If this is the case, what is probably being observed is the response of juvenile characteristics as affected with competition.

APPENDIX C

MEANS OF CHARACTERISTIC VARIABLES IN VIRGINIA PINE AND WHITE PINE BY STAND AND BY FAMILY WITHIN STAND

Table C-1. Mean Values of Characteristics Measured in Virginia Pine after Fourteen Growing Seasons

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
1	1	12	7.7	12.3	4.2	0.012	14.8	0.040
	2	8	7.7	11.8	3.9	0.011	13.0	0.035
	3	16	7.8	10.7	4.2	0.009	14.2	0.030
	6	16	8.1	11.6	4.0	0.011	13.2	0.037
	7	12	8.0	12.6	3.7	0.013	11.0	0.040
	9	12	8.7	13.2	4.6	0.014	16.8	0.050
	12	16	8.1	11.9	4.2	0.012	14.1	0.038
	13	16	8.0	11.9	3.8	0.012	12.4	0.040
	15	16	8.0	11.4	3.8	0.011	12.3	0.036
Stand Mean		124	8.0	11.9	4.0	0.012	13.5	0.038
2	1	16	8.2	11.1	4.0	0.010	13.0	0.033
	3	16	7.9	10.6	3.7	0.009	11.2	0.030
	4	16	7.8	11.2	4.1	0.010	13.6	0.032
	7	8	8.1	11.2	4.1	0.010	13.5	0.033
	8	16	7.6	10.2	3.3	0.009	9.4	0.027
	9	16	7.7	10.9	3.8	0.010	12.2	0.031
	10	8	7.9	10.9	4.1	0.010	14.0	0.032
	11	16	7.6	10.2	3.7	0.009	12.0	0.028
	12	12	8.0	11.2	3.8	0.010	11.5	0.033
	14	12	8.1	10.6	3.7	0.009	11.4	0.030
Stand Mean		136	7.9	10.8	3.8	0.010	12.0	0.031
3	2	16	8.0	10.6	3.9	0.009	12.9	0.030
	4	16	7.7	9.4	3.5	0.007	10.0	0.023
	5	16	7.8	10.5	3.7	0.009	11.1	0.028
	6	12	7.9	10.2	3.8	0.008	11.7	0.027
	7	16	8.0	10.1	4.0	0.009	13.2	0.028
	8	16	7.4	10.5	3.8	0.009	12.2	0.030
	9	12	7.8	10.2	4.0	0.008	13.1	0.027
	10	16	8.0	11.4	3.9	0.010	12.2	0.033
	12	16	8.2	12.5	4.5	0.013	17.0	0.042
	14	16	7.8	10.2	3.4	0.009	10.1	0.028
	15	16	8.2	11.1	4.2	0.010	14.4	0.032
Stand Mean		168	7.9	10.6	3.9	0.009	12.5	0.030

Table C-1 (continued)

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
4	1	16	8.3	11.6	4.2	0.011	14.5	0.037
	2	16	8.1	10.5	3.9	0.009	12.3	0.030
	3	12	8.1	11.8	4.4	0.012	15.7	0.038
	4	12	7.7	10.9	3.8	0.010	11.6	0.030
	5	16	8.2	12.0	4.2	0.012	14.7	0.040
	6	16	8.2	11.8	4.3	0.011	15.2	0.038
	7	16	7.8	10.6	4.1	0.009	13.9	0.030
	8	12	8.2	11.9	4.6	0.011	17.3	0.038
	9	16	8.0	11.5	3.8	0.011	12.3	0.035
	10	12	7.2	10.2	3.8	0.008	12.2	0.025
	12	16	8.3	11.8	4.3	0.011	14.9	0.038
	13	16	8.1	10.8	4.2	0.010	14.2	0.031
	14	16	8.0	11.4	4.1	0.011	14.0	0.035
Stand Mean		192	8.0	11.3	4.1	0.010	14.1	0.034
6	2	16	8.2	12.5	4.5	0.013	17.0	0.042
	3	16	8.3	11.9	4.3	0.012	15.1	0.038
	4	12	7.8	10.6	3.8	0.009	12.4	0.029
	6	12	7.8	11.0	3.7	0.010	11.4	0.031
	7	16	7.4	10.9	4.0	0.010	13.1	0.029
	8	16	8.2	11.5	3.9	0.011	12.8	0.037
	9	8	7.9	11.0	3.7	0.010	11.2	0.032
	10	16	7.7	11.2	4.2	0.010	14.8	0.032
	11	8	7.6	11.6	4.4	0.011	15.2	0.033
	12	16	8.3	12.4	4.4	0.012	15.9	0.042
	14	16	7.9	10.2	4.1	0.008	13.5	0.027
	15	16	7.9	11.8	4.2	0.011	14.8	0.036
Stand Mean		168	7.9	11.4	4.1	0.011	14.1	0.034
7	1	16	7.9	10.7	3.7	0.009	11.1	0.030
	4	12	8.2	12.3	4.4	0.012	15.9	0.041
	5	12	7.8	10.2	3.6	0.009	10.8	0.027
	6	12	7.1	10.5	3.6	0.009	11.2	0.027
	8	16	8.1	11.3	4.1	0.010	13.7	0.035
	10	12	8.2	11.3	4.4	0.010	16.1	0.035
	11	12	8.1	11.3	3.8	0.011	11.6	0.035
	13	12	8.0	10.7	3.9	0.009	12.7	0.030
	14	16	8.3	13.7	5.0	0.015	19.9	0.051
	15	16	7.9	10.9	3.9	0.010	12.8	0.033
Stand Mean		136	8.0	11.3	4.1	0.011	13.7	0.035

Table C-1 (continued)

