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I am submitting herewith a dissertation written by George Rink entitled "Variation in Open-Pollinated Progeny Plantations of Virginia Pine (Pinus virginiana Mill.)." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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VARIATION IN OPEN-POLLINATED PROGENY PLANTATIONS OF VIRGINIA PINE (*PINUS VIRGINIANA* MILL.)

A Dissertation

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Doctor of Philosophy

Degree

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ABSTRACT

The objectives of this study were to evaluate genetic and environmental sources of variation in height, diameter at half-height, volume of wood per tree, branch length, and branch diameter in juvenile Virginia pine. Five-year data from approximately 40,000 open-pollinated progeny of random trees from 12 natural stands in Tennessee and Kentucky were analyzed; data were measurements of individual progenies from 128 half-sib families outplanted at six locations in Kentucky, Tennessee, and Alabama. In addition, wood samples were obtained from one of the six plantations to estimate the heritability of wood specific gravity. Soil samples were collected from another plantation in an attempt to assess and account for high environmental sources of variance.

Individual location analyses disclosed that variance components for each source of variation, expressed as a percent of total variation, were relatively similar from location to location. Of the five characteristics evaluated, height growth consistently had the highest family-within-stand variance while branch diameter had the lowest.

Since variance components from the combined location analyses, including five of the six plantations, are based on numbers of stands and of families within stands different from those in the individual location analyses, comparison of variance components from the two types of analyses is not strictly valid. Generally, however, variance

components in the combined analyses are similar in magnitude to those in the individual location analyses.

Neither of the two levels of genotype x environment interaction evaluated (the interaction of location with stand and the interaction of location with family-within-stand) accounted for substantial amounts of phenotypic variance although the corresponding main effects were statistically significant; the sum of these interaction variance components accounted for a maximum of two percent of the phenotypic variance.

When compared with two-year estimates, five-year heritability estimates derived from individual location analyses seem to increase in uniformity. Heritability estimates based on variance components from the combined location analyses are in close agreement with averages derived from six individual locations; averages of estimates from individual location analyses are within one standard error of estimates from combined location analyses.

The family-within-stand effect for wood specific gravity was significant at only the 10 percent level of probability while the stand effect was significant at the one percent level, indicating that more improvement in this characteristic may be obtained by stand selection than by family-within-stand selection. There was no evidence of any significant genetic effect on amount of wood extractives; apparently this trait is primarily controlled by environmental variables.

Analyses of soil variables at a strip mine site in Kentucky

disclosed that 25 percent of total variation in tree height may be accounted for by three variables (pH, conductivity of soil saturation extract and exchangeable aluminum or exchangeable acidity).

Expected gains were computed on the basis of a hypothetical roguing of each plantation using three selection schemes. Gains from a three-stage selection system, which included stand selection, family selection, and within-family selection, ranged from a low of 23.5 to a high of 61.9 percent over mean unselected stem volume. Similar expected gains were obtained with a two-stage selection system (no stand selection); although the two-stage selection resulted in greater gains at two plantations, these greater gains were offset by losses of a similar magnitude at the four remaining plantations. Mass selection, the third selection scheme, resulted in gains of between 13 and 27 percent of the expected gains from the two-stage selection.

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CHAPTER I

INTRODUCTION

Virginia pine (*Pinus virginiana* Mill.) possesses two traits which make it a desirable species for management on a large scale. First, Virginia pine characteristically has high yields of wood per acre on average or poor sites in the Mid-South (Thor, 1964). When compared with loblolly (*Pinus taeda* L.) and shortleaf pines (*Pinus echinata* Mill.), Virginia pine outgrows both species on the poorest sites of the Cumberland Plateau-Sand Mountain area of Alabama, Georgia and Tennessee (Allen, 1961). Similarly, after five years Virginia pine was tallest of 11 conifers planted on strip mines in Pennsylvania (Czapowskyj, 1970). High yields for this species were reported also by Burton (1960), Fenton and Bond (1964) and Slocum and Miller (1953). Second, Virginia pine wood has good pulping qualities (Thor, 1964). Primarily for these reasons thousands of acres of marginal lands have been regenerated with this species (Evans, 1971). However, until recently all Virginia pine regeneration was done with unimproved stock. For example, of the 10,512 pounds of seed collected from the North Carolina State University Cooperative Pine Orchards in 1971, only 187 pounds, or approximately two percent, were Virginia pine seed (North Carolina State University, 1972). If these marginal sites are to be used to their fullest potential they should be regenerated with improved seed; this implies that additional seed orchards of Virginia pine will have to be established.

The primary objective of this study was to evaluate genetic and environmental sources of variation and their interaction with respect to height, diameter at half-height, stem volume, branch length, branch diameter and wood specific gravity in plantation grown juvenile Virginia pine. Another objective was to determine genetic gains which could be expected if seedling seed orchards were established. It is hoped that these data will aid in establishment of seed orchards of Virginia pine.

CHAPTER II

REVIEW OF LITERATURE

Ecology of the Species

Virginia pine has been characterized as a disaster species with most effective reproduction after fires and on badly eroded old fields. On better sites it is a transitional species soon replaced by hardwoods; like most pioneer species, it is extremely intolerant of competition and requires direct sunlight. While it is more tolerant of low soil moisture than most pine species, it is not usually found on poorly drained soils (Fowells, 1965).

Although Virginia pine grows well on a wide variety of sites, it grows best on clay, loam, and sandy loam and grows poorly on shaly and very sandy soils (Fowells, 1965). However, when compared with loblolly and shortleaf pines in the Virginia Piedmont, the site index of Virginia pine was the least sensitive to soil factors. In attempting to predict site index of this physiographic province, Kormanik (1966) found that of 60 site variables investigated, the three that affected growth of Virginia pine most were thickness of the A horizon and the estimated percent water at field capacity of the A_2 and A_3B_1 horizons. It was suggested that most woodland sites had a site index between 60 and 70 and that Virginia pine would be superior to loblolly or shortleaf pine on those sites considered least productive, especially on dry upland soils and those lacking a B horizon. Kundt

(1972) reported that root development of the species varies greatly; shallow root systems were observed on shallow soils while on deep soils trees had tap roots of 8 to 10 feet.

The range of Virginia pine extends from Long Island and southern New York southeast to north Georgia and central Alabama. East of the Appalachian mountains it is found on the Coastal Plain of New Jersey, Maryland, Delaware, and northern Virginia, as well as the Piedmont of Virginia, North and South Carolina, and Georgia. The western part of the species range extends from central Pennsylvania through southeast Ohio and southward to parts of western Kentucky and Tennessee (Fowells, 1965).

Natural Variation

The first suggestion that racial variation patterns may be present in Virginia pine was by Allen (1961). In his study of site index relationships on the Cumberland Plateau and Sand Mountain areas of Alabama, Georgia, and Tennessee, best growth was found in the northern part of the study area. This observation could not be explained by soil or precipitation factors and it was concluded that it may be the result of racial variation.

Thor (1964) investigated natural variation in wood properties of Virginia pine in Tennessee and Kentucky. He reported a clinal variation pattern for tracheid length on the Cumberland Plateau and Mountains with tracheids increasing in length from south to north. No definite pattern was observed for other wood characteristics.

Provenance and Progeny Tests

One of the initial steps in tree improvement programs is the establishment of provenance tests. Ideally, seed from several parts of the species range are planted in an area to determine which source will provide the best growth in the area to be regenerated. Genys (1966) reported on such a seed source test of Virginia pine with 17 provenances outplanted in Pennsylvania, Maryland, and Tennessee. Seven year results indicated that trees from sources on the Atlantic Coastal Plain and Tennessee provided better growth in the Maryland and Tennessee locations than trees from more northerly or mountainous sources. However, at the Pennsylvania test location, on a poor site outside the species range, trees from higher elevation sources had 90 to 100 percent survival while trees from southern sources had over 50 percent mortality.

Following provenance testing, the next step in the normal progression of a tree breeding program is the progeny testing phase; the best phenotypes are selected from the most promising provenances and their progeny compared to determine the relative breeding value of the selections. One way of doing this is to collect seed from wind-pollinated phenotypes and compare growth in replicated progeny tests. If superior phenotypes are selected from the best provenances, the resulting variance components and heritability estimates can be applied only to those superior provenances where collections were made and to the specific population of selected trees. An alternative approach would be to collect seed from randomly selected dominant or codominant

trees in random stands. The identity of the seed could be maintained both with respect to stand and mother tree. Since both stands and mother trees in these stands are selected randomly, the resulting variance components and heritabilities would be applicable to all the populations from which collections were made. Furthermore, if the stand collections are thought of as provenances, such a progeny test may also serve as a seed source test.

The first report of such a progeny test was by Wright and Bull (1963) and consisted of open-pollinated progeny from 290 red pine (Pinus resinosa Ait.). A similar progeny test was established at The University of Tennessee with Virginia pine. This test consisted of wind-pollinated progeny from 128 mother trees from 12 stands in Kentucky and Tennessee outplanted at six locations. Two-year results from this test indicated that trees from three stands in the Great Valley Physiographic province consistently provided outstanding growth at most planting locations (Evans and Thor, 1971).

Heritability Estimates

A heritability estimate is generally used as a guide to the amount of improvement possible in a metric trait. More specifically, it estimates the proportion of phenotypic variance which can be attributed to additive genetic effects. It is only this portion of the phenotypic variance which can be consistently exploited for breeding purposes. Heritability estimates also serve as a guide to the degree of correspondence between phenotype and genotype; to what degree can the phenotype be used as a selection criterion (Falconer, 1960). This is

important since all measurements made on trees are phenotypic measurements. The size of a heritability estimate then indicates:

a. Whether a breeding program will result in improvement of a trait and if it does, approximately how much can be expected.

b. Which kind of breeding program will be most appropriate.

Among crop breeders one of the most popular methods of estimating heritability is the offspring-parent regression. Although this method has also been used in forest tree breeding, it is not well adapted for such use since the difference between a trait measured on juvenile progeny and the same trait measured on mature parents is of such a magnitude that it may be better to consider them as separate traits. In such cases the correlation of offspring with parent may be a more reliable estimate of heritability than the offspring-parent regression (Steinhoff and Hoff, 1971). In addition, the progeny are usually grown on a site different from that of the parent and therefore, the heritability estimates derived from regression and correlation techniques are confounded with environmental effects.

Most narrow-sense heritability estimates in forest tree breeding are derived by variance component methods. Unfortunately, many of the early heritability estimates are either biased or erroneous. Good discussions of the erros in many of these estimates may be found in the literature (Namkoong, Snyder, and Stonecypher, 1966; Stonecypher, 1966; Evans, 1971). One of the most common flaws in published heritabilities is that they are usually computed from experiments represented in only one environment. No estimate of genotype-environment interaction can be computed from such experiments. Since there is no way to

extract this interaction from the additive genetic variance component, the result may be an inflated heritability estimate if it is applied to a site other than the test location. For example, Stonecypher (1966) obtained a heritability of 0.20 for height of two-year old loblolly pine at one location and 0.04 at another location. The heritability of two-year height for combined locations after the genotype-location interaction had been removed from the family variance component was 0.10.

The majority of heritability estimates based on variance-component methods are computed using analysis of variance techniques. This approach results in least-squares estimates of variance components as long as there are data in all classifications and there are very few missing observations. Unfortunately, many heritability estimates are based on analysis of variance techniques with unbalanced data. For example, the variance components and heritabilities for Virginia pine based on two-year data (Evans, 1971) were estimated by analysis of variance although all plots with less than two trees were omitted from the calculations. The resulting variance components and heritabilities are not maximum-liklihood-least-squares estimates and may be biased.

Heritability of Height Growth

Evans (1971) obtained highly variable heritability estimates from one- and two-year data; estimates ranged from 0.16 to 0.48 at age two and from 0.17 to 0.44 at age one. Although there was not much change in these estimates from age one to age two (the average heritability for all locations was 0.28 for both one- and two-year data), there was

a wide range in the magnitude of estimates among locations for both years. Heritability estimates for height of juvenile Virginia pine were obtained also by Kundt (1972) from a diallel analysis; at age two months $\hat{h}^2$ = 0.09, at age seven months $\hat{h}^2$ = 0.14, and at age 10 months $\hat{h}^2$ = 0.11. These estimates compare with heritabilities of height growth in loblolly pine of 0.14 to 0.10 at age one-year and 0.20 to 0.04 at age two-years (Stonecypher, 1966).

Heritability estimates derived from such young plant material should be viewed with caution. For example, in western white pine (Pinus monticola Dougl.) total height at the end of each of the first four years from seed was significantly correlated with seed weight. Analysis was therefore restricted to fourth-year data in which heritability of height growth was found to be only 6.6 percent (Squillace, Bingham, Namkoong, and Robinson, 1967). More recent data from research with slash pine (Pinus elliottii Engelm.) indicate that seed-size ef effects may persist for eight years or more (Dr. T. O. Perry, North Carolina State University, personal communication). However, Kundt (1972) found no evidence of such a correlation in Virginia pine.

Analysis of incomplete diallel crosses in one-, two-, and three-year old eastern white pine (Pinus strobus L.) revealed that heritabilities for height decline with older plant material, in one case from 0.59 for crosses at age one to 0.16 for crosses at age three. Two reasons were proposed for this decline in heritability; first, a relative increase in environmental sources of error, and second, a reduction in genetic variance in growth caused by a convergence in

growth curves. Since there was no evidence of a decrease in the amount of variation associated with additive genetic components, it was concluded that the lower heritabilities of the older trees could be attributed to increased among- and within-plot sources of environmental variance. In this same experiment, analysis of three-year old open-pollinated material yielded a heritability estimate of 0.28 for height growth (Kriebel, Namkoong, and Usanis, 1972).

Heritability of Diameter Growth

Reports of heritabilities of diameter growth are much less prevalent than for height, probably due to the fact that most heritability estimates are based on juvenile trees. Researchers may feel also that since diameter growth is strongly affected by environmental and spacing factors, detection of genetic control may be more difficult than with height. In addition, no standardized method of measuring diameter has been developed for seedlings; even when diameter at breast height (d.b.h.) can be obtained on trees five years old and younger, such a d.b.h. may not have much meaning. Kundt (1972) obtained a heritability estimate of 0.03 for diameter of 10-month old Virginia pine where diameter was measured at ground level. However, the range of diameters was very narrow, and it was suggested that this range would increase with age. Evans (1971) reported estimates of heritability between 0.08 and 0.41 for two-year old seedlings (average heritability for all locations was 0.20) when diameter was measured at half-height. These estimates are somewhat lower than the 0.32 heritability estimate

reported for five-year old loblolly pine (half-height diameter measurement) by Stonecypher and Zobel (1966).

Heritability of Branching Characteristics

Wood of Virginia pine has so many knots that Slocum and Miller (1953) stated that wood of this species is unsuitable for quality lumber and should be considered primarily for pulpwood purposes. However, knotty wood is also undesirable for pulpwood (Curran, 1938). In response to these objections most tree improvement programs include as selection criteria for superior trees characteristics such as pruning ability and branch angle. Unfortunately, there are few reports of heritability estimates of such characteristics.

Preliminary results of Trousdell, Dorman, and Squillace (1963) indicate that crown form and branch length in young loblolly pine are inherited traits. Their measurements were based on a limited number of progeny from parents selected for either good or poor crown form, and therefore, the heritability estimates are probably biased and not applicable to the species as a whole. Their results confirmed the work of Peters and Goddard (1961) where a high positive correlation between tree height and the product of length and diameter of branches ($r = 0.87$) was found in five-year old slash pine. However, in both studies there were individual trees having superior height growth as well as small crowns and small limbs, indicating a potential for breeding trees for rapid height growth and small branches. Similar results were obtained in a preliminary study of 22-month old seedlings of Virginia pine; although the shortest seedlings had the shortest branches, the

progeny of one controlled cross had both superior height growth and short branches (Kundt, 1972).

A study of 31 clones of Pinus densiflora S et Z. indicated broad-sense heritability estimates of 0.465, 0.753, and 0.774 for number of branches per whorl, branch angle, and internode length, respectively (Kwak, Noh, and Choi, 1972). In Virginia pine Kundt (1972) obtained a narrow-sense heritability of 0.21 for number of branch whorls on 10-month old seedlings (each node was counted as a branch whorl if it had more than one branch).

Narrow-sense heritability estimates for branch length and branch diameter of two-year old Virginia pine were reported by Evans (1971). For branch length (measured on the longest branch in the first most nearly perfect whorl), heritability estimates ranged from 0.08 to 0.47 with a mean of 0.21 while for branch diameter (the same branch was measured for both length and diameter), heritability estimates ranged from 0.05 to 0.40 with a mean of 0.16.

Heritability of Wood Specific Gravity

Because wood specific gravity is an indicator of pulping qualities and strength properties of wood, it has been incorporated in most selection systems for superior phenotypes of the southern pines (Thor, 1964). Heritability estimates of wood specific gravity of southern pines have been reported by numerous workers; narrow-sense heritability estimates for two- and three-year old unextracted loblolly pine wood were reported by Stonecypher, Cech, and Zobel (1964) to be 0.56 and 0.72, respectively. At age five heritability estimates for unextracted

wood of loblolly pine were 0.73 and 0.64 for extracted wood (Stonecypher and Zobel, 1966). Similarly, Van Buijtenen (1962) estimated narrow-sense heritability of unextracted wood of open-pollinated loblolly pine progeny to be between 0.64 and 1.00, although the heritability estimate for two-year old controlled-pollinated progeny was only 0.37. Although no estimates of heritability of Virginia pine wood have been reported, in a natural variation survey of wood properties of this species, Thor (1964) found that the among-tree variance component accounted for 68 percent of total variance of specific gravity of extracted wood, indicating that specific gravity may be an inherited trait in this species also.

Genotype-Environment Interactions

A genotype-environment interaction is defined as a lack of uniformity of response of two or more groups of plants grown in two or more environments when the groups possess some degree of genetic similarity; one group may demonstrate good growth in one environment but mediocre growth in another. Such an interaction may manifest itself in one of two ways. First, there may be differences in rank of genotypes in the different environments and second, the relative superiority of genotypes may differ although the ranks may remain the same. Presence of the first kind of interaction may necessitate the selection of different genotypes for different locations in order to maximize gain (Squillace, 1970).

Crop breeders generally use the genotype x environment interaction as an indicator of the stability of a genotype for a

characteristic under consideration or how adaptable a genotype is to varying environments. There seems to be a trend in plant breeding to develop varieties which are adapted to a relatively broad range of environments as opposed to the more conventional approach of breeding varieties for specific localities. Development of such stable varieties requires consideration of stability parameters related to the genotype-environment interactions as well as yield and productivity data (Reich and Atkins, 1970).

Wricke (1962) proposed a method of partitioning the genotype x environment interaction sum of squares directly into the contribution of individual varieties using a series of two-way tables. The yield of each variety at a location is subtracted from the mean yield of all cultivars at that location; the resulting deviations are squared and their sum is subtracted from the total sum of squares for each variety, resulting in the contribution of that variety to the interaction sum of squares. A relatively stable variety will make a lower contribution to this interaction sum of squares than a less stable variety.

Eberhart and Russell (1966) used a regression approach to rate the the stability of a variety. By their method the genotype x environment interaction sum of squares is partitioned into two parts; the sum of squares due to regression of a varietal yield on the average yield of all varieties in that environment and the sum of squares of deviations unexplained by regression. The most desirable varieties had a regression coefficient of

approximately 1.0, a high mean yield, and deviations from regression approximating zero.

Morgenstern and Teich (1969) compared the methods of Wricke (1962) and Eberhart and Russell (1966) for evaluation of phenotypic stability of height growth of jack pine (Pinus banksiana Lamb.) provenances. The two methods yielded similar results. They suggested that, after initial studies have defined selection areas, the application of stability criteria in forestry shows promise for the development of an environmental index; such an index would be used in the selection of adaptable races and would be superior to selection on the basis of mean performance.

The importance of the genotype x environment interaction has long been recognized in forestry as witnessed by the long standing rule of thumb that local seed sources of a given species should be used in regenerating a site. However, more recently this rule of thumb has been seriously questioned. It has been pointed out that best growth occurs in areas where environmental conditions are optimum for that species and that perhaps sources from such areas can be used more extensively. In areas where environmental variables are less than optimum there may be a loss in vigor at the expense of adaptation to less productive sites (Namkoong, 1969).

Most reports of such interactions in forestry are on the provenance level. These reports frequently indicate that the seed source x environment interaction accounts for only a small part of the total variation. For example, King (1965) found that the seed source x

plantation variance component never accounted for more than six percent of the total variation in a Scotch pine (Pinus sylvestris L.) provenance test and that this was only one-sixth of the seed source variance component for height growth. In reporting interactions in 8- to 12-year old provenance and progeny tests of 11 species, Wright (1973) found that genetic and site effects are generally higher than the genotype x environment interaction. He proposed that many such interactions are artifacts traceable to details of nursery practice or plantation establishment. Likewise, in reporting 10-year results for loblolly pine in the Southwide Pine Seed Source Study, Wells and Wakeley (1966) stated that "considering the diversity of the planting locations, the most surprising and informative point about these interactions is that they are so small."

The relatively small magnitude of these interaction variance components in provenance studies may not be surprising considering the structure of the gene pool in a provenance selection. If the assumption that most forest trees are heterozygous for most characteristics is true, a seed source collection from random trees in a provenance will probably most closely resemble a hybrid blend with considerable genetic diversity. Many crop breeders have reported that genetic diversity such as in a mixture of heterozygotes or of different genotypes results in more stable, phenotypically consistent performance than that observed in more genetically uniform populations (Allard, 1961; Reich and Atkins, 1970).

Reports of genotype x environment interactions in progeny tests

are sparse in the forestry literature. Stonecypher (1966) found that the interaction component for loblolly pine was low for first- and second-year height and high for survival, relative to the family variance component. In Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), however, Campbell (1972) found that the family x location interactions were a significant part of the total variation for juvenile height growth. Few families consistently demonstrated superior performance over all locations and seasons; it was suggested that a breeding program to develop widely adapted strains would require progeny evaluation over many environments.

Assumptions Regarding Parent and Progeny Populations

In order to interpret additive components of variance in a progeny test, Stonecypher (1966) listed a series of assumptions to be made about parent and progeny populations from which these components were derived. Most of these assumptions are based on the Hardy-Weinberg Equilibrium. The assumptions are:

a. Diploid, Mendelian inheritance.

b. Parent populations are in linkage equilibrium.

c. Parents and progeny are not inbred and are random members of non-inbred populations.

d. Open-pollinated progeny are half-sibs.

e. No epistasis.

f. No maternal effects.

Of these, assumptions c and d have been seriously questioned and warrant some discussion.

Most genetic variation studies in forest trees assume that parent trees within a stand are unrelated. The assumption is made because there is no way of determining the degree of relationship among random trees in a stand. The coefficient of inbreeding, which is an expression of this degree of relationship among parent trees, is a function of the amount of inbreeding in the current generation and the average inbreeding coefficients of the parents in the previous generation (Franklin, 1971a). Since in most cases such estimates are not available, there is no way to translate genetic variances from one generation to the next unless it is assumed that gene frequency is one-half and there is no dominance (Namkoong, 1966).

Franklin (1971a) estimated the average coefficient of inbreeding of loblolly pine parent trees on an old field site to be so low (0.0003) that for all practical purposes it could be ignored. The low inbreeding coefficient was interpreted as being an indicator of the small number of selfed seedlings which became established and reached sexual maturity despite appreciable levels of inbreeding at fertilization. This severe inbreeding depression has been suggested as a means of decreasing the number of inbred seedlings outplanted; since inbred seedlings are usually noticeably shorter than outcrossed trees they could be culled in the nursery (Kraus and Squillace, 1964). However, in slash pine the correlation between nursery and field inbreeding depressions was only 0.38, indicating that selfs are not always recognizable during nursery roguing. In one case a selfed family was only six percent shorter in the nursery but 30 percent shorter after five years in the field (Snyder, 1972).

Results of an electrophoretic-peroxidase variation study in a natural forest of Thujopsis dolobrata L. contradict these assumptions. In this study trees in a radius of 20 to 25 meters had isozyme patterns so similar that Sakai and Miyazaki (1972) considered them to be members of the same family. They concluded that genetically related trees of this species grow in proximity to each other and are not scattered. Unlike pines, however, there seem to be indications that vegetative reproduction is common in this species; this would account for the high relationship among trees.

Many studies use estimates of natural selfing as a measure of inbreeding. Kraus and Squillace (1964) found self-fertility in slash pine to average 18 percent on the basis of controlled crosses of seven trees, with a range of 4 to 36 percent, suggesting that individual trees differ in their capability for self-fertilization. Fowler (1965) estimated that natural selfing in red pine probably does not exceed 10 percent in closed stands, although in small isolated stands a much higher proportion of self-fertilized seeds can be expected. In loblolly pine, estimates of selfing varied with position in the crown; in the upper crowns, estimates of self-fertilization averaged seven percent, whereas in lower crown estimates ran as high as 34 percent (Franklin, 1971a). In another report, Franklin (1971a) emphasized that many estimates of selfing based on frequency of mutant phenotypes may be biased because they do not take into account embryonic mortality.

Self-fertility is not a prerequisite for inbreeding; Namkoong (1966) emphasized that estimates of genetic variances derived from

open-pollinated progeny may be biased due to natural inbreeding resulting from relationship of the seed parent with its pollinator, relationship of pollinators among themselves, or the presence of only a few effective pollinators. He suggested that although the failures of the assumptions may be small, until the extent of these failures is determined genetic variance components derived from such tests should be regarded with caution.

In open-pollinated progeny tests the family component is interpreted as being one-quarter of the additive genetic variance. This interpretation is dependent upon the assumption that all progeny are half-sibs. However, due to synchronized time of flowering of some clones and other assortative pollination mechanisms, some of the progeny may be full sibs (Squillace and Bengtson, 1961).

The fact that some assortative pollination mechanism occurs in Virginia pine can be seen from the data of Kundt (1972). Of 22 clones used in a modified diallel mating experiment, none of the clones displayed 100 percent crossability in terms of the number of successful crosses with other clones. Crossability ranged from 86 percent for the highest to 19 percent for the clone with the lowest number of successful crosses with other clones. Such assortative pollination mechanisms may result in a degree of relationship among some progeny closer than that of half-sibs. If this is the case, the family variance component should estimate between one-half and one-quarter of the additive variance (Squillace and Bengtson, 1961).

Gains

Expected response or gain as defined by Falconer (1960) is the product of selection intensity, the appropriate phenotypic standard deviation and the heritability. This product is used to evaluate the relative merits of different selection schemes in terms of the progress which can be expected by breeding for the character in question.

In forest tree breeding, selection is commonly practiced in several stages. Response may be realized due to phenotypic selection of wild parent trees, followed by a gain from selection of best families in an open-pollinated progeny test and again due to selection of best individuals in these families. Expected gains from such multi-stage selection systems can be computed by the additive methods of Namkoong, Snyder, and Stonecypher (1966). Expected gains resulting from such a selection scheme are:

$$G = i_1\left(\frac{\sigma^2 A}{\sigma_1}\right) + i_2\left(\frac{1/4\,\sigma^2 A_1}{\sigma_2}\right) + i_3\left(\frac{3/4\,\sigma^2 A_1}{\sigma_3}\right)$$

where

$$\sigma_1^2 = \sigma_W^2 + \sigma_P^2 + \sigma_{GE}^2 + \sigma_G^2$$

$$\sigma_2^2 = \frac{\sigma_T^2 + n\sigma_P^2}{NRS} + \frac{\sigma_{GE}^2}{E} + 1/4\,\sigma_{A_1}^2$$

$$\sigma_3^2 = \sigma_W^2 + \sigma_P^2 + \sigma_{GE}^2 + 3/4\,\sigma_{A_1}^2 + \sigma_D^2$$

and σ_A^2 equals total additive genetic variance for a large random mating population. The among family variance component ($\sigma_{A_1}^2$) usually represents the additive genetic variance component. In most cases the genetic variance is assumed to be regenerated as a result of

recombination between parental and progeny generations. Therefore,

$\sigma^2_{A_1} = \sigma^2_A$;

σ^2_T = error variance of the small plot or microsite.

σ^2_W = within-plot or individual tree variance component.

σ^2_P = among-replication variance component.

σ^2_{GE} = genotype x environment interaction variance component.

σ^2_G = total genetic variance component.

σ^2_D = total genetic variance component.

i_1 = first stage selection intensity (mass selection).

i_2 = second stage selection intensity (among-family selection).

i_3 = third stage selection intensity (within-family selection).