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
8	3	16	7.7	10.1	3.8	0.009	11.8	0.027
	4	12	7.8	10.8	3.7	0.010	11.5	0.032
	5	16	7.6	10.4	4.0	0.009	13.0	0.028
	6	12	8.0	11.4	4.4	0.010	15.2	0.034
	8	16	8.1	11.4	4.3	0.011	15.5	0.036
	9	16	7.8	10.4	3.8	0.009	11.4	0.029
	10	12	7.5	10.5	4.1	0.009	13.7	0.028
	11	16	8.2	11.7	4.2	0.011	14.7	0.038
	12	8	7.9	11.4	4.2	0.011	14.4	0.034
	13	12	8.0	10.9	4.0	0.010	13.4	0.031
	14	8	7.3	10.2	3.7	0.009	12.2	0.026
	15	16	8.2	11.2	4.1	0.010	13.9	0.035
Stand Mean		160	7.9	10.9	4.0	0.010	13.4	0.032
9	1	16	7.7	10.8	3.6	0.009	11.2	0.030
	3	12	7.5	10.1	4.0	0.009	13.4	0.027
	4	16	7.9	10.6	3.8	0.009	12.7	0.031
	5	16	8.2	11.2	4.0	0.010	13.4	0.035
	6	16	7.6	10.9	3.6	0.010	11.3	0.031
	7	12	7.6	10.5	3.8	0.009	12.2	0.028
	9	12	8.1	10.6	4.0	0.009	13.3	0.029
	10	16	7.6	10.1	3.8	0.008	11.9	0.027
	11	12	8.0	10.8	4.2	0.009	14.3	0.030
	12	16	7.9	11.6	4.5	0.011	16.8	0.036
	13	16	8.2	12.2	4.1	0.012	13.7	0.040
Stand Mean		160	7.8	10.9	4.0	0.010	13.9	0.031
10	2	12	8.2	11.2	4.1	0.010	13.3	0.034
	3	16	8.2	11.1	4.1	0.010	13.9	0.033
	4	16	8.3	12.3	4.5	0.012	16.4	0.041
	5	12	8.1	11.1	4.2	0.010	14.6	0.033
	6	16	8.3	11.8	4.3	0.011	15.1	0.038
	9	12	8.0	11.1	4.2	0.010	15.0	0.033
	10	12	7.8	11.0	4.4	0.010	16.1	0.032
	11	16	8.4	12.5	4.6	0.013	17.3	0.043
	14	16	8.4	13.3	4.9	0.014	19.5	0.049
	15	16	8.0	12.4	4.0	0.013	13.5	0.041
Stand Mean		144	8.2	11.8	4.3	0.011	15.6	0.038

Table C-1 (continued)

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
11	1	16	8.4	12.1	4.5	0.012	16.1	0.040
	2	16	7.7	11.2	3.9	0.010	13.0	0.033
	3	16	8.2	12.4	4.6	0.012	16.7	0.041
	4	16	8.4	12.6	4.5	0.013	16.3	0.044
	5	12	8.1	11.5	4.1	0.011	13.7	0.036
	6	12	8.2	12.4	4.6	0.012	17.1	0.041
	7	8	8.6	12.6	4.6	0.013	16.9	0.046
	8	16	7.9	11.4	4.0	0.010	13.3	0.034
	9	16	8.3	12.7	4.6	0.014	17.2	0.047
	10	8	7.7	10.8	3.6	0.009	11.2	0.030
	11	8	7.9	10.6	3.8	0.009	11.5	0.030
	14	12	8.1	11.3	4.3	0.011	15.1	0.036
	15	8	8.0	10.8	3.9	0.010	13.5	0.033
Stand Mean		164	8.1	11.8	4.3	0.011	15.0	0.038
12	5	16	7.9	11.4	4.0	0.011	13.0	0.034
	6	16	8.2	11.8	4.4	0.011	15.9	0.039
	7	16	8.4	12.1	4.6	0.012	17.0	0.041
	10	16	7.9	11.4	4.1	0.011	13.4	0.034
	12	16	8.2	11.2	4.1	0.010	14.0	0.035
	14	16	8.1	12.2	4.5	0.012	16.9	0.041
	15	16	8.1	11.1	3.9	0.010	12.5	0.034
Stand Mean		112	8.1	11.6	4.2	0.011	14.7	0.037
13	1	16	7.8	11.0	4.0	0.010	13.8	0.032
	2	16	7.8	10.8	3.7	0.010	13.0	0.034
	3	12	8.1	10.6	3.9	0.009	12.6	0.030
	4	16	8.1	12.2	4.5	0.012	16.6	0.040
	6	16	7.9	11.2	4.1	0.010	14.2	0.035
	7	16	8.1	11.2	4.0	0.010	13.1	0.034
	9	16	8.0	11.9	4.4	0.012	15.6	0.038
	11	16	8.0	10.9	4.2	0.010	14.1	0.032
	14	16	8.3	12.5	4.7	0.013	17.9	0.043
	15	16	8.0	11.9	4.6	0.011	17.0	0.037
Stand Mean		156	8.0	11.5	4.2	0.011	14.8	0.035

[a]Stand identification numbers are as given in Table 2 (p. 16).

Table C-2. Mean Values of Characteristics Adjusted for DRI Competition in Virginia Pine after Fourteen Growing Seasons

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
1	1	12	7.7	11.8	4.3	0.012	15.4	0.038
	2	8	7.9	11.8	4.1	0.011	14.3	0.037
	3	16	7.8	10.7	4.0	0.009	13.1	0.031
	6	16	8.1	12.1	4.2	0.012	14.0	0.038
	7	12	8.0	12.6	4.0	0.012	12.9	0.040
	9	12	8.5	11.9	4.1	0.011	13.7	0.038
	12	16	8.0	11.5	4.2	0.011	14.6	0.035
	13	16	7.9	11.8	4.0	0.012	14.0	0.040
	15	16	7.9	11.2	3.8	0.011	12.9	0.035
Stand Mean		124	8.0	11.7	4.1	0.011	13.8	0.037
2	1	16	8.1	11.4	4.1	0.011	14.2	0.036
	3	16	7.9	11.0	3.9	0.010	13.1	0.033
	4	16	7.9	11.7	4.2	0.011	14.3	0.035
	7	8	8.0	11.1	4.1	0.010	13.9	0.034
	8	16	7.8	11.1	3.8	0.010	12.8	0.034
	9	16	7.8	11.4	4.1	0.011	13.7	0.034
	10	8	7.8	10.5	3.9	0.009	13.1	0.032
	11	16	7.7	10.9	4.0	0.010	13.4	0.033
	12	12	7.7	10.4	3.7	0.009	11.6	0.029
	14	12	8.1	10.4	3.8	0.009	12.4	0.030
Stand Mean		136	7.9	11.0	4.0	0.010	13.3	0.033