The overall expected gains equation is then broken into three parts, corresponding to the three stages of selection. The gain resulting from phenotypic selection of parent trees, assuming gains are realized from mass selection, is:

$$\frac{i_1 \sigma^2_{A_1}}{\sigma_1}$$

This is followed by expected response due to selection of the best families in the progeny test:

$$i_2 \frac{1/4\sigma^2_{A_1}}{\sigma_2}$$

The last term in the equation represents the expected gain in response to selection of the best phenotypes in the most promising families:

$$i_3 \frac{3/4\sigma^2_{A_1}}{\sigma_3}$$

In the latter term, gain is based on total genetic variance after the variance among half-sibs is removed.

Evans (1971) modified this approach to compute gains from selection in the two-year old Virginia pine heritability study. Since there was no phenotypic selection in choosing parent trees for establishment of the open-pollinated progeny test, it was assumed that initial gains from mass selection were zero. Expected gains were computed using the formula:

$$G = i_4 \frac{\sigma^2_{F(S)}}{\sigma_1} + i_5 \frac{3\sigma^2_{F(S)}}{\sigma_2}$$

where

$$\sigma^2_1 = \frac{\sigma^2_W}{NR} + \frac{\sigma^2_{F(S)R}}{R} + \sigma^2_{F(S)}$$

$$\sigma^2_2 = \sigma^2_W + \sigma^2_{F(S)R}$$

$\sigma^2_{F(S)}$ = among-family-within-stand variance component.

σ^2_W = within-plot variance component.

$\sigma^2_{(RxF)/S}$ = family-within-stand x replication interaction variance component.

E = environment.

N = number of trees in a plot.

R = number of replications.

i_4 = among-family selection intensity.

i_5 = within-family selection intensity.

Expected gains for height growth were computed for two selection schemes as applied to a single plantation of the progeny test. Expected gains were computed selecting the tallest families within the seven tallest of 12 parent stands, and alternatively selecting the tallest families without regard to stand origin. Both schemes resulted in similar gains; expected response was computed to be 21 percent of the unselected population means.

It may be a significant point that in the first selection scheme of Evans (1971), stand selection was applied in calculating gains. Evans (1971) and Rink and Thor (1973) treated gains from stand selection as a deviation between means of selected and unselected stands; gains in response to family and within-family selection were added to this deviation.

The expected gains for height growth reported by Evans (1971) in Virginia pine compare favorably with reports of gains with other species. For example, Squillace, Bingham, Namkoong, and Robinson (1967) estimated 11.9 percent gain for juvenile growth rate in western white pine resulting from a combination of phenotypic parental selection and genotypic selection in a progeny test. Snyder (1969) compared gains in height increment which could be realized from parental selection as opposed to family selection in eight-year-old longleaf pine (Pinus palustris Mill.); gains resulting from parental selection were 12 percent while 35 percent could be achieved by family selection in the progeny test. Gains for height growth as a result of mass selection in Virginia pine would be only five percent,

approximately one-fourth of the expected response from multistage selection (Evans, 1971). Gains in height increment of two- and three-year old seedlings of Douglas-fir in response to mass selection were estimated to be between 8.0 and 22.6 percent of the mean (Campbell, 1972).

CHAPTER III

MATERIALS AND METHODS

I. SELECTION OF PARENT POPULATIONS

The plantations comprising this experiment were established in 1967 from open-pollinated seed collected from 13 stands in Kentucky and Tennessee. Parent stands were selected from the three predominant physiographic regions of Kentucky and Tennessee: The Coastal Plain, Cumberland Plateau and Mountains, and The Great Valley. Nine of these stands were in Tennessee and four in Kentucky (Figure 1); all were even-aged natural stands of average or better than average quality established on abandoned fields with site indices ranging from 60 to 87 feet (Thor, 1966). With one exception (stand number 10), none had been subjected to any silvicultural treatment or management; stand number 10 was a United States Forest Service seed production area which had been heavily thinned to remove undesirable trees. The parent stands ranged in age from 28 to 53 years. Stands younger than age 25 were not accepted because parent trees were used also in a wood property study requiring samples obtained at breast height and representing the wood between the tenth and twentieth growth rings. Old stands were not used because pruning and branching characteristics could not be objectively compared with those of younger stands. Stand and respective site characteristics are summarized in Table 1.

Within each stand 15 trees were selected as potential parent

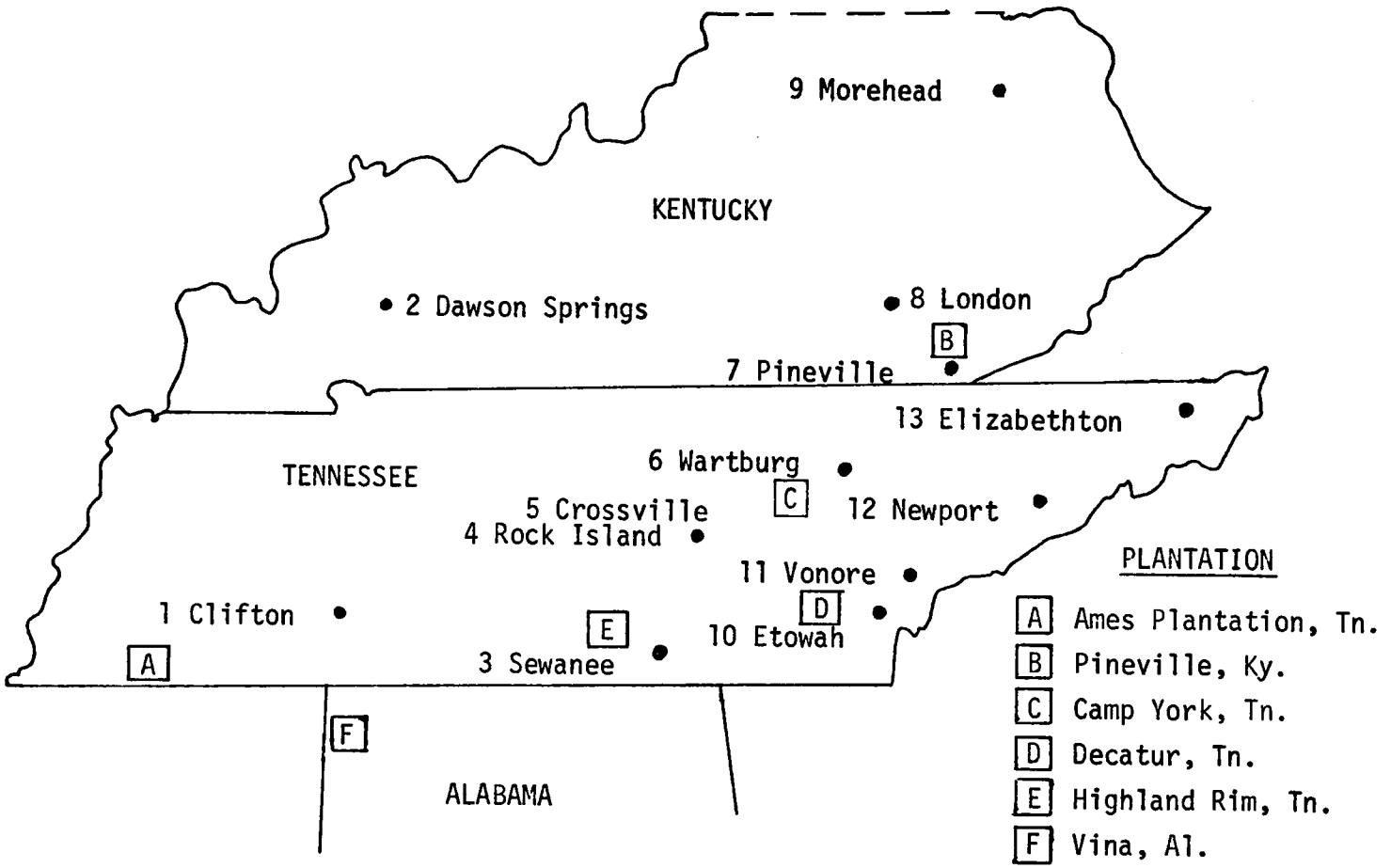


Figure 1. Location of parent stands and plantation sites in Kentucky, Tennessee, and Alabama.

TABLE 1. Location, Cooperator, Site Index, d.b.h., and Age of Parent Stand. (Averages Are Based on 15 Trees Per Stand)

Stand Number	Physiographic Region	Location	Cooperator	Site Index (Feet at 50 Years)	d.b.h. (Inches)	Age (Years)
1	Coastal Plain	Clifton, Tennessee	The University of Tennessee	75	9.0	28
2	Coastal Plain	Dawson Springs, Kentucky	Kentucky State Division of Forestry	69	11.6	52
3	Cumberland Plateau	Sewanee, Tennessee	U. S. Forest Service	73	9.7	34
4	Highland Rim	Rock Island, Tennessee	The University of Tennessee	74	10.2	42
5	Cumberland Plateau	Crossville, Tennessee	Hiwassee Land Company	68	9.0	37
6	Cumberland Mountains	Wartburg, Tennessee	The University of Tennessee	87	8.9	35
7	Cumberland Mountains	Pineville Kentucky	Kentucky State Division of Forestry	82	9.5	42
8	Cumberland Plateau	London, Kentucky	U. S. Forest Service	83	10.9	47
9	Cumberland Plateau	Morehead, Kentucky	U. S. Forest Service	69	8.8	32

TABLE 1 (continued)

Stand Number	Physiographic Region	Location	Cooperator	Site Index (Feet at 50 Years)	d.b.h. (Inches)	Age (Years)
10	Great Valley	Etowah, Tennessee	U. S. Forest Service	81	9.0	34
11	Great Valley	Vonore, Tennessee	Hiwassee Land Company	60	9.8	53
12	Great Valley	Newport, Tennessee	The University of Tennessee	75	9.7	42
13	Great Valley	Elizabethton, Tennessee	U. S. Forest Service	64	11.1	43

trees from which seed collections could be made. The only criteria used in selecting these trees were that they be dominant or codominant and that they could be climbed safely. Although poor, average, and excellent phenotypes were included, these criteria may have resulted in a slight sampling bias toward taller and sturdier trees. Abundant cone production was not a selection criterion.

Since most abandoned fields in Kentucky and Tennessee are only a few acres in size, individual trees had to be selected within a small area; some parent trees were several hundred feet apart while some were adjacent to each other. Again, stand number 10 was an exception; since all undesirable trees had been removed, most of the remaining trees had to be used.

II. SEEDLING PRODUCTION

It was estimated that a minimum of 200 cones would be required from each tree in order to produce enough seedlings to represent each parent tree at all planting locations. Even though Virginia pine is characterized as a prolific cone producer, it was recognized that some individuals would not fulfill expectations. As a result, cone collection was aimed at obtaining 200 cones from 10 of the original 15 trees by extending collection from September and October 1963 through the cone maturation dates of 1964 and 1965. The required number of cones were obtained from most parent trees.

Cone harvesting was accomplished both by climbing trees and by cutting them. After extraction from cones, the seeds were stored at 40°F in plastic bags until sowing.

Seeds were germinated and grown in the spring of 1966 in unreplicated plots at the Norris, Tennessee, nursery of the Tennessee Valley Authority. After one growing season the seedlings were lifted, sorted into bundles of 10 seedlings per family, and tagged. During this sorting process all small and deformed seedlings were culled, and only healthy seedlings were retained. Seedlings were packed in damp sphagnum moss and wrapped with seedling wrapper paper prior to shipment to cooperators for outplanting.

Of the original 195 trees selected as parents, only 12 yielded enough seedlings to be included in the experiment. Since a half-sib family is defined as open-pollinated progeny of a single mother tree, a maximum of 12 half-sib families could be outplanted. Unfortunately, the number of progeny produced by parent trees varied so that the maximum number of families could be planted only at the Highland Rim plantation. Ninety families were represented at four locations, while only 57 families were planted at the Pineville, Kentucky, plantation due to an insufficient number of seedlings. The numbers of families from each stand planted at each location are listed in Table 2.

III. DESCRIPTION OF PLANTATION SITES

The six plantation sites were selected on the basis of land available from cooperators and a desire to represent the widest possible array of sites of Virginia pine in the southernmost part of its natural range, including all the major physiographic provinces in this area. Once the general location was determined, the specific

TABLE 2. Number of Families Per Stand Planted at Each Test Site

Stand Number	Number of Families Per Test Site[1]						Total
	A	B	C	D	E	F	
1	4	0	0	0	9	1	14
2	8	3	9	9	10	9	48
3	8	3	10	9	11	10	51
4	10	9	10	10	13	10	62
6	9	4	10	8	12	10	53
7	10	10	10	10	10	10	60
8	9	4	9	8	12	7	49
9	8	6	8	7	11	7	47
10	9	10	9	10	10	10	58
11	9	3	8	10	13	9	52
12	0	0	0	0	7	0	7
13	6	5	7	9	10	7	44
Total	90	57	90	90	128	90	545

[1]A = Ames Plantation, Tennessee; B = Pineville, Kentucky; C = Camp York, Tennessee; D = Decatur, Tennessee; E = Highland Rim, Tennessee; F = Vina, Alabama.

planting site was selected by cooperating personnel not directly involved in the experiment. For example, reforestation personnel of the Hiwassee Land Company selected an abandoned field for the Decatur, Tennessee, site while nonacademic personnel of The University of Tennessee selected a poor upland hardwood site at Ames Plantation which had been scheduled for conversion to pine. Since most plantations required tracts of land approximately 10 acres in size (including border rows), availability of tracts of land of suitable size was often a deciding factor in selecting a planting site. Site descriptions are summarized in Tables 3 and 4; Table 3 describes location, elevation, and soil factors and some of the climatic variables of the plantations are presented in Table 4.

Initially, a seventh planting site was located at Oak Ridge, Tennessee, but a power failure at the Tennessee Valley Authority seedling storage facility resulted in the destruction of the plant material which was to be used for this plantation.

Site preparation varied with the amount and kind of vegetation at each location. The Pineville site required no site preparation since it had no vegetation cover at the time of planting; it had been graded into a gently rolling bench six months prior to planting. All other plantations required disking, burning, mistblowing with 2,4,5-T, or some combination of these (Table 5).