Table C-2 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
3	2	16	8.0	11.0	4.1	0.010	13.9	0.033
	4	16	7.9	10.8	3.9	0.010	12.7	0.034
	5	16	7.9	11.0	3.8	0.010	12.0	0.032
	6	12	7.9	10.9	4.1	0.010	14.3	0.034
	7	16	7.9	10.2	4.0	0.009	14.0	0.031
	8	16	7.5	11.1	4.0	0.011	13.5	0.034
	9	12	7.6	10.0	3.8	0.009	12.4	0.028
	10	16	7.9	11.0	4.0	0.010	13.3	0.031
	12	16	8.2	12.1	4.4	0.012	15.6	0.039
	14	16	7.8	10.7	3.8	0.010	12.6	0.033
	15	16	8.1	11.4	4.2	0.011	14.3	0.035
Stand Mean		168	7.9	11.0	4.0	0.010	13.5	0.033
4	1	16	8.0	10.9	4.0	0.010	13.9	0.035
	2	16	8.1	11.0	4.1	0.010	14.3	0.033
	3	12	8.0	11.4	4.2	0.011	14.7	0.037
	4	12	7.8	11.2	3.8	0.010	12.1	0.032
	5	16	8.0	10.7	3.6	0.009	11.0	0.030
	6	16	8.2	12.2	4.5	0.012	16.1	0.041
	7	16	7.8	11.0	4.2	0.010	14.3	0.033
	8	12	8.2	11.8	4.3	0.011	14.7	0.036
	9	16	7.8	11.1	3.9	0.011	13.6	0.034
	10	12	7.3	10.6	3.9	0.009	12.6	0.030
	12	16	8.2	11.8	4.2	0.011	14.6	0.038
	13	16	8.1	11.4	4.3	0.011	15.5	0.036
	14	16	8.1	11.3	4.0	0.010	13.0	0.034
Stand Mean		192	8.0	11.3	4.1	0.010	13.9	0.034

Table C-2 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
6	2	16	8.0	11.3	4.0	0.010	13.2	0.033
	3	16	8.2	11.5	4.2	0.011	14.5	0.036
	4	12	7.6	10.3	3.7	0.009	11.8	0.028
	6	12	7.8	10.9	3.8	0.009	12.2	0.030
	7	16	7.4	10.8	3.8	0.010	12.4	0.031
	8	16	8.2	11.7	4.1	0.011	13.4	0.036
	9	8	7.9	11.4	4.1	0.011	14.3	0.036
	10	16	7.5	10.6	3.7	0.009	11.4	0.028
	11	8	7.6	11.2	4.1	0.010	13.1	0.031
	12	16	8.2	11.9	4.3	0.011	14.9	0.037
	14	16	7.9	10.4	3.9	0.009	12.8	0.029
	15	16	8.0	11.7	4.2	0.011	14.6	0.035
Stand Mean		168	7.9	11.1	4.0	0.010	13.2	0.033
7	1	16	7.9	10.8	3.8	0.010	12.2	0.031
	4	12	8.0	10.7	3.8	0.009	11.7	0.029
	5	12	7.6	10.5	3.8	0.010	13.2	0.032
	6	12	7.2	10.6	3.8	0.010	12.6	0.031
	8	16	8.1	11.3	4.2	0.010	14.8	0.034
	10	12	8.3	11.7	4.6	0.011	17.2	0.037
	11	12	8.1	11.6	4.0	0.011	13.0	0.037
	13	12	7.8	10.4	3.8	0.009	12.5	0.032
	14	16	8.4	12.9	4.6	0.013	16.3	0.042
	15	16	8.0	11.5	4.2	0.011	14.5	0.037
Stand Mean		136	8.0	11.3	4.1	0.010	13.9	0.034

Table C-2 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
8	3	16	7.8	11.0	4.0	0.010	14.0	0.034
	4	12	7.9	11.1	3.8	0.010	12.3	0.033
	5	16	7.8	10.9	4.1	0.010	13.9	0.033
	6	12	8.1	11.8	4.4	0.011	15.4	0.035
	8	16	8.1	11.1	4.0	0.010	12.9	0.033
	9	16	7.8	10.7	3.9	0.010	12.4	0.031
	10	12	7.6	10.6	4.1	0.009	14.0	0.031
	11	16	8.1	11.3	4.0	0.011	13.5	0.035
	12	8	7.7	10.9	3.9	0.010	12.5	0.031
	13	12	7.8	10.6	3.9	0.009	13.4	0.030
	14	8	7.4	10.4	3.8	0.009	12.4	0.029
	15	16	8.2	10.9	4.0	0.010	13.5	0.032
Stand Mean		160	7.9	11.0	4.0	0.010	13.4	0.032
9	1	16	7.9	11.2	3.8	0.010	12.0	0.033
	3	12	7.7	11.3	4.2	0.011	14.7	0.037
	4	16	7.9	10.8	3.9	0.010	13.0	0.031
	5	16	8.1	11.3	4.0	0.011	13.4	0.035
	6	16	7.7	11.2	4.0	0.010	13.6	0.034
	7	12	7.8	11.1	4.1	0.010	13.3	0.031
	9	12	8.2	11.4	4.2	0.011	14.7	0.036
	10	16	7.5	9.9	3.5	0.009	10.8	0.028
	11	12	8.0	11.3	4.3	0.011	15.1	0.035
	12	16	7.9	11.5	4.3	0.011	15.5	0.036
	13	16	8.3	12.5	4.4	0.012	15.6	0.041
Stand Mean		160	7.9	11.2	4.1	0.010	13.7	0.034