Several of the sites included obstacles which had to be avoided at the time of planting in order to maintain the great possible uniformity within replications. The Camp York site had remnants of barracks

TABLE 3. Location, Physiography, Elevation, and Soil Properties of Plantations

Item	Plantation A Ames	B Pineville	C Camp York	D Decatur	E Highland Rim	F Vina
Plantation location	Fayette County, Tennessee	Bell County, Kentucky	Cumberland County, Tennessee	Meigs County, Tennessee	Franklin County, Tennessee	Franklin County, Alabama
Longitude	89°20'	84°35'	85°10'	84°40'	86°10'	88°05'
Latitude	35°05'	36°40'	35°55'	35°30'	35°20'	34°25'
Physiography[1]	Coastal Plain	Cumberland Mountains	Cumberland Plateau	Great Valley	Highland Rim	Coastal Plain
Elevation (feet)	450	2200	1900	1000	1000	650
Topography	Gently rolling	Gently rolling	Gentle slope	South aspect of low ridge	Gentle slope	Top of low ridge
Soil series	Ruston[2]	Strip mine spoils	Hartsells[3]	DeKalb[4]	Dickson[5]	Guin[6]
Soil texture	Sandy loam	Coarse sand and sand-stone fragments	Sandy loam	Silt loam	Silt loam	Sandy loam

TABLE 3 (continued)

Item	Plantation					
	A Ames	B Pineville	C Camp York	D Decatur	E Highland Rim	F Vina
Soil depth	Deep	Surface	18 inches to bedrock[3]	Variable	18 inches to fragipan[5]	Variable

[1]Fenneman, N. B. 1938. Physiography of Eastern United States. McGraw-Hill Book Co., New York, N. Y. 714 pp.

[2]Flowers, R. L. 1964. Soil Survey of Fayette County, Tennessee. U.S.D.A. Series 1960, No. 13. 98 pp.

[3]Hubbard, E. H., B. L. Matzer, and M. E. Austin. 1950. Soil Survey of Cumberland County, Tennessee. U.S.D.A. Series 1938, No. 25. 107 pp.

[4]Sweet, A. T., J. H. Agee, and W. E. Hearn. 1919. Soil Survey of Meigs County, Tennessee. U.S.D.A. Field Operations of the Bureau of Soils, 21st Report. pp. 1253-1286.

[5]Love, T. R., L. D. Williams, and W. H. Proffitt. 1959. Soil Survey of Coffee County, Tennessee. U.S.D.A. Series 1956, No. 5. 112 pp.

[6]Sherad, H. and R. A. Young. 1965. Soil Survey of Franklin County, Alabama. U.S.D.A. Series 1961, No. 19. 80 pp.

TABLE 4. Climatic Description of Plantations. (Averages Are Based on the Period 1931-1955)

Item	Plantation					
	A Ames[1]	B Pineville[2]	C Camp York[1]	D Decatur[1]	E Highland Rim[1]	F Vina[3]
Mean annual precipitation (inches)	53.12	45.48	53.53	51.71	53.48	49.92
Month with maximum mean precipitation (inches)	January 6.18	March 4.97	January 5.97	March 5.84	January 6.19	January 5.96
Month with minimum mean precipitation (inches)	October 2.78	October 2.15	October 2.70	September 2.55	October 2.56	October 2.34
Mean daily temperature for month of July (°F)	80.3	77.3	73.8	79.0	77.6	81.2
Mean daily temperature for month of January (°F)	42.6	40.5	37.8	41.3	41.5	44.9

TABLE 4 (continued)

Item	Plantation					
	A Ames[1]	B Pineville[2]	C Camp York[1]	D Decatur[1]	E Highland Rim[1]	F Vina[3]
Average length of freeze-free period (number of days)	205	185	176	192	196	232

[1]Dickson, R. R. 1960. Climates of the states - Tennessee. U. S. Dept. of Commerce Weather Bureau No. 60-40. 15 pp.

[2]Anderson, O. K. 1959. Climates of the states - Kentucky. U. S. Dept. of Commerce Weather Bureau No. 60-15. 15 pp.

[3]Long, A. R. 1959. Climates of the states - Alabama. U. S. Dept. of Commerce Weather Bureau No. 60-1. 15 pp.

TABLE 5. Cooperators Involved at Each Planting Site, Previous Land Usage, and Site Preparation Techniques Used at Each Site

Item	Plantation					
	A Ames	B Pineville	C Camp York	D Decatur	E Highland Rim	F Vina
Cooperator	Ames Plantation	U. S. Forest Service	The University of Tennessee	Hiwassee Land Company	The University of Tennessee	Auburn University
Previous land usage	Upland oak-hickory forest	Strip mine graded to a bench	Pasture and World War II prisoner of war camp	Abandoned field	Pasture	Abandoned field
Site preparation	Clearcut and mist-blown with 2,4,5-T	None	Mistblown with 2,4,5-T and disked	Clearcut windrowed	Light disking	Burned and disked

foundations. The Vina site was dissected by gullies and the Decatur site contained an area so eroded that the B_1 horizon was exposed. The latter site contained areas where bare rock was exposed, and old windrows from trees cut prior to planting remained. In all plantations replications and row plots were arranged to avoid such obstacles. The Ames and Highland Rim sites were the most uniform of the plantations with respect to site characteristics.

IV. OUTPLANTING DESIGN

Individual plantations were arranged in randomized complete block design with stands and families within stands randomized in blocks. Half-sib families were planted in 10-tree row plots.

All plantations consisted of 10 replications with the exception of Vina and Pineville which were comprised of nine replications. Spacing between trees was four feet within family-row plots and eight feet between rows at all locations except Pineville where spacing was three feet by five feet, respectively. Two border rows were planted around each plantation; these consisted of a mixture of half-sib progenies.

Since the plantations differed in number of half-sib families, number of replications, and between-tree spacing, they differed also in the amount of land area occupied. Excluding border rows, the Highland Rim plantation was 9.4 acres; the Pineville plantation was two acres. All others were 6.6 acres in size.

V. MEASUREMENTS AND SAMPLING

Five-year measurements were performed on all plantations at the end of the 1971 growing season. Measurements included:

1. Total height to the nearest foot.

2. Stem diameter at the midpoint of the total height of each tree (half-height) to the nearest 0.1 inch.

3. Diameter of the largest branch nearest to the half-height measurement point, to the nearest 0.1 inch.

4. Length of the above branch to the nearest foot.

Total height and stem diameter measurements were used also to compute individual tree volumes using a volume prediction equation for young loblolly pine (Perry and Roberts, 1964):

$$V = (10.62D^2H)/1728$$

where

V = volume in cubic feet.

D = stem diameter at half-height in inches.

H = total height in feet.

In addition, wood cores were obtained from the Highland Rim plantation in order to investigate the heritability of several wood properties. During August 1972, when the trees were in their sixth growing season, 11 mm wood cores were collected from 738 trees, representing 123 half-sib families from 12 seed sources. The third and seventh trees were bored in each 10-tree family-row plot in three of the 10 replications present. In plots where the third or seventh tree was missing, the next tree in line was sampled. Cores with pitch

pockets, knots, or visible amounts of compression wood were not accepted. Since trees were bored between 12 and 18 inches above ground level, only trees which were relatively straight and had a fairly clear bole in this stem section were accepted. Trees under four inches in diameter at one foot above ground level were not sampled since cores from such trees often crumbled upon extraction. Total height and diameter at half-height measurements used in calculation of volumes and weights of wood per tree were obtained from five-year data. All cores were extracted with alcohol and benzene for 16 hours followed by extraction with alcohol for six hours. Extractives in grams per cubic centimeter were determined by subtracting the specific gravity of each core before and after extraction (Rink and Thor, 1973).

In an attempt to more fully account for differences in height growth through a combination of genetic parameters and specific site characteristics, it was decided to evaluate soil samples at the Pineville plantation. In the spring of 1974, when the plantation was seven years old, soil samples and tree heights were obtained to determine the effect of chemical characteristics of the spoil on height growth. Four of the nine replications were used; they were selected because variation in height (based on coefficients of variation) was similar and because of the fact that mean height at age five was significantly different among these four replications. Twenty-seven systematically selected sample spots were used in each replication to obtain the height of four trees and two soil samples, one from the upper six inches and one from between six and 12 inches in soil depth. Five determinations were made from each soil sample: active acidity

(pH in water), extractable phosphorus, conductivity of the saturation extract, exchangeable acidity, and exchangeable Al^{++}. Exchangeable H^{+} was obtained by subtraction of the exchangeable Al^{++} from exchangeable acidity (Thor et al., in press).

VI. STATISTICAL ANALYSIS

Preliminary analyses consisted of analyses of variance for each location; the five characteristics were analyzed on an individual-tree basis in accordance with Henderson's (1953) "Method 1." All effects were assumed to be random. The linear model for these analyses is:

$$Y_{R(F/S)W} = M + S_S + R_R + SR_{SR} + F/S_{F/S} + (RxF)/S_{(RxF)/S} + E_{R(F/S)W}$$

where

$Y_{R(F/S)W}$ = individual observation.

M = mean.

S_S = stand effect, S = 1,...,i, where i = number of stands.

R_R = replication effect, R = 1,...,j, where j = number of replications.

SR_{SR} = effect of interaction of stand and replication.

$F/S_{F/S}$ = family-within-stand effect, F/S = 1,...,p, where p = number of families within a stand.

$(RxF)/S_{(RxF)/S}$ = effect of within-stand interaction of family with replication.

$E_{R(F/S)W}$ = within-plot (residual) effect, W = number of individual trees in one family plot.

The analysis of variance, expected mean squares, and heritability

equation are presented in Table 6. The analysis was performed on an IBM 360 Model 65 computer at The University of Tennessee Computing Center with a program written for this study by The University of Tennessee Program Services. The program had no provision for missing cells; all plots with fewer than two trees were deleted from the analysis. Variance components were obtained by the conventional method of equating expected mean squares to observed values and solving for the appropriate component.

In addition, a combination of Henderson's (1953) "Method 1" and "Method 3" were used to arrive at an analysis of variance combined across all locations. Although an overall least-squares analysis such as Henderson's (1953) "Method 3" would have been preferred, the size of the variance-covariance matrix generated by a complete model precluded such an analysis.

The initial attempt at a combined analysis included an analysis of variance shown in Table 7, Model A; this was an attempt to apply Henderson's (1953) "Method 1" and resulted in negative sums of squares. In order to avoid the negative sums of squares and obtain least squares estimates of mean squares, the analysis was partitioned into three models (Models A, B, and C; Table 7). The Maximum Likelihood General Purpose Program ("Harvey Procedure") of the Statistical Analysis System (Goodnight and Barr, 1973) was used for Models B and C. The latter approach is an application of Henderson's (1953) "Method 3." The ANOVA procedure of the Statistical Analysis System

TABLE 6. Analysis of Variance, Expected Mean Squares, and Heritability Equation for Individual Location Analyses

Source of Variation	d.f.	Expected Mean Squares[1]
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	(F-1)(R-1)S	$\sigma^2_W + W\sigma^2_{(RxF)/S}$
Within plot (= residual)	(W-1)RFS	σ^2_W

[1]See following page for explanation of symbols. Expected mean squares were determined in accordance with the method of Schultz (1955).

TABLE 6 (continued)

[1]Explanation of symbols:

σ^2_W = within-plot variance component.

$\sigma^2_{(RxF)/S}$ = variance component for interaction of replication with family within stand.

$\sigma^2_{F/S}$ = family-within-stand variance component.

σ^2_{RxS} = variance component for interaction of replication with stand.

σ^2_S = among-stand variance component.

σ^2_R = among-replication variance component.

W = average number of plants per plot = $\frac{1}{((RxF)/S)-1}\left[\sum_{R=1}^{j}\sum_{F/S=1}^{p}(t) - \frac{\sum_{R=1}^{j}\sum_{F/S=1}^{p}(t)^2_{F/S}}{\sum_{R=1}^{j}\sum_{F/S=1}^{p}(t)_{F/S}}\right]$, where t = number of trees in each plot.

R = number of replications.

F = average number of families within stands = $\frac{1}{(RS-1)}\left[\sum_{R=1}^{j}\sum_{S=1}^{i}(fm) - \frac{\sum_{R=1}^{j}\sum_{S=1}^{i}(fm)^2_S}{\sum_{R=1}^{j}\sum_{S=1}^{i}(fm)_S}\right]$, where fm = number of families within each stand.

S = number of stands.

Table 6 (continued)

$$h^2 = \frac{4\sigma^2_{F/S}}{\sigma^2_W + \sigma^2_{(RxF)/S} + \sigma^2_{F/S}} .$$

$$h^2 = \frac{4s^2_{F/S}}{s^2_W + s^2_{(RxF)/S} + s^2_{F/S}} , \text{ each } s^2 \text{ being an estimate of the}$$

corresponding σ^2.

TABLE 7. Analyses of Variance and Expected Mean Squares of Three Models into Which the Combined Location Analysis Was Partitioned. Analysis C Was Computed Separately for Each Parent Stand

Source of Variation	d.f.	Expected Mean Squares[1]
Model A		
Locations	L-1	$\sigma^2_W + k_{18}\sigma^2_{(RxF)/L,S} + k_{19}\sigma^2_{(SxR)/L} + k_{20}\sigma^2_{R/L} + k_{21}\sigma^2_{LS} + k_{22}\sigma^2_{(LxF)/S} + k_{23}\theta^2_L$
Replications within location	(R-1)L	$\sigma^2_W + k_{15}\sigma^2_{(RxF)/L,S} + k_{15}\sigma^2_{(SxR)/L} + k_{17}\sigma^2_{R/L}$
Stands	S-1	$\sigma^2_W + k_{12}\sigma^2_{(RxF)/L,S} + k_{13}\sigma^2_{(SxR)/L} + k_{14}\sigma^2_S$
Stands x location	(S-1)(L-1)	$\sigma^2_W + k_9\sigma^2_{(RxF)/L,S} + k_{10}\sigma^2_{(SxR)/L} + k_{11}\sigma^2_{LS}$
(Stands x replications)/location	(S-1)(S-1)L	$\sigma^2_W + k_7\sigma^2_{(RxF)/L,S} + k_8\sigma^2_{(SxR)/L}$
Families in stands	(F-1)S	$\sigma^2_W + k_4\sigma^2_{(RxF)/L,S} + k_5\sigma^2_{(LxF)/S} + k_6\sigma^2_{F/S}$
(Families x location)/stand	(L-1)(F-1)S	$\sigma^2_W + k_2\sigma^2_{(RxF)/L,S} + k_3\sigma^2_{(LxF)/S}$

TABLE 7 (continued)

Source of Variation	d.f.	Expected Mean Squares[1]
(Families x replications)/(location, stand)	(F-1)(R-1)L,S	$\sigma_W^2 + k_1\sigma^2_{(RxF)/L,S}$
Within plot (= residual)	(W-1)RF(S)L	σ_W^2
Model B		
Locations	(L-1)	$\sigma_W^2 + k_3\sigma^2_{LxS} + k_4\theta^2_L$
Stands	(S-1)	$\sigma_W^2 + k_2\sigma_S^2$
Locations x stands	(L-1)(S-1)	$\sigma_W^2 + k_1\sigma^2_{LxS}$
Residual	(W-1)	σ_W^2
Model C		
Families	(F-1)	$\sigma_W^2 + k_5\sigma_F^2$

TABLE 7 (continued)

Source of Variation	d.f.	Expected Mean Squares[1]
Locations	(L-1)	$\sigma^2_W + k_3\sigma^2_{LxF} + k_4\theta^2_L$
Families x locations	(F-1)(L-1)	$\sigma^2_W + k_2\sigma^2_{LxF}$
Replications within locations	(F-1)L	$\sigma^2_W + k_1\sigma^2_{R/L}$
Residual	(W-1)	σ^2_W

[1]Explanation of symbols:

σ^2_W = within-plot variance component.