Table C-2 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
10	2	12	8.1	10.9	3.8	0.010	11.7	0.031
	3	16	8.3	11.4	4.2	0.010	14.0	0.035
	4	16	8.2	11.6	4.1	0.010	13.7	0.035
	5	12	8.1	11.3	4.2	0.010	14.5	0.034
	6	16	8.3	11.6	4.2	0.011	14.5	0.036
	9	12	8.0	11.0	4.2	0.010	14.9	0.033
	10	12	8.2	12.1	4.6	0.012	16.4	0.038
	11	16	8.3	12.1	4.3	0.012	14.8	0.038
	14	16	8.4	12.9	4.8	0.013	18.7	0.044
	15	16	8.1	12.6	4.3	0.013	15.1	0.041
Stand Mean		144	8.2	11.8	4.3	0.011	14.9	0.037
11	1	16	8.4	11.9	4.4	0.011	15.5	0.036
	2	16	7.7	11.0	4.0	0.010	13.4	0.033
	3	16	8.2	12.3	4.4	0.012	15.7	0.040
	4	16	8.2	11.7	4.3	0.011	15.0	0.037
	5	12	8.1	11.2	4.1	0.010	14.2	0.034
	6	12	8.0	11.4	4.1	0.011	14.5	0.035
	7	8	8.3	11.4	4.2	0.011	14.7	0.037
	8	16	8.0	11.5	4.1	0.011	13.6	0.034
	9	16	8.2	12.1	4.4	0.012	15.8	0.041
	10	8	7.8	11.3	4.0	0.011	14.0	0.035
	11	8	7.8	10.8	4.0	0.010	14.0	0.033
	14	12	7.9	10.9	3.7	0.010	11.7	0.034
	15	8	7.8	10.8	3.9	0.010	13.8	0.035
Stand Mean		164	8.1	11.5	4.2	0.011	14.4	0.036

Table C-2 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
12	5	16	8.0	11.6	4.1	0.011	13.2	0.034
	6	16	8.1	11.0	4.0	0.010	13.5	0.033
	7	16	8.4	11.8	4.4	0.011	15.5	0.035
	10	16	8.1	11.6	4.2	0.011	14.2	0.034
	12	16	8.1	11.0	4.0	0.010	13.1	0.033
	14	16	7.9	11.4	4.1	0.011	14.7	0.037
	15	16	8.2	11.4	4.2	0.011	14.5	0.036
Stand Mean		112	8.1	11.4	4.1	0.011	14.1	0.034
13	1	16	8.1	11.9	4.3	0.011	15.2	0.038
	2	16	8.0	11.4	4.0	0.011	13.6	0.037
	3	12	8.1	11.1	4.1	0.010	13.8	0.034
	4	16	8.2	11.7	4.3	0.011	15.2	0.036
	6	16	7.7	10.6	3.9	0.010	13.0	0.031
	7	16	8.2	11.6	4.0	0.011	12.9	0.035
	9	16	8.2	11.8	4.3	0.011	15.0	0.036
	11	16	8.1	11.0	4.2	0.010	13.9	0.032
	14	16	8.4	12.3	4.6	0.012	16.5	0.040
	15	16	8.1	11.8	4.3	0.011	14.5	0.034
Stand Mean		156	8.1	11.5	4.2	0.011	14.4	0.035

[a]Stand identification numbers are as given in Table 2 (p. 16).

Table C-3. Mean Values of Characteristics Measured in White Pine after Eleven Growing Seasons

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
1	1	40	7.2	12.2	4.4	0.012	15.6	0.046
	2	36	6.4	11.7	4.3	0.012	15.2	0.039
	3	40	5.8	10.1	3.6	0.009	12.2	0.031
	4	40	6.2	10.4	3.8	0.009	12.2	0.031
	5	40	6.0	9.7	3.7	0.008	12.0	0.028
	6	40	6.3	11.4	4.0	0.011	13.3	0.037
	7	36	6.4	11.2	3.7	0.011	11.9	0.037
	8	36	5.8	9.4	3.6	0.008	10.9	0.025
	9	36	6.4	10.8	4.0	0.010	13.3	0.033
	10	40	6.6	12.0	4.2	0.012	14.8	0.041
Stand Mean		384	6.3	10.9	3.9	0.010	13.2	0.035
2	1	40	6.2	10.5	3.7	0.009	11.6	0.031
	2	40	6.5	11.2	4.1	0.011	14.1	0.036
	3	40	6.7	10.9	4.0	0.010	13.4	0.035
	4	40	6.4	11.5	4.0	0.011	13.0	0.038
	5	40	6.7	12.2	4.1	0.012	14.2	0.043
	6	40	6.7	11.1	4.1	0.010	13.7	0.036
	7	40	5.3	9.4	3.3	0.008	9.8	0.023
	8	40	6.8	11.2	4.2	0.010	14.2	0.037
	9	40	6.4	9.6	3.6	0.008	11.0	0.025
	10	40	7.0	11.5	4.2	0.011	14.2	0.040
Stand Mean		400	6.5	10.9	3.9	0.010	12.9	0.034
3	1	36	6.5	11.4	4.0	0.010	13.5	0.037
	2	32	7.0	11.4	4.2	0.011	14.3	0.038
	3	32	6.2	9.9	3.7	0.008	11.8	0.028
	4	32	6.6	10.9	4.0	0.010	13.7	0.035
	5	28	6.1	10.3	4.0	0.009	13.3	0.029
	6	32	6.1	9.9	3.6	0.008	11.3	0.028
	7	32	6.5	11.2	4.2	0.011	14.3	0.036
	8	32	5.7	10.2	3.7	0.009	11.8	0.028
	9	36	6.4	10.9	4.3	0.010	15.2	0.034
	10	32	6.2	10.6	3.9	0.010	12.8	0.032
Stand Mean		324	6.3	10.7	4.0	0.010	13.2	0.033