$\sigma^2_{(RxF)/L,S}$ = within-location-and-stand variance component for the interaction of family with replication.

$\sigma^2_{(LxF)/S}$ = within-stand variance component for the interaction of family with location.

$\sigma^2_{F/S}$ = family-within-stand variance component.

TABLE 7 (continued)

$\sigma^2_{(SxR)/L}$ = within-location variance component for the interaction of stand with replication.

σ^2_{LxS} = variance component for interaction of location with stand.

σ^2_S = among-stand variance component.

$\sigma^2_{R/L}$ = replication-within-location variance component.

σ^2_L = among-location effect.

W = number of trees per plot.

R = number of replications.

F = number of families.

S = number of stands.

L = number of locations.

$$h^2 = \frac{4\sigma^2_{F/S}}{\sigma^2_W + \sigma^2_{(RxF)/L,S} + \sigma^2_{(LxF)/S} + \sigma^2_{F/S}}$$

Again, $\hat{h}^2$ was calculated using s^2 values derived from observed mean squares.

was used for Model A. Sums of squares from these models were variously combined into a final analysis of variance; a description of this final analysis will follow.

Expected mean squares for the model used for the analysis of variance combined across all locations are presented in Table 8. All effects were assumed to be random except location which was fixed. The linear model for this analysis is:

$$Y_{LR(F/S)W} = M + L_L + R/L_{R/L} + S_S + SL_{SL} + F/S_{F/S} + (LF)/S_{(LF)/S} + E_{LR(F/S)} + W_{LR(F/S)W}$$

where

$Y_{LR(F/S)W}$ = individual observation.

M = mean.

L_L = location effect, L = 1,...,q, where q = number of locations.

$R/L_{R/L}$ = effect of replications within locations, R/L = 1,...,j, where j = number of replications at a given location.

S_S = stand effect, S = 1,...,i, where i = number of stands.

SL_{SL} = effect of interaction of stand with location.

$F/S_{F/S}$ = family-within-stand effect, F/S = 1,...,p, where p = number of families in a given stand.

$(LF)/S_{(LF)/S}$ = effect of within-stand interaction of location with family.

$E_{LR(F/S)}$ = term resulting from pooling effects for interaction of stand with replication in location and of family with replication-within-location-and-stand (Error A).

$W_{LR(F/S)W}$ = within-plot effect, W = number of individual trees per family plot.

TABLE 8. Analysis of Variance and Expected Mean Squares for Analysis Combined Across Locations

Line Number	Source of Variation	d.f.	Expected Mean Squares[1]
1	Locations	L-1	$\sigma^2_W + k_{13}\sigma^2_E + k_{14}\sigma^2_{R/L} + k_{15}\sigma^2_{LxS} + k_{16}\sigma^2_{(LxF)/S} + k_{17}\theta^2_L$
2	Replications in locations	(R-1)L	$\sigma^2_W + k_{11}\sigma^2_E + k_{12}\sigma^2_{R/L}$
3	Stands	S-1	$\sigma^2_W + k_9\sigma^2_E + k_{10}\sigma^2_S$
4	Stands x locations	(S-1)(L-1)	$\sigma^2_W + k_7\sigma^2_E + k_8\sigma^2_{LxS}$
5	Families in stands	(F-1)S	$\sigma^2_W + k_4\sigma^2_E + k_5\sigma^2_{(LxF)/S} + k_6\sigma^2_{F/S}$
6	(Locations x families)/stands	(L-1)(F-1)S	$\sigma^2_W + k_2\sigma^2_E + k_3\sigma^2_{(LxF)/S}$
7	Error A	L[(F-1)(R-1)S + (S-1)(R-1)]	$\sigma^2_W + k_1\sigma^2_E$
8	Residual (within plot)	(W-1)RF(S)L	σ^2_W

[1]See following page for explanation of symbols. Expected mean squares were determined in accordance with the method of Schultz (1955).

TABLE 8 (continued)

[1]Explanation of symbols:

σ^2_W = within-plot variance component.

σ^2_E = variance component for Error A.

$\sigma^2_{(LxF/S)}$ = variance component for the interaction of location with family-within-stand.

$\sigma^2_{F/S}$ = family-within-stand variance component.

σ^2_{LxS} = variance component for the interaction of location with stand.

σ^2_S = among-stand variance component.

$\sigma^2_{R/L}$ = replication-within-location variance component.

σ^2_L = among-location effect.

W = number of trees per plot.

R = number of replications.

F = number of families.

S = number of stands.

L = number of locations.

The "Harvey" program computes least-squares estimates of variance components and "k" coefficients for all components (in other words, for the terminal variance component and coefficient of each main-effect component in the expected mean square) except interaction effects. However, since the program provides inverse elements of segments of the inverse matrix for each effect, "k" coefficients can be computed for these interactions using the "direct method" of Harvey (1960);

$$k = \frac{1}{m}\left(\sum_{ii} Z^{ii} - \frac{1}{d.f.}\sum_{ij}\sum Z^{ij}\right)$$

where

d.f. = number of degrees of freedom for the effect in the sample of data.

m = number of subclasses.

$\sum_{ii} Z^{ii}$ = sum of diagonal elements of the appropriate segments of the matrix.

$\sum_{ij}\sum Z^{ij}$ = sum of off-diagonal elements of that matrix.

The resulting "k" coefficient is divided into the difference between the two appropriate mean squares to obtain an estimate of the variance component.

A line-by-line description of the derivation of the sums of squares in the overall analysis (Table 8) will follow. Sums of squares for lines 1, 3, and 4 were obtained directly from Model B (Table 7, page 47). Sums of squares for lines 5 and 6 were derived by summing the sum of squares for the respective line in Model C (Table

7, page 47) over all parent stands. The respective sum of squares was then divided by the appropriate sum of degrees of freedom to obtain an extimate of the mean square. Sums of squares for lines 2 and 8 were obtained directly from Model A (Table 7). Although an estimate of line 2 was also included in Model C (Table 7), it was thought that a combined estimate from the latter model may have been confounded with stands and therefore was not used. The sum of squares for line 7 was obtained by subtracting from the residual in Model B (Table 7) the sum of squares for lines 2, 5, 6, and 8 (Table 8, page 52). The resulting sum of squares is actually a pooled estimate of the combined sum of squares of two interactions, the interaction of stands with replications within locations, and the interaction of families with replications within locations and stands (as shown in Model A, Table 7). Since mean squares for these two interactions were of approximately equal magnitude, it was decided to pool them.

The "Harvey" program requires that terminal rows and columns of a variance-covariance matrix to be inverted contain no blank cells. To meet this requirement some of the observations had to be deleted from the combined locations analysis. For example, families in stand 12, represented only at the Highland Rim plantation, were deleted from the analysis. In addition, the Pineville plantation, containing only 57 families, was also excluded from this analysis. These deletions minimized the number of blank cells in the matrices with as little as possible loss in family representation; after deletions, 85 percent of

the progenies remained in the combined locations analysis. The number of families from stands represented, after deletions, are presented in Table 9.

TABLE 9. Number of Families from Each Stand, at Each Location Included in the Combined Location Analysis (After Deletions)

Stand Number	Number of Families Per Test Site[1]					Total
	A	C	D	E	F	
1	4	0	0	4	0	8
2	8	9	9	9	9	44
3	8	9	9	11	10	47
4	10	10	10	11	10	51
6	9	10	8	11	10	48
7	10	10	10	10	10	50
8	9	9	8	11	7	44
9	8	8	7	8	7	38
10	9	9	10	10	10	48
11	9	8	10	10	9	46
13	6	7	9	9	7	38
Total	90	89	90	104	89	462

[1]A = Ames Plantation, Tennessee; C = Camp York, Tennessee; D = Decatur, Tennessee; E = Highland Rim, Tennessee; F = Vina, Alabama.

CHAPTER IV

RESULTS AND DISCUSSION

I. INDIVIDUAL LOCATION ANALYSES

Mean stand and family-within-stand values for five-year height and diameter at half-height are presented in Tables A-1 and A-2, respectively (Appendix).

Mean squares, degrees of freedom, and levels of significance for individual location analyses of variance, for five stem and branch characteristics, are presented in Tables 10 through 15. The most outstanding feature of these analyses is the frequency of significance of replication, stand, and family-within-stand effects and the effect of the interaction of families within stands with replications for all characteristics.

These effects are significant at the one percent level for all locations except Pineville; for Pineville (Table 11) stand effects are not significant for any characteristics and the family-within-stand effect is not significant for branch length. The family-within-stand effect for branch diameter for this plantation is significant at the five percent level but with respect to height, diameter, and volume of wood per tree it is significant at the one percent level. Both replication and the interaction of replication with families in stands are significant at the one percent level.

Significance for the interaction of stand with replication was

TABLE 10. Degrees of Freedom, Mean Squares, and Levels of Significance for Five Characteristics Evaluated at Ames Plantation, Tennessee. Stem and Branch Diameter Mean Squares Presented Times 100

Item	d.f.	Height	Diameter	Branch Diameter	Branch Length	Volume Per Tree
Replications	9	133.79**	789.22**	271.45**	41.67**	0.279**
Stands	10	81.16**	133.43**	24.00**	6.28**	0.067**
Replications x stands	90	4.32^{NS}	13.53^{NS}	3.15^{NS}	0.68^{NS}	0.006^{NS}
Families/stands	79	16.01**	23.98**	5.27**	1.28**	0.010**
(Replications x families)/stands	687	4.03**	11.61**	3.50**	0.60**	0.004**
Within plot	5903	1.70	6.09	1.94	0.40	0.002

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 11. Degrees of Freedom, Mean Squares, and Levels of Significance for Five Characteristics Evaluated at Pineville, Kentucky. Stem and Branch Diameter Mean Squares Presented Times 100

Item	d.f.	Height	Diameter	Branch Diameter	Branch Length	Volume Per Tree
Replications	8	376.63**	220.27**	22.04**	23.65**	0.042**
Stands	9	31.14^{NS}	56.43^{NS}	4.88^{NS}	1.12^{NS}	0.007^{NS}
Replications x stands	72	9.93^{NS}	20.36^{NS}	3.12^{NS}	1.02^{NS}	0.004^{NS}
Families/stands	47	15.82**	32.85**	4.94*	1.54^{NS}	0.006**
(Replications x families)/stands	360	8.97**	19.97**	3.57**	1.14**	0.003**
Within plot	3096	2.11	5.90	1.37	0.45	0.001

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 12. Degrees of Freedom, Mean Squares, and Levels of Significance for Five Characteristics Evaluated at Camp York, Tennessee. Stem and Branch Diameter Mean Squares Presented Times 100

Item	d.f.	Height	Diameter	Branch Diameter	Branch Length	Volume Per Tree
Replications	9	94.49**	350.30**	174.28**	13.34**	0.117**
Stands	9	80.99**	433.69**	63.29**	16.07**	0.124**
Replications x stands	81	8.40*	25.68^{NS}	6.41^{NS}	1.51^{NS}	0.009**
Families/stands	80	20.50**	73.76**	14.90**	3.85**	0.024**
(Replications x families)/stands	670	6.27**	20.52**	5.31**	1.39**	0.006**
Within plot	4971	2.53	10.29	3.36	0.79	0.003

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 13. Degrees of Freedom, Mean Squares, and Levels of Significance for Five Characteristics Evaluated at Decatur, Tennessee. Stem and Branch Diameter Mean Squares Presented Times 100

Item	d.f.	Height	Diameter	Branch Diameter	Branch Length	Volume Per Tree
Replications	9	544.00**	825.74**	161.37**	52.61**	0.366**
Stands	9	68.13**	218.10**	24.03**	6.27**	0.074**
Replications x stands	81	4.03^{NS}	11.27^{ns}	3.69^{NS}	0.84^{ns}	0.004^{NS}
Families/stands	80	16.29**	33.15**	7.81**	2.31**	0.012**
(Replications x families)/stands	575	5.94**	15.53**	4.61**	1.05**	0.005**
Within plot	3859	2.07	7.27	2.64	0.48	0.002

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 14. Degrees of Freedom, Mean Squares, and Levels of Significance for Five Characteristics Evaluated at Highland Rim, Tennessee. Stem and Branch Diameter Mean Squares Presented Times 100

Item	d.f.	Height	Diameter	Branch Diameter	Branch Length	Volume Per Tree
Replications	9	98.11**	350.33**	31.13*	3.93^{NS}	0.221**
Stands	11	88.27**	441.27**	71.33**	13.71**	0.262**
Replications x stands	99	4.99*	13.02*	7.09^{NS}	0.80^{NS}	0.008*
Families/stands	116	20.31**	60.14**	11.39**	2.53**	0.039**
(Replications x families)/stands	1013	3.78**	10.28**	5.98**	0.78**	0.006**
Within plot	10192	1.72	7.27	4.36	0.55	0.004

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 15. Degrees of Freedom, Mean Squares, and Levels of Significance for Five Characteristics Evaluated at Vina, Alabama. Stem and Branch Diameter Mean Squares Presented Times 100

Item	d.f.	Height	Diameter	Branch Diameter	Branch Length	Volume Per Tree
Replications	8	79.96**	1442.25**	176.11**	34.23**	0.388**
Stands	10	84.89**	260.00**	43.04**	6.84**	0.158**
Replications x stands	80	4.71^{NS}	19.23^{NS}	3.85^{NS}	0.61^{NS}	0.011^{NS}
Families/stands	79	19.51**	48.80**	8.11**	1.76**	0.027**
(Replications x families)/stands	629	4.66**	18.26**	4.23**	0.75**	0.008**
Within plot	6645	1.59	8.48	2.40	0.41	0.004

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

indicated only at the Camp York and Highland Rim plantations; at Camp York (Table 12) this interaction was significant for height at the five percent level and for volume of wood per tree at the one percent level while at Highland Rim (Table 14) height, diameter, and volume of wood per tree were all significant at the five percent level.