Table C-3 (continued)

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
4	1	32	5.5	8.4	3.1	0.006	8.6	0.019
	2	36	5.7	9.1	3.4	0.007	10.6	0.024
	3	28	6.0	8.6	3.3	0.006	9.6	0.021
	4	40	5.6	9.2	3.4	0.008	11.1	0.025
	5	40	6.2	10.4	3.9	0.010	12.8	0.032
	6	32	6.0	9.8	3.6	0.009	11.7	0.029
	7	36	5.6	9.5	3.5	0.008	11.3	0.026
	8	32	4.8	7.4	2.7	0.005	6.8	0.013
	9	28	5.3	8.2	3.2	0.006	9.0	0.018
	10	36	5.7	9.1	3.2	0.007	9.6	0.023
Stand Mean		340	5.6	9.0	3.4	0.007	10.2	0.023
5	2	32	6.2	10.5	3.8	0.009	12.0	0.031
	3	32	5.6	9.7	3.7	0.008	11.9	0.025
	5	24	6.2	10.0	3.9	0.009	12.5	0.028
	6	28	5.9	10.3	4.1	0.009	13.8	0.029
	7	28	5.2	8.8	3.1	0.007	8.3	0.019
	8	28	6.0	9.4	3.6	0.007	11.1	0.024
	9	32	6.4	10.5	3.8	0.009	12.2	0.032
	10	28	6.2	11.6	4.4	0.011	15.4	0.035
Stand Mean		232	6.0	10.1	3.8	0.009	12.1	0.028
6	1	24	6.8	12.2	4.6	0.012	16.1	0.043
	2	36	6.0	10.9	3.8	0.010	12.2	0.033
	3	20	5.4	9.7	3.6	0.008	11.6	0.026
	4	40	5.7	9.8	3.6	0.008	11.1	0.026
	5	36	5.6	10.6	3.6	0.010	11.4	0.033
	6	32	5.9	10.4	3.6	0.010	11.8	0.034
	7	32	4.9	7.8	3.1	0.005	8.6	0.013
	8	28	5.4	9.5	3.3	0.008	9.8	0.026
	9	24	5.9	10.2	3.8	0.009	12.2	0.029
	10	28	6.7	11.4	4.3	0.011	15.7	0.040
Stand Mean		300	5.8	10.2	3.7	0.009	11.9	0.030

Table C-3 (continued)

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
7	1	32	6.8	11.6	4.6	0.011	17.0	0.039
	2	12	7.0	11.5	4.2	0.011	14.3	0.038
	3	28	5.2	8.5	3.1	0.006	8.4	0.017
	4	32	5.7	9.5	3.5	0.008	10.3	0.023
	5	24	6.2	9.7	3.7	0.008	10.3	0.012
	6	28	5.6	10.3	3.8	0.009	12.5	0.029
	7	20	6.7	10.6	4.0	0.009	14.1	0.034
	8	28	6.2	11.4	4.0	0.011	14.1	0.037
	9	20	6.2	9.6	3.7	0.008	11.6	0.027
	10	28	6.3	9.7	3.7	0.008	12.2	0.030
Stand Mean		252	6.1	10.2	3.8	0.009	12.6	0.029
8	1	28	6.2	10.2	3.9	0.009	12.4	0.028
	2	28	6.2	11.0	4.3	0.010	14.9	0.032
	3	28	6.2	9.6	3.8	0.008	11.7	0.025
	4	32	6.1	9.3	3.5	0.007	10.1	0.024
	5	16	6.1	11.4	4.3	0.011	14.9	0.033
	6	32	5.9	10.9	3.6	0.010	11.1	0.033
	7	32	6.7	12.2	4.3	0.012	15.1	0.042
	8	20	6.3	10.4	3.8	0.009	11.8	0.031
	9	36	6.3	10.6	4.0	0.010	13.5	0.032
	10	32	6.9	11.0	4.3	0.010	15.2	0.036
Stand Mean		284	6.3	10.6	4.0	0.010	13.0	0.032
9	1	20	4.2	7.2	2.4	0.004	5.1	0.010
	2	20	4.4	5.6	2.7	0.003	7.1	0.007
	3	32	5.5	9.0	3.2	0.007	9.5	0.023
	4	24	5.1	8.2	3.0	0.006	8.8	0.020
	5	32	5.3	8.9	3.1	0.007	8.8	0.022
	6	20	4.1	6.0	2.7	0.003	6.9	0.008
	7	28	4.7	7.4	2.8	0.005	6.9	0.014
	8	24	4.6	7.2	3.1	0.005	8.4	0.013
	9	16	6.2	9.2	3.6	0.008	12.1	0.029
	10	24	5.2	7.6	2.9	0.005	7.4	0.016
Stand Mean		240	5.0	7.7	3.0	0.006	8.1	0.017

Table C-3 (continued)