Variance component estimates for each characteristic are presented in Tables 16 through 20. Direct comparison of these estimates from location to location is probably not valid since they are based on plantations containing different numbers of families and replications and since they are located on widely differing sites. However, by presenting these components as a percent of total variation within each plantation, comparison among locations becomes more meaningful. For example, the largest source of variation in every case is the within-plot component (s^2_W); for each characteristic evaluated this component accounts for at least 50 percent of total variation at each plantation and in some cases it accounts for over 90 percent. Similarly, the replication x stand interaction variance component ($s^2_{(RS)}$) accounts for less than two percent of total variation in all plantations and for every characteristic.

1. Variance Components for Height Growth

In general, components which reflect pure genetic sources of variance in height are low. In four of the six locations, the family-within-stand variance component ($s^2_{F/S}$) accounts for between 7.9 and 5.8 percent of total variation (Table 16). Since this component is

TABLE 16. Estimates of Variance Components for Individual Location Analyses of Height. Numbers in Parentheses Indicate the Percent Contribution of the Respective Component to Total Variation at that Plantation

Location	σ^2_W	$\sigma^2_{(RxF)/S}$	$\sigma^2_{F/S}$	σ^2_{FS}	σ^2_S	σ^2_R	Total
Ames Plantation	(69.1)	(12.3)	(6.3)	(1.8)	(4.3)	(7.8)	
	1.6977	0.3021	0.1555	0.0045	0.1052	0.1911	2.4561
Pineville	(50.9)	(22.9)	(2.5)	(0.6)	(1.0)	(22.2)	
	2.1121	0.9486	0.1054	0.0242	0.0401	0.9211	4.1515
Camp York	(70.9)	(15.3)	(5.8)	(1.0)	(2.8)	(4.1)	
	2.5339	0.5467	0.2080	0.0365	0.1003	0.1479	3.5733
Decatur	(49.8)	(15.2)	(4.1)	*	(2.8)	(28.1)	
	2.0737	0.6326	0.1694	0	0.1166	1.1712	4.1635
Highland Rim	(75.1)	(9.8)	(7.9)	(0.6)	(3.1)	(3.6)	
	1.7146	0.2248	0.1801	0.0127	0.0700	0.0814	2.2836
Vina	(69.4)	(14.6)	(7.8)	(0.0)	(4.2)	(4.0)	
	1.5870	0.3331	0.1786	0.0007	0.0965	0.0910	2.2869

*Actual calculated value for this component was less than zero.

TABLE 17. Estimates of Variance Components for Individual Location Analyses of Stem Diameter (at Half-Height); Variance Components Presented Times 100. Numbers in Parentheses Indicate the Percent Contribution of the Respective Component to Total Variation at that Plantation

Location	σ^2_W	$\sigma^2_{(RxF)/S}$	$\sigma^2_{F/S}$	σ^2_{RS}	σ^2_S	σ^2_R	Total
Ames Plantation	(73.3)	(8.6)	(1.9)	(0.4)	(2.1)	(13.8)	
	6.0931	0.7130	0.1599	0.0312	0.1746	1.1449	8.3167
Pineville	(68.5)	(22.6)	(2.3)	(0.1)	(0.8)	(5.8)	
	5.9038	1.9460	0.1980	0.0099	0.0646	0.5021	8.6245
Camp York	(74.5)	(10.8)	(5.6)	(0.6)	(4.4)	(4.0)	
	10.2922	1.4954	0.7782	0.0887	0.6095	0.5577	13.8228
Decatur	(65.6)	(12.2)	(2.6)	*	(3.7)	(15.9)	
	7.2652	1.3533	0.2882	0	0.4104	1.7665	11.0836
Highland Rim	(82.0)	(3.7)	(6.1)	(0.3)	(4.5)	(3.3)	
	7.2673	0.3278	0.5432	0.0288	0.3971	0.2950	8.8592
Vina	(71.0)	(8.9)	(3.1)	(0.1)	(2.6)	(14.4)	
	8.4792	1.0587	0.3676	0.0129	0.3106	1.7205	11.9495

*Actual calculated value for this component was less than zero.

TABLE 18. Estimates of Variance Components for Individual Location Analyses of Volume Wood Per Tree; Variance Components Presented Times 1000. Numbers in Parentheses Indicate the Percent Contribution of the Respective Component to Total Variation at that Plantation

Location	σ^2_W	$\sigma^2_{(RxF)/S}$	$\sigma^2_{F/S}$	σ^2_{RS}	σ^2_S	σ^2_R	Total
Ames Plantation	(68.9)	(10.4)	(2.6)	(0.9)	(3.2)	(14.2)	
	1.9623	0.2954	0.0728	0.0241	0.0906	0.4030	2.8482
Pineville	(67.4)	(23.2)	(2.2)	(0.4)	(0.3)	(6.6)	
	0.9767	0.3361	0.0323	0.0057	0.0041	0.0950	1.4499
Camp York	(71.3)	(11.4)	(6.9)	(1.4)	(4.2)	(4.8)	
	2.7857	0.4452	0.2683	0.0551	0.1656	0.1860	3.9059
Decatur	(60.4)	(10.9)	(3.2)	*	(3.8)	(21.8)	
	2.1788	0.3929	0.1161	0	0.1355	0.7850	3.6083
Highland Rim	(78.2)	(4.8)	(7.7)	(0.5)	(4.9)	(3.9)	
	3.6877	0.2255	0.3645	0.0211	0.2322	0.1860	4.7170
Vina	(72.0)	(9.6)	(4.7)	(0.7)	(3.8)	(9.2)	
	3.5631	0.4749	0.2311	0.0342	0.1898	0.4560	4.9491

*Actual calculated value for this component was less than zero.

TABLE 19. Estimates of Variance Components for Individual Location Analyses of Branch Diameter; Variance Components Presented Times 100. Numbers in Parentheses Indicate the Percent Contribution of the Respective Component to Total Variation at that Plantation

Location	σ^2_W	$\sigma^2_{(RxF)/S}$	$\sigma^2_{F/S}$	σ^2_{RS}	σ^2_S	σ^2_R	Total
Ames Plantation	(74.8) 1.9372	(7.8) 0.2016	(0.9) 0.0229	* 0	(1.2) 0.0310	(15.3) 0.3960	2.5887
Pineville	(78.5) 1.3705	(17.5) 0.3049	(1.2) 0.0210	* 0	(0.1) 0.0011	(2.7) 0.0475	1.7450
Camp York	(80.5) 3.3633	(6.8) 0.2849	(3.4) 0.1402	(0.5) 0.0188	(1.9) 0.0812	(6.9) 0.2884	4.1768
Decatur	(77.7) 2.6261	(9.5) 0.3234	(1.5) 0.0523	* 0	(1.1) 0.0372	(10.1) 0.3420	3.3910
Highland Rim	(93.0) 4.3561	(3.8) 0.1764	(1.3) 0.0590	(0.3) 0.0117	(1.3) 0.0617	(0.5) 0.0210	4.6859
Vina	(82.6) 2.4002	(6.8) 0.1977	(1.6) 0.0468	* 0	(1.8) 0.0522	(7.2) 0.2083	2.9052

*Actual calculated values for these components were less than zero.

TABLE 20. Estimates of Variance Components for Individual Location Analyses of Branch Length. Numbers in Parentheses Indicate the Percent Contribution of the Respective Component to Total Variation at that Plantation

Location	σ^2_W	$\sigma^2_{(RxF)/S}$	$\sigma^2_{F/S}$	σ^2_{RS}	σ^2_S	σ^2_R	Total
Ames Plantation	(79.2)	(5.2)	(1.8)	(0.2)	(1.6)	(12.0)	
	0.3986	0.0264	0.0088	0.0012	0.0080	0.0605	0.5035
Pineville	(73.9)	(15.8)	(1.0)	*	*	(9.4)	
	0.4487	0.0960	0.0061	0	0	0.0568	0.6076
Camp York	(82.6)	(9.1)	(3.8)	(0.2)	(2.2)	(2.1)	
	0.7892	0.0872	0.0361	0.0021	0.0208	0.0203	0.9557
Decatur	(66.7)	(13.1)	(2.9)	*	(1.3)	(16.0)	
	0.4771	0.0937	0.0206	0	0.0090	0.1145	0.7149
Highland Rim	(90.5)	(4.0)	(3.1)	(0.0)	(1.0)	(0.4)	
	0.5513	0.0244	0.0191	0.0002	0.0117	0.0027	0.6094
Vina	(80.6)	(7.4)	(2.4)	*	(1.5)	(8.1)	
	0.4054	0.0374	0.0121	0	0.0077	0.0407	0.5033

*Actual calculated values for these components were less than zero.

assumed to estimate one-quarter of the additive genetic variance, the total additive genetic variance component for height is probably between 20 and 25 percent. At Pineville and Decatur the family-within-stand components are even lower, accounting for only 2.5 and 4.1 percent of their respective total variation. The stand components (s_S^2) are between one-half and two-thirds the magnitude of the family-within-stand components.

The single largest source of variance is the within-plot component (s_W^2); this component accounts for between 49.8 and 75.1 percent of total variance. At two of the locations, Pineville and Decatur, the within-plot component, as a percent of the total, is considerably lower, although the absolute value of this component at these plantations is among the highest. These large within-plot components reflect the site heterogeneity in these two plantations; of the six plantations, the Pineville and Decatur sites are the most nonuniform. Despite the large replication components at these locations, indicating that much of the environmental variation was successfully removed, most of the variation remained at the within-plot level. A third plantation, Camp York, also had a high within-plot variance, probably the result of remnants of roads and buildings randomly scattered throughout the site and competition from existing vegetation. Because of the random distribution of these remnants, replication layout could not remove this source of variation. The larger within-plot variance resulting from the site heterogeneity is reflected also by the greater magnitude of total variance at these three plantations.

Variance components for the interaction of families in stands with replications account for from 9.8 at Highland Rim, the most uniform site, to 22.9 percent of total variation at Pineville, the most heterogeneous site. Since this component is a measure of the consistency of performance of families in stands in all replications, large components indicate that some site heterogeneity is present within replications and that different families show different growth rates under variable site conditions.

The high s^2_W and $s^2_{(RxF)/S}$ at Pineville may explain the low family within-stand variance component; expression of the latter component may be masked by the former.

Variance components for the interaction of replications with stands account for less than two percent of total variance for height growth.

2. Variance Components for Diameter Growth

Variance components reflecting pure genetic sources of variation in diameter growth (Table 17, page 67) are of the same relative magnitude as for height, although more variable from location to location. The family-within-stand component accounts for between 1.9 and 6.1 percent of total variance while between 0.8 and 4.5 percent of total variance could be attributed to the stand component.

The largest source of variance, the within-plot component, accounts for between 65.6 and 82.0 percent of total variance. In terms

of absolute numbers, the highest s_W^2 is from Camp York (10.3) data while the lowest if from Pineville data (5.9).

The high within-plot component at Camp York is partially the result of random site variation due to remnants of buildings and roads and competition. In addition, two species of voles (Microtus ochrogaster and Microtus pinetorum) have damaged almost all the trees by feeding on bark and roots of trees. Numerous trees were killed when these voles girdled them, especially in the first few years after plantation establishment (Dimmick and Dietrich, 1970). Mortality resulting from vole damage may have resulted in increased diameter growth of adjacent trees; the resulting variance in diameter growth would be part of the within-plot variance component.

The low within-plot variance at Pineville is a reflection of the poor growing conditions on this site. Growing conditions were so severe on this strip mine site that variation in diameter between the slowest and fastest growing trees was small. This low variance probably resulted in part from taking diameter measurements at half-height; this measurement is taken on a sliding scale with the result that there is some loss of variation which would have appeared if the measurement had been taken at breast-height.

Variance components for the interaction of families in stands with replications for diameter, as for height, reflect site heterogeneity within replications. At the most variable plantation, Pineville, this component accounted for 22.6 percent of total variation while at Highland Rim, the most homogeneous site, it accounted for only 3.7 percent.

Large replication variance components were obtained at Ames Plantation, Decatur, and Vina, where this component accounted for 13.8, 15.9, and 14.4 percent of total variance, respectively. Since diameter growth is affected by spacing factors, it was thought that the high replication variance component may be a reflection of differential survival in different replications. However, survival data indicated very small differences in diameter between replications with highest and lowest survival. Apparently, competition among trees for light, water, and nutrients has not yet progressed to a degree where diameter growth is affected. The large replication components are probably a reflection of the efficiency of replication layout in accounting for random environmental variation.

3. Variance Components for Volume Per Tree

Since volume of wood per tree is a function of both diameter and height, variance components for volume (Table 18, page 68) would be expected to reflect variation in height and diameter. In general, where variance components for height and diameter are high the corresponding variance components for volume are also high.

The highest sources of pure genetic variation are found at the Highland Rim site, the most uniform plantation; $s^2_{F/S}$ and s^2_S account for 7.7 and 4.9 percent of total variation, respectively.

4. Variance Components for Branch Characteristics

Variance components for branch diameter (Table 19, page 69) and branch length (Table 20, page 70) generally display similar variation

patterns. Neither $s^2_{F/S}$ nor s^2_S account for appreciable amounts of variation for either characteristics; the sum of these two pure genetic components accounts for five percent or less of total variation. These low components may reflect the young age of these plantations. It may not be possible to detect expression of genetic patterns of branch characteristics five years after plantation establishment. However, the high components for interaction of families in stands with replications for both branch characteristics at Pineville and for branch length at Decatur indicate that some genetic expression of branch traits to varying site conditions of variable replications may be masked by these interaction effects.

As with all other traits, the within-plot component accounts for between 75 and 93 percent of total variation in both branch diameter and branch length.

5. Heritability Estimates

Five-year heritability estimates are presented in Table 21 along with one- and two-year estimates derived by Evans (1971). Between ages two and five the mean heritability of all characteristics (based on six plantations) has decreased. The decrease in mean heritabilities may be the result of a decrease in the family-within-stand component or an increase in the components for the interaction of families in stands with replications, and the within-plot component. A decrease in the family-in-stand component could be accounted for by a combined decrease in nursery and seed-size effects. It is likely that nursery

TABLE 21. Estimates of Heritability[1] of Height, Stem Diameter at Half-Height, Volume of Wood Per Tree, Branch Diameter, and Branch Length Derived from One-, Two-, and Five-Year Measurements

Location	One-Year[2] Height	Two-Year[2] Height	Five-Year Height	Two-Year[2] Diameter	Five-Year Diameter	Five-Year Volume Per Tree	Two Year[2] Branch Diameter	Five-Year Branch Diameter	Two-Year[2] Branch Length	Five-Year Branch Length
Ames Plantation	0.17	0.16	0.289	0.08	0.092	0.125	0.05	0.042	0.08	0.081
Pineville	0.33	0.23	0.133	0.16	0.098	0.096	0.14	0.050	0.16	0.044
Camp York	0.27	0.28	0.253	0.21	0.248	0.307	0.15	0.148	0.17	0.158
Decatur	0.20	0.22	0.236	0.16	0.129	0.173	0.10	0.069	0.21	0.139
Highland Rim	0.44	0.48	0.340	0.41	0.267	0.341	0.40	0.051	0.47	0.128
Vina	0.30	0.34	0.340	0.20	0.148	0.217	0.14	0.071	0.20	0.106
Mean	0.285	0.285	0.265	0.203	0.164	0.210	0.163	0.072	0.215	0.109

[1]Narrow sense heritability $h^2 = \frac{4\sigma^2_{F/S}}{\sigma^2 + \sigma^2_{(RxF)/S} + \sigma^2_{F/S}}$.

[2]Evans, R. M. 1971. Estimates of genetic and environmental variances and heritabilities for natural populations of Virginia pine (Pinus virginiana Mill.). Unpublished M.S. Thesis, The University of Tennessee, Knoxville, Tennessee.

effects may have been present in this experiment at the time of outplanting since the seedlings were in unreplicated plots in the nursery and considerable variation in bed density was observed at the time of lifting. Accompanying a loss of nursery effects an increase in within-plot variance would be expected since growth variables would reflect microsite differences to a greater extent. Higher components for the interaction of families-in-stands with replications would occur as an expression of increased response of families to site variability within and among replications.

Height Growth

In comparing five-year estimates of heritability of height with one- and two-year estimates, the most significant trend which emerges is that, excluding the Pineville site, estimates seem to be increasing in uniformity. Between ages two and five heritability of height increased at some locations such as Ames Plantation, Decatur, and Vina, while decreasing at others, such as Camp York and Highland Rim.

In general, heritability estimates reflect the magnitude of the family-within-stand variance component. Highland Rim and Vina had the highest five-year estimates of heritability of height with $\hat{h}^2 = 0.340$; relative to $s^2_{F/S}$ at other plantations, the family-within-stand variance component at Highland Rim and Vina accounted for more variation than at other plantations. Similarly, $s^2_{F/S}$ at Pineville accounts for less variation than at any other plantation and the heritability estimate here is also lowest. This low estimate also reflects high within-plot variance and interaction ($s^2_{(RxF)/S}$).

Volume Per Tree

Volume of wood per tree is a composite characteristic computed from height and diameter measurements. Fluctuation in heritability estimates from location to location would, therefore, be expected to reflect variation in the size of variance components of height and diameter. Since diameter measurements are squared in the computational formula for volumes while height measurements are included only to the first power, heritability estimates of volumes should resemble more closely the patterns of diameter viariance components. However, estimates of heritability of volume are consistently larger than estimates of heritability of diameter at all locations except Pineville where they are almost equal.

Heritability estimates of volume per tree at age five range from a low of 0.096 at Pineville to a high of 0.341 at Highland Rim; all other locations have values intermediate to these. No volumes were computed from one- and two-year data.

Branch Characteristics

Estimates of heritability estimates of branch diameter are less than 0.1 at all locations except Camp York. These low values reflect the low family-within-stand variance components. Such small values would be expected if genetic factors have not had time to exert contol.

Heritability estimates of branch length ranged from a low of 0.081 at Ames Plantation to a high of 0.158 at Camp York with intermediate estimates from other locations. Estimates of heritability of branch length were larger than heritability estimates of branch

diameter at all locations except Pineville, indicating that in juvenile trees this trait would be more responsive to selection than branch diameter.

6. Wood Specific Gravity and Extractive Content

Mean squares, degrees of freedom, and levels of significance for extracted specific gravity and extractive content are presented in Table 22 and estimates of variance components in Table 23.

Extracted Wood Specific Gravity

Both replication and stand effects were significant at the one percent level of probability while the family-within-stand effect was significant at only the 10 percent level. The small family variance component is rather surprising. If, as with other species of southern pines, specific gravity were a highly heritable complex trait, the family component should be relatively high (Zobel et al., 1972). The low family and high stand mean square do not correspond with the natural variation pattern in Virginia pine where variance in extracted specific gravity had a significant among-tree component but was nonsignificant among stands (Thor, 1964).

Site characteristics may mask genetic differences among stands in natural populations. The highly significant among-replication effect would tend to confirm this environmental effect although the replication variance component accounts for only four percent of total variation.

A New Duncan's Multiple Range Test distinguishing among stand means is presented in Table 24. The test shows that, in general, the stands

TABLE 22. Degrees of Freedom, Mean Squares, and Levels of Significance for Extracted Wood Specific Gravity and Extractives (Times 1000)

Item	d.f.	Specific Gravity	Extractives
Replications	2	5.964**	0.237**
Stands	11	3.451**	0.017^{NS}
Replications x stands	22	0.318^{NS}	0.011^{NS}
Families/stands	111	0.691^{NS}	0.014^{NS}
(Replications x families)/stands	222	0.563^{NS}	0.012^{NS}
Within plot	369	0.439	0.009

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 23. Estimates of Variance Components for Extracted Specific Gravity and Extractive Content; Variance Components Presented Times 10000. Numbers in Parentheses Indicate the Percent Contribution of the Respective Component to Total Variation

Item	σ^2_W	$\sigma^2_{(RxF)/S}$	$\sigma^2_{F/S}$	σ^2_{RxS}	σ^2_S	σ^2_R	Total
Extracted specific gravity	(73.9)	(10.5)	(3.6)	*	(8.3)	(3.8)	
	4.3842	0.6245	0.2121	0	0.4899	0.2249	5.9356
Extractives	(77.5)	(11.5)	(2.7)	*	(0.7)	(7.7)	
	0.09311	0.0138	0.0032	0	0.0008	0.0092	0.12011

*Actual calculated values were less than zero.

TABLE 24. Duncan's New Multiple Range Test for Specific Gravity and Coefficients of Variation for Open-Pollinated Progeny from Stands

Number	Stand Location	Stand Mean[1]	C.V. Percent
2	West Kentucky (Dawson Springs)	0.41015	5.33
12	Great Valley (Newport, Tennessee	0.40643	5.60
9	Cumberland Plateau (Morehead, Kentucky)	0.40544	5.35
4	Eastern Rim (Rock Island, Tennessee)	0.40536	5.94
1	West Tenn (Clinton)	0.40250	5.90
13	Great Valley (Elizabethton, Tennessee)	0.40237	5.93
10	Great Valley (Etowah, Tennessee)	0.39615	4.87
7	Eastern Ridge (Pineville, Kentucky)	0.39380	6.62
11	Great Valley (Vonore, Tennessee)	0.39356	4.87
8	Cumberland Plateau (London, Kentucky)	0.39201	5.92
6	Cumberland Mountains (Wartburg, Tennessee)	0.39189	5.99
3	Cumberland Plateau (Sewanee, Tennessee)	0.38633	6.65

[1]Means connected with the same line are not significantly different from each other, $P > 0.05$.

can be separated into two groups, those with high wood densities and those with low densities. Stand numbers 2, 12, 9, and 4 fall into the high category and are also the stands which fall into the extremes of the species range in Tennessee and Kentucky while the five stands with low specific gravity are all from the central part of the range sampled. The coefficients of variation (Table 24) for each stand indicate that the magnitude of wood density variation within stands is approximately equal.

Heritability of extracted specific gravity was estimated to be 0.162 by the variance component method, 0.129 by the regression method, and 0.183 by the correlation method. These estimates are low compared to values obtained for other species. In the case of the variance-component method this result is a reflection of the low family and the high stand variance component. The estimates obtained by the three methods seem to be in fairly close agreement, although each has drawbacks as enumerated by Van Buijtenen (1962).

Extractive Content

Since the analysis of variance showed a very low and statistically nonsignificant family effect, no estimate of heritability of this characteristic was computed. The stand component was also nonsignificant.

The trees in this plantation were in their sixth growing season at the time cores were extracted and heartwood depositions were not expected; therefore, the extractive content should be low. Extractives ranged between 2.6 and 10.3 percent of extracted wood weight,

considerably higher than the two to four percent obtained by Zobel et al. (1972) for juvenile wood of loblolly and slash pine, but similar to that produced between the tenth and twenty-fifth growth ring in young Virginia pine (Thor, 1964). Virginia pine stands older than 50 years have from two to three times the amount of extractives observed in younger stands, indicating that heartwood initiation is rather late in this species.

Only the replication effect was significant in the analysis of variance; the replication variance component accounted for almost eight percent of the total variation, indicating strong environmental influence on extractive content. Stonecypher and Zobel (1966) obtained similarly high replication and low among-family mean squares for extractive percentages in loblolly pine.

Correlations Among Characteristics

Table 25 lists correlation coefficients between various characteristics. The most noteworthy of these is the significant positive correlation between progeny specific gravity and progeny diameter, $r = 0.235$. With the exception of Thor and Brown (1963), who obtained a similar positive correlation for juvenile loblolly pine ($r = 0.201$), most reports show negative correlations between diameter and wood densities of southern pines. In the present case, although this correlation was significant, only 5.5 percent of the variation in offspring wood specific gravity was accounted for by variation in progeny diameter. By itself, diameter would not be a very efficient indirect selection criterion for high wood density, but it is encouraging that

TABLE 25. Phenotypic Correlation Coefficients Between Wood Properties and Diameter of Parent Trees and Progeny Resulting from Wind Pollinations

Correlation Between:	Correlation Coefficient
Progeny specific gravity and progeny extractives	.135*
Progeny specific gravity and progeny d.i.b.[1]	.235*
Progeny specific gravity and parent specific gravity	.091*
Progeny specific gravity and parent extractives	.087*
Progeny extractives and progeny d.i.b.	.078*
Progeny extractives and parent specific gravity	.025[NS]
Progeny extractives and parent extractives	-.053[NS]
Progeny d.i.b. and parent specific gravity	-.083*
Progeny d.i.b. and parent extractives	.010[NS]

[1]Progeny diameter inside bark data from measurements of core lengths obtained at one foot above ground level.

[NS]Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

selection for rapid juvenile diameter growth will not result in decreased specific gravity.

A similar situation exists with respect to the correlations between progeny wood specific gravity and other progeny and parent characters. All of these correlations are statistically significant, but none accounts for much of the variation in specific gravity of progeny trees.

The positive correlation between progeny specific gravity and progeny extractives indicates that trees with greater wood density tend to have a greater extractive content. The small negative and nonsignificant correlation between progeny extractives and parent extractives indicates very little genetic control over extractive content. Therefore, the positive correlation between progeny specific gravity and progeny extractives is most likely an "environmental" relationship.

7. Pineville Soil Analysis

Soil samples were analyzed in an effort to determine which variables were responsible for the high environmental variance components for height growth; at this plantation s_R^2 accounted for 22.2 percent of total variance in five-year height (Table 16, page 66). At the time soil samples were collected, total height of four trees surrounding the collection point was measured. The analysis of variance based on average height of these four trees per plot is shown in Table 26 along with variance components and the percent contribution of these components to total variance. The analysis disclosed that

TABLE 26. Degrees of Freedom, Mean Squares, Levels of Significance, Variance Components, and Percent of Total Variance of Mean Height of Four Trees Immediately Adjacent to Plot from Which Soil Samples Were Collected at Pineville, Kentucky Plantation

Source of Variation	d.f.	Mean Square	Variance Component	Percent of Total Variance
Replication	3	149.6883**	5.16120	59.78
Strata	8	10.3148**	0.85520	9.90
Error	96	2.6181	2.61806	30.32

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

almost 60 percent of total variation in height could be attributed to the replication variance component and 30 percent to the among-plot component. Only 10 percent could be accounted for by strata (replications were subdivided into strata which were parallel to the existing slope).

Mean squares, degrees of freedom, levels of significance, variance components, and their percent contribution to total variance for five soil variables evaluated are presented in Tables 27 through 31. A common feature of these tables is that each table contains an analysis of the appropriate variable in the upper six inches of soil, the analysis of that variable in soil between six inches and 12 inches beneath the surface followed by the analysis of the average of this variable for the upper and lower samples combined. Since the correlation between a variable in the upper six inches of soil and the same variable in the lower six inches (Table 32) was highly significant in every case, sampling at one level may have been sufficient at this location.

In the analyses of soil variables the bulk of the variability was accounted for by the within-plot (error) variance component. This component accounted for a maximum of 99.67 percent of total variation of pH of the upper six inches of soil (Table 27) and a minimum of 40.30 percent for the conductivity of the saturation extract of the upper layer of soil (Table 29). The replication variance component always accounted for less variation in a single spoil characteristic than in height variation.

TABLE 27. Degrees of Freedom, Mean Squares, Levels of Significance, Variance Components, and Percent of Total Variance of pH of Upper Six Inches of Soil, Lower Six Inches of Soil, and Average pH of These Two Samples

Item	Replications (3 d.f.)	Strata (8 d.f.)	Error (96 d.f.)
pH of soil 0-6 inches			
Mean square	0.243[NS]	0.222[NS]	0.229
Variance component	0.001	0[1]	0.229
Percent of total variance	0.33	0	99.67
pH of soil 6-12 inches			
Mean square	0.720[NS]	0.956*	0.393
Variance component	0	0.063	0.393
Percent of total variance	0	13.74	86.26
pH of average of 0-6 and 6-12 soil samples			
Mean square	0.416[NS]	0.499[NS]	0.250
Variance component	0	0.028	0.250
Percent of total variance	0	9.95	90.05

[1]Actual calculated value was less than zero.