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
10	1	24	5.1	7.9	2.8	0.006	7.4	0.016
	2	32	5.5	9.6	3.7	0.008	11.6	0.022
	3	32	5.1	8.4	3.2	0.006	9.2	0.018
	4	40	5.4	8.2	3.2	0.006	8.8	0.016
	5	28	5.4	9.4	3.5	0.008	10.6	0.023
	6	40	5.8	9.6	3.5	0.008	10.2	0.024
	7	40	6.3	10.5	3.9	0.009	12.5	0.030
	8	24	3.4	4.8	1.7	0.002	3.1	0.005
	9	24	4.9	7.9	3.0	0.006	8.1	0.015
	10	20	5.7	9.8	3.4	0.008	10.0	0.024
Stand Mean		304	5.3	8.8	3.3	0.007	9.4	0.020
11	1	40	6.3	10.9	3.9	0.010	12.8	0.033
	2	40	6.8	12.0	4.3	0.012	14.8	0.043
	3	36	6.7	11.9	4.3	0.012	15.3	0.040
	4	32	6.9	12.0	3.9	0.012	13.0	0.042
	5	40	6.9	12.0	4.5	0.012	16.3	0.042
	6	36	6.5	11.6	3.8	0.011	12.1	0.038
	7	40	7.0	12.7	4.2	0.013	14.2	0.048
	8	40	7.0	12.6	4.4	0.013	15.7	0.047
	9	36	6.3	11.6	4.1	0.011	14.2	0.038
	10	36	6.2	10.6	3.6	0.010	10.9	0.032
Stand Mean		376	6.7	11.8	4.1	0.012	14.0	0.040
12	1	40	6.1	11.1	3.8	0.010	12.7	0.035
	2	40	6.6	11.9	4.2	0.012	14.2	0.040
	3	40	6.7	12.2	4.1	0.012	13.6	0.041
	4	40	6.2	11.0	4.0	0.010	13.4	0.035
	5	40	7.3	12.7	4.4	0.013	15.5	0.050
	6	36	6.3	10.0	3.8	0.008	12.4	0.028
	7	40	7.1	12.2	4.3	0.012	14.9	0.044
	8	36	6.5	11.2	4.0	0.010	13.4	0.035
	9	40	6.4	11.0	3.9	0.010	12.7	0.035
	10	36	7.0	12.5	4.3	0.013	14.9	0.047
Stand Mean		388	6.6	11.6	4.1	0.011	13.8	0.039

Table C-3 (continued)

Stand[a]	Family	N	Height (m)	DBH (cm)	Crown (m)	BA (m^2)	CA (m^2)	Volume (m^3)
13	1	32	6.7	11.3	3.9	0.011	13.1	0.037
	2	40	7.3	11.6	4.6	0.011	17.6	0.043
	3	36	7.1	11.1	4.0	0.010	13.6	0.037
	4	36	6.5	10.4	4.0	0.009	13.7	0.032
	5	36	6.8	11.9	4.2	0.012	15.2	0.041
	6	40	7.0	12.4	4.1	0.013	14.2	0.046
	7	40	6.8	12.0	4.2	0.012	14.9	0.042
	8	40	6.5	10.4	3.8	0.009	12.2	0.032
	9	40	7.3	12.1	4.4	0.012	16.2	0.046
	10	32	7.3	11.4	4.1	0.011	13.6	0.041
Stand Mean		372	6.9	11.5	4.1	0.011	14.5	0.040

[a]Stand identification numbers are as given in Table 1 (p. 15).

Table C-4. Mean Values of Characteristics Adjusted for DRI Competition in White Pine after Eleven Growing Seasons

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
1	1	40	6.7	11.2	4.9	0.011	13.6	0.038
	2	36	6.0	10.5	4.7	0.010	12.7	0.031
	3	40	5.8	10.1	4.6	0.009	12.2	0.031
	4	40	6.1	10.5	4.6	0.010	12.2	0.031
	5	40	6.2	10.3	4.7	0.009	13.1	0.032
	6	40	6.3	11.0	4.7	0.010	12.6	0.034
	7	36	6.2	10.7	4.6	0.010	12.2	0.036
	8	36	6.0	10.1	4.6	0.009	12.4	0.030
	9	36	6.5	11.1	4.9	0.010	13.4	0.036
	10	40	6.7	12.1	5.1	0.012	14.5	0.040
Stand Mean		384	6.2	10.8	4.7	0.010	12.9	0.034
2	1	40	6.2	10.9	4.6	0.010	11.9	0.033
	2	40	6.3	11.0	4.9	0.010	13.5	0.033
	3	40	6.4	10.6	4.8	0.009	12.7	0.031
	4	40	6.5	11.6	4.8	0.011	12.9	0.038
	5	40	6.5	11.6	4.9	0.011	13.7	0.037
	6	40	6.4	10.6	4.7	0.010	12.7	0.033
	7	40	5.7	10.2	4.6	0.009	12.5	0.031
	8	40	6.6	10.7	4.9	0.010	13.5	0.033
	9	40	6.3	10.2	4.6	0.009	11.6	0.028
	10	40	6.7	11.2	4.9	0.010	13.7	0.037
Stand Mean		400	6.4	10.9	4.8	0.010	12.9	0.033

Table C-4 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
3	1	36	5.9	10.5	4.6	0.009	11.7	0.030
	2	32	6.3	10.2	4.6	0.009	11.7	0.029
	3	32	5.9	9.7	4.4	0.008	11.1	0.026
	4	32	6.0	10.2	4.6	0.009	12.4	0.029
	5	28	6.3	10.4	4.7	0.009	12.5	0.031
	6	32	5.7	9.3	4.3	0.008	10.7	0.024
	7	32	6.1	10.4	4.7	0.009	12.3	0.031
	8	32	5.8	10.5	4.6	0.010	11.9	0.031
	9	36	6.2	10.6	4.9	0.009	13.6	0.031
	10	32	6.2	10.7	4.7	0.010	12.9	0.034
Stand Mean		324	6.0	10.2	4.6	0.009	12.1	0.030
4	1	32	5.9	9.9	4.4	0.009	11.2	0.029
	2	36	5.8	10.0	4.5	0.009	12.1	0.029
	3	28	6.2	10.1	4.5	0.009	11.6	0.030
	4	40	5.8	9.8	4.4	0.009	11.5	0.029
	5	40	6.4	11.1	4.9	0.010	13.3	0.035
	6	32	6.3	11.0	4.8	0.011	13.6	0.036
	7	36	6.0	10.6	4.7	0.010	13.2	0.035
	8	32	5.6	9.4	4.3	0.008	11.0	0.027
	9	28	5.5	9.6	4.4	0.009	11.1	0.027
	10	36	5.8	10.1	4.4	0.009	11.4	0.030
Stand Mean		340	5.9	10.2	4.6	0.009	12.0	0.031

Table C-4 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
5	2	32	6.2	10.2	4.6	0.009	12.1	0.031
	3	32	5.6	9.5	4.5	0.008	11.7	0.026
	5	24	6.1	10.2	4.7	0.009	12.0	0.028
	6	28	6.0	10.2	4.8	0.009	13.2	0.030
	7	28	5.6	9.8	4.5	0.009	11.6	0.028
	8	28	6.1	10.2	4.7	0.009	13.0	0.031
	9	32	6.1	10.1	4.5	0.009	11.9	0.031
	10	28	5.9	10.6	4.8	0.010	13.4	0.030
Stand Mean		232	5.9	10.1	4.6	0.009	12.4	0.029
6	1	24	6.4	11.3	4.8	0.011	13.3	0.037
	2	36	6.0	10.9	4.6	0.010	11.9	0.034
	3	20	5.8	10.0	4.6	0.009	12.0	0.029
	4	40	5.7	9.9	4.4	0.009	11.3	0.028
	5	36	5.8	10.6	4.6	0.010	11.8	0.032
	6	32	5.9	10.4	4.7	0.010	12.9	0.034
	7	32	5.3	9.4	4.4	0.008	11.2	0.026
	8	28	5.9	10.4	4.6	0.010	11.5	0.032
	9	24	5.9	10.6	4.7	0.010	13.2	0.033
	10	28	6.0	10.1	4.7	0.009	12.9	0.029
Stand Mean		300	5.9	10.3	4.6	0.009	12.1	0.032

Table C-4 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
7	1	32	6.5	11.1	5.1	0.010	15.1	0.036
	2	12	6.6	10.7	4.9	0.010	13.5	0.034
	3	28	5.8	9.7	4.4	0.009	11.2	0.028
	4	32	5.8	10.1	4.4	0.009	11.2	0.029
	5	24	6.1	10.1	4.6	0.009	11.9	0.029
	6	28	5.6	9.9	4.6	0.009	12.2	0.029
	7	20	6.2	9.8	4.7	0.008	12.7	0.027
	8	28	5.9	10.3	4.5	0.009	11.9	0.030
	9	20	6.2	9.6	4.4	0.008	11.1	0.028
	10	28	6.0	9.7	4.6	0.008	12.3	0.028
Stand Mean		252	6.0	10.1	4.6	0.009	12.3	0.030
8	1	28	5.9	9.7	4.4	0.008	11.1	0.027
	2	28	5.8	10.1	4.8	0.009	13.0	0.026
	3	28	6.4	10.6	4.8	0.009	12.9	0.032
	4	32	6.2	10.1	4.5	0.009	11.6	0.030
	5	16	5.7	10.6	4.7	0.010	12.7	0.028
	6	32	5.6	9.7	4.3	0.008	9.9	0.027
	7	32	6.4	10.9	4.8	0.010	13.0	0.034
	8	20	6.3	10.4	4.7	0.010	12.7	0.033
	9	36	5.9	10.0	4.7	0.009	12.9	0.029
	10	32	6.1	9.9	4.7	0.009	12.7	0.029
Stand Mean		284	6.0	10.2	4.6	0.009	12.2	0.029

Table C-4 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
9	1	20	5.0	9.3	4.1	0.008	9.9	0.025
	2	20	5.5	8.8	4.4	0.008	11.7	0.027
	3	32	5.6	9.8	4.3	0.009	11.0	0.028
	4	24	5.4	9.0	4.3	0.008	11.5	0.026
	5	32	5.6	9.6	4.4	0.008	11.4	0.027
	6	20	5.2	8.6	4.3	0.008	11.1	0.025
	7	28	5.5	9.4	4.2	0.009	10.7	0.029
	8	24	5.6	9.5	4.6	0.009	12.4	0.029
	9	16	6.3	10.0	4.8	0.009	13.7	0.035
	10	24	5.6	9.1	4.2	0.008	9.9	0.024
Stand Mean		240	5.5	9.3	4.4	0.008	11.3	0.028
10	1	24	5.6	9.3	4.2	0.008	10.1	0.026
	2	32	5.7	10.0	4.6	0.009	12.4	0.027
	3	32	5.6	9.8	4.5	0.009	11.8	0.027
	4	40	5.8	9.6	4.4	0.008	10.8	0.027
	5	28	5.2	8.7	4.2	0.007	10.4	0.022
	6	40	6.0	10.2	4.6	0.009	12.0	0.030
	7	40	6.0	10.0	4.6	0.008	11.7	0.027
	8	24	5.1	9.0	4.1	0.008	10.6	0.029
	9	24	5.3	9.3	4.3	0.008	10.9	0.026
	10	20	5.5	9.7	4.4	0.008	11.2	0.024
Stand Mean		304	5.6	9.6	4.4	0.008	11.3	0.027

Table C-4 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
11	1	40	6.3	11.0	4.8	0.010	12.7	0.033
	2	40	6.5	10.7	4.7	0.010	12.5	0.034
	3	36	6.3	10.9	4.9	0.010	13.2	0.032
	4	32	6.4	10.5	4.6	0.009	11.9	0.033
	5	40	6.4	10.8	4.8	0.010	13.1	0.033
	6	36	6.5	11.2	4.8	0.010	12.9	0.035
	7	40	6.4	11.1	4.6	0.011	12.2	0.037
	8	40	6.5	11.4	4.9	0.011	14.0	0.040
	9	36	6.2	10.9	4.9	0.010	12.9	0.032
	10	36	6.1	10.2	4.5	0.009	11.1	0.029
Stand Mean		376	6.4	10.9	4.7	0.010	12.7	0.034
12	1	40	6.1	10.6	4.7	0.010	12.8	0.033
	2	40	6.4	11.4	4.9	0.011	13.1	0.035
	3	40	6.4	11.2	4.7	0.010	11.6	0.034
	4	40	6.4	11.1	4.8	0.010	12.8	0.035
	5	40	6.7	11.5	4.9	0.011	13.6	0.040
	6	36	6.4	10.3	4.8	0.009	13.0	0.032
	7	40	6.5	11.1	4.8	0.010	12.6	0.035
	8	36	6.4	11.1	4.8	0.010	12.7	0.034
	9	40	6.5	11.2	4.8	0.010	13.0	0.035
	10	36	6.7	11.4	4.9	0.011	13.5	0.040
		388	6.5	11.1	4.8	0.010	12.9	0.035

Table C-4 (continued)

Stand[a]	Family	N	H-WOUT$_2$ (m)	D-WOUT$_2$ (cm)	C-WOUT$_2$ (m)	B-WOUT$_2$ (m^2)	CA-WOUT$_2$ (m^2)	V-WOUT$_2$ (m^3)
13	1	32	6.5	11.3	4.7	0.011	12.5	0.036
	2	40	6.8	11.2	5.1	0.010	15.1	0.037
	3	36	6.9	10.9	5.0	0.010	13.7	0.034
	4	36	6.4	10.5	4.8	0.009	13.3	0.030
	5	36	6.6	11.5	5.0	0.011	14.0	0.036
	6	40	6.5	11.2	4.8	0.010	13.1	0.036
	7	40	6.4	11.0	4.8	0.010	13.1	0.034
	8	40	6.2	10.5	4.7	0.009	12.6	0.032
	9	40	6.5	11.3	4.9	0.011	13.8	0.037
	10	32	6.8	10.9	4.7	0.010	12.5	0.035
Stand Mean		372	6.6	11.0	4.9	0.010	13.4	0.035

[a]Stand identification numbers are as given in Table 1 (p. 15).

APPENDIX D

COMPUTATION TIME AND COSTS FOR STATISTICAL ANALYSES AND DATA SET MANIPULATION

Table D-1. Computation Time and Costs of Analyses Performed in Terms of Central Processing Unit (CPU)[a] Usage

Analysis	Virginia Pine		White Pine	
	CPU Time[b]	CPU Cost[c]	CPU Time	CPU Cost
Preliminary Study	(N = 312)		(N = 400)	
Correlations and Duncan's New Multiple Range Tests	0:17.19	$0.93	0:10.32	$0.56
Regressions	0:33.31	$1.81	0:36.79	$1.99
Competitive Intensity Coefficients	0:01.65	$0.09	0:01.02	$0.06
Preliminary Total	0:52.15	$2.83	0:48.13	$2.61
Main Study	(N = 1820)		(N = 4196)	
Means	0:23.71	$1.29	0:47.63	$2.58
Correlations	0:28.59	$1.55	0:53.24	$2.89
Regressions	1:40.17	$5.43	4:05.49	$13.31
ANOVA and VARCOMP	1:58:27.24	$385.37	4:05:53.92	$799.99
Heritabilities and Gains	0:03.08	$0.16	0:02.87	$0.16
Pearson Correlations	2:31.41	$8.21	4:20.18	$14.10
Multiple Regressions	5:09.65	$16.79	7:40.14	$24.95
ANCOVA (Slope Tests)	1:05.28	$3.54	2:04.52	$6.75
Spearman Rank Order Correlations	1:39.77	$5.41	2:02.64	$6.65
Means by Stand and by Family	1:17.33	$4.19	1:51.95	$6.07
Main Total	2:12:46.11	$431.94	4:29:42.49	$877.45
Grand Total	2:13:38.25	$434.77	4:30:30.62	$880.06

Table D-1 (continued)

Note. Considerable time and costs were expended in developing the programs to calculate DDI and DRI competitive effects. Actual computation expense in manipulating the data sets, once the methods were perfected, are given in Table D-2.

[a]All analyses were performed using the Statistical Analysis System (SAS, 79) Computer Software Package on an IBM 360 computer.

[b]Time units are hours:minutes:seconds.centiseconds.

[c]Costs are in 1981 dollars.

Table D-2. Computation Time and Costs of Data Set Manipulation in Terms of Central Processing Unit (CPU)[a] Usage

Operation performed	Virginia Pine		White Pine	
	CPU Time[b]	CPU Cost[c]	CPU Time	CPU Cost
Derivation of TREESIZE Factor Coefficients	1:43.46	$5.61	1:13.15	$3.96
Computation of DDI and DRI Competition Variables	11:03.42	$35.95	28:34.95	$92.99
Random Sampling	8:12.00	$26.68	22:18.54	$72.60
Total	20:58.88	$68.24	52:06.64	$169.55

[a]All operations were performed using the Statistical Analysis System (SAS, 79) Computer Software Package on an IBM 360 computer.

[b]Time units are hours:minutes:seconds.centiseconds.

[c]Costs are in 1981 dollars.

VITA

Basil Eugene Pinker was born in Fredericksburg, Virginia, on October 17, 1953. He grew up in Dahlgren, Virginia, where he attended a local elementary school. He later attended James Monroe High School in Fredericksburg from which he was graduated in June 1972. The following September he enrolled in the University of Virginia, and four years later, in May 1976, he received his Bachelor of Arts with Distinction degree with a major in environmental science.

Following a short (six month) interlude in which he worked for Technassociates, Inc., in Washington, D.C., as an environmental technician, he enrolled in West Virginia University in January of 1977 to pursue study leading to a Master of Science degree in forestry. While attending W.V.U. he was employed as a Graduate Research Assistant.

In May of 1980, he received his M.S. degree in forestry after having already begun work toward his doctorate at The University of Tennessee in Knoxville in September of 1979. He was supported at U.T. by a Graduate Research Assistantship and received the Doctor of Philosophy degree with a major in ecology in December 1982.

The author is a member of Phi Kappa Phi, Gamma Sigma Delta, and Xi Sigma Pi national honorary societies and the Tau Kappa Epsilon international fraternity.