[NS]Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 28. Degrees of Freedom, Mean Squares, Levels of Significance, Variance Components, and Percent of Total Variance of Extractable Phosphorus of Upper Six Inches of Soil, Lower Six Inches of Soil, and Average of These Two Samples

Item	Replications (3 d.f.)	Strata (8 d.f.)	Error (96 d.f.)
Extractable phosphorus of soil 0-6 inches			
Mean square	170.939[NS]	44.957**	10.288
Variance component	4.666	3.852	10.288
Percent of total variance	24.81	20.48	54.70
Extractable phosphorus of soil 6-12 inches			
Mean square	121.583[NS]	30.289**	9.897
Variance component	3.381	2.266	9.897
Percent of total variance	21.75	14.58	63.67
Extractable phosphorus of average of 0-6 and 6-12 soil samples			
Mean square	143.695[NS]	36.375**	8.865
Variance component	3.975	3.057	8.865
Percent of total variance	25.00	19.23	55.77

[NS]Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 29. Degrees of Freedom, Mean Squares, Levels of Significance, Variance Components, and Percent of Total Variance of Conductivity of Saturation Extract of Upper Six Inches of Soil, Lower Six Inches of Soil, and Average of These Two Samples

Item	Replications (3 d.f.)	Strata (8 d.f.)	Error (96 d.f.)
Conductivity of saturation extract of soil 0-6 inches			
Mean square	0.0430**	0.0029*	0.0011
Variance component	0.0015	0.0002	0.0011
Percent of total variance	52.67	7.03	40.30
Conductivity of saturation extract of soil 6-12 inches			
Mean square	0.0430^{NS}	0.0117**	0.0033
Variance component	0.0012	0.0009	0.0033
Percent of total variance	21.39	17.17	61.43
Conductivity of saturation extract of average of 0-6 and 6-12 soil samples			
Mean square	0.0425*	0.0061*	0.0015
Variance component	0.0014	0.0005	0.0015
Percent of total variance	39.82	14.94	45.24

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 30. Degrees of Freedom, Mean Squares, Levels of Significance, Variance Components, and Percent of Total Variance of Exchangeable Acidity of Upper Six Inches of Soil, Lower Six Inches of Soil, and Average of These Two Samples

Item	Replications (3 d.f.)	Strata (8 d.f.)	Error (96 d.f.)
Exchangeable acidity of soil 0-6 inches			
Mean square	14.6778*	2.6912[NS]	2.5850
Variance component	0.4440	0.01180	2.5850
Percent of total variance	14.60	0.39	85.01
Exchangeable acidity of soil 6-12 inches			
Mean square	25.0431*	4.6509[NS]	4.0693
Variance component	0.7553	0.0646	4.0693
Percent of total variance	15.45	1.32	83.23
Exchangeable acidity of average of 0-6 and 6-12 soil samples			
Mean square	18.6248*	3.1154[NS]	2.8157
Variance component	0.5744	0.0333	2.8157
Percent of total variance	16.78	0.97	82.25

[NS]Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 31. Degrees of Freedom, Mean Squares, Levels of Significance, Variance Components, and Percent of Total Variance of Exchangeable Aluminum of Upper Six Inches of Soil, Lower Six Inches of Soil, and Average of These Two Samples

Item	Replications (3 d.f.)	Strata (8 d.f.)	Error (96 d.f.)
Exchangeable Al^{++} of soil 0-6 inches			
Mean square	7.2032**	0.9394^{NS}	1.4040
Variance component	0.2320	0[1]	1.4040
Percent of total variance	14.18	0	85.82
Exchangeable Al^{++} of soil 6-12 inches			
Mean square	8.8464^{NS}	2.6205^{NS}	1.9882
Variance component	0.2306	0.0703	1.9882
Percent of total variance	10.07	3.07	86.86
Exchangeable Al^{++} of average of 0-6 and 6-12 soil samples			
Mean square	7.4839*	1.3959^{NS}	1.4223
Variance component	0.2255	0[1]	1.4223
Percent of total variance	13.68	0	86.32

[1]Actual calculated values was less than zero.

^{NS}Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

TABLE 32. Significant Correlation Coefficients Between Soil Variables and Height of Virginia Pine at Pineville, Kentucky

Correlation Between:	Correlation Coefficient
Height and conductivity, 0-6 inches	-0.403**
Height and exchangeable acidity, 0-6 inches	0.218*
Height and exchangeable Al^{++}, 0-6 inches	0.219*
Height and extractable phosphorus	0.257**
Height and conductivity, 6-12 inches	-0.302**
Height and exchangeable acidity, 6-12 inches	0.211*
Height and exchangeable Al^{++}, 6-12 inches	0.212*
pH, 0-6 inches and exchangeable acidity, 0-6 inches	-0.749**
pH, 0-6 inches and exchangeable Al^{++}, 0-6 inches	-0.753**
pH, 0-6 inches and pH, 6-12 inches	0.662**
pH, 0-6 inches and conductivity, 6-12 inches	-0.189*
pH, 0-6 inches and exchangeable acidity, 6-12 inches	-0.510**
pH, 0-6 inches and exchangeable Al^{++}, 6-12 inches	-0.523**
Exchangeable acidity, 0-6 inches and exchangeable Al^{++}, 0-6 inches	0.973*
Exchangeable acidity, 0-6 inches and extractable phosphorus, 0-6 inches	0.423**
Exchangeable acidity, 0-6 inches and pH, 6-12 inches	-0.551**
Exchangeable acidity, 0-6 inches and exchangeable acidity, 6-12 inches	0.740**
Exchangeable acidity, 0-6 inches and exchangeable Al^{++}, 6-12 inches	0.727**
Exchangeable acidity, 0-6 inches and extractable phosphorus, 6-12 inches	0.419**
Exchangeable Al^{++}, 0-6 inches and extractable phosphorus, 0-6 inches	0.404**
Exchangeable Al^{++}, 0-6 inches and pH, 6-12 inches	-0.536**
Exchangeable Al^{++}, 0-6 inches and exchangeable acidity, 6-12 inches	0.706**

TABLE 32 (continued)

Correlation Between:	Correlation Coefficient
Exchangeable Al^{++}, 0-6 inches and exchangeable Al^{++}, 6-12 inches	0.704**
Exchangeable Al^{++}, 0-6 inches and extractable phosphorus, 6-12 inches	0.401**
Extractable phosphorus, 0-6 inches and exchangeable acidity, 6-12 inches	0.253**
Extractable phosphorus, 0-6 inches and exchangeable Al^{++}, 6-12 inches	0.208**
Extractable phosphorus, 0-6 inches and extractable phosphorus, 6-12 inches	0.845**
pH, 6-12 inches and conductivity, 6-12 inches	-0.237*
pH, 6-12 inches and exchangeable acidity, 6-12 inches	-0.622**
pH, 6-12 inches and exchangeable Al^{++}, 6-12 inches	-0.602**
Exchangeable acidity, 6-12 inches and exchangeable Al^{++}, 6-12 inches	0.975**

*$P < 0.05$.

**$P < 0.01$.

Table 33 contains mean values for all spoil characteristics as well as standard deviations and maximum and minimum values for these characteristics. The large range of values observed for all characteristics is an indication of the great site variability existing within this two-acre strip mine plantation.

The analysis of active acidity (pH, Table 27, page 89) indicates that this variable was randomly distributed; neither replications nor strata accounted for a significant portion of variability in either the upper or lower samples of soil. Also, active acidity was not significantly correlated with tree height.

Although the replication effect is not statistically significant for extractable phosphorus (Table 28, page 90) while the strata effect is highly significant, the replication variance component accounts for slightly more of the total variance than the strata component. Highly significant positive correlations exist between extractable phosphorus and tree height, exchangeable aluminum, and exchangeable acidity.

The replication effect of conductivity of the saturation extract was highly significant in the upper six inches of soil and nonsignificant in the sample from six to 12 inches beneath the surface; the corresponding variance components accounted for 53 and 21 percent of total variation. The conductivity of the upper six inches of soil in one replication (Replication 9) was approximately twice as high as in all others, and height growth in this replication was significantly less than in all others. In addition, it was observed that there was almost no litter accumulation on the soil surface in this replication

TABLE 33. Mean, Standard Deviation, Minimum and Maximum Values of Tree Height and 12 Spoil Characteristics

Characteristic	Mean	Standard Deviation	Minimum Value	Maximum Value
Tree height, feet	8.5	2.7	4.0	15.0
Active acidity, pH				
0-6 inches	4.5	0.5	3.6	6.3
6-12 inches	4.5	0.7	3.0	7.4
Conductivity, mmhos/cm				
0-6 inches	0.091	0.049	0.028	0.300
6-12 inches	0.116	0.071	0.026	0.440
Exchangeable acidity, meq/100 g				
0-6 inches	3.2	1.7	0.1	8.3
6-12 inches	3.2	2.2	0.1	15.6
Exchangeable Al^{++}, meq/100 g				
0-6 inches	2.2	1.2	0.0	6.4
6-12 inches	2.2	1.5	0.0	11.4
Extractable phosphorus, ppm				
0-6 inches	4.8	4.2	0.3	24.8
6-12 inches	4.5	3.8	0.7	23.1

while a thin litter layer had begun to accumulate in other replications. Initially, it was thought that the poor height growth in Replication 9 was the indirect result of low buffering action due to lack of organic matter in the upper soil layer. However, the difference in conductivity between upper and lower soil samples was equal in all replications indicating that the presence of organic matter has not significantly affected conductivity. Apparently, height growth is inversely related to conductivity as a result of the relationship of the conductivity with free acids in the soil.

Although replication effects of exchangeable acidity were significant at the 0.05 level, the replication variance component accounted for only 15 to 17 percent of total variation. Exchangeable acidity was highly significantly correlated with the most spoil characteristics except conductivity.

The replication variance component of exchangeable aluminum accounted for 10 to 14 percent of total variance and was highly significantly correlated with most spoil characteristics. In addition, exchangeable aluminum was significantly positively correlated with height. If aluminum toxicity were prevalent in this area as implied by Berg and Vogel (1973), correlation coefficients should have been negative; perhaps levels of aluminum encountered at this plantation are below some toxic threshold.

Although the mean height of trees at this plantation was significantly (0.05 or 0.01 level) correlated with most spoil characteristics, the best multiple regression equations accounted for only 25 percent

of variation in height growth:

$$Y = 0.32 + 1.7\ (pH) - 16.2\ (Conduc.) + 1.0\ (Exch.\ Al^{++})$$ or

$$Y = 0.60 + 1.6\ (pH) - 16.1\ (Conduc.) + 0.69\ (Exch.\ ac.).$$

(Exchangeable acidity and exchangeable aluminum could not be included in the same regression equation because they were so highly correlated; by including them a singular matrix was encountered.) According to these models, height growth increased with higher pH (less active acidity), lower conductivity, and more exchangeable aluminum or exchangeable acidity. A negative relationship of conductivity with height growth would be expected if conductivity is an indicator of free acid availability. Exchangeable Al^{++} and exchangeable acidity are related to soil texture, and are probably indicators that more clay or organic material resulted in improved tree growth on this excessively well-drained site. However, the inclusion of pH in these multiple regressions is surprising, since pH was not significantly correlated with height. Apparently the presence of pH is a reflection of a high correlation with both exchangeable aluminum and exchangeable acidity (but not high enough to cause singularity of matrices).

II. COMBINED LOCATION ANALYSES

Mean squares, degrees of freedom, and levels of significance for five stem and branch characteristics are presented in Table 34. The lack of statistically nonsignificant effects in these analyses is a result of the large number of degrees of freedom in error terms used to test for significance.

TABLE 34. Degrees of Freedom, Mean Squares, and Levels of Significance for Combined Location Analysis for Five Characteristics Evaluated. Stem and Branch Diameter and Volume Per Tree Mean Squares Presented Times 100

Source of Variation	d.f.	Mean Squares				
		Height	Diameter	Volume/Tree	Branch Diameter	Branch Length
Locations	4	5879.0250	18316.7933	584.1694	7208.1176	1019.3638
Replications in locations	44	192.0913**	720.0787**	26.1942**	161.6549**	29.3728**
Stands	10	318.0985**	1160.8997**	50.6665**	171.2118**	33.7744**
Stands x locations	37	13.3023**	47.6577**	1.9936**	8.2010**	2.2688**
Families in stands	93	55.1121**	118.9125**	5.9909**	19.4111**	5.6187**
(Locations x families)/ stands	318	7.0431**	24.1873**	0.9550**	5.8299*	1.3163**
Error A[1]	3917	4.9899**	15.3992**	0.6010**	4.9792**	0.9004**
Residual (within plot)	29749	1.8851	7.8263	0.2974	3.1356	0.5179

[1]Sums of squares for the interaction of stand with replication within location and for the interaction of families with replication within location and stand were pooled to obtain sums of squares for Error A.

[NS]Not statistically significant, $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

Estimates of variance components are presented in Table 35. It should be noted that the percent contribution of each component to phenotypic variance (Table 35) is not directly comparable to percent contribution of variance components to total variance in the individual location analyses. In the combined analyses no variance components were computed either for replication within location or for the interaction of stand with replication in locations; therefore, percent contribution of these to total variance could not be computed. In addition, since locations were assumed to be fixed, no variance component was available corresponding to this source of variation. Generally, however, variance components in combined location analyses are similar in magnitude to those in the individual location analyses. Standard errors of family-within-stand variance components were 12 to 21 percent of their respective family variance component.

Of all characteristics, the family-within-stand variance component is greatest in relative magnitude for height growth, followed by the component for volume of wood per tree, and lowest for branch diameter. The stand variance components for height, diameter, and volume are of equal magnitude, accounting for approximately 4.5 percent of phenotypic variance, twice as much as for branch traits.

The components for the two interactions, σ^2_{LxS} and $\sigma^2_{(LxF)/S}$ appear to be so small that for practical purposes they can be disregarded; the combined total of these interaction components accounts for only one percent or less of phenotypic variance. However, it should be noted that these components are based on least squares estimates of k

TABLE 35. Estimates of Variance Components and Heritability Derived from the Combined Location Analysis. Variance Components for Stem and Branch Diameter and Volume Per Tree Presented Times 100. Numbers in Parentheses Indicate Percent Contribution to Phenotypic Variance

Component	Height	Diameter	Volume/Tree	Branch Diameter	Branch Length
σ^2_S	(4.20) 0.1077	(4.12) 0.3942	(4.65) 0.0172	(1.64) 0.0572	(1.89) 0.0113
σ^2_{LxS}	(0.25) 0.0065	(0.26) 0.0251	(0.30) 0.0011	(0.07) 0.0025	(0.18) 0.0011
$\sigma^2_{F/S}$	(6.35) 0.1629	(3.34) 0.3201	(4.62) 0.0171	(1.32) 0.0460	(2.44) 0.0146
S.E.$(\sigma^2_{F/S})$[1]	±0.0272	±0.0589	±0.0030	±0.0097	±0.0028
$\sigma^2_{(LxF)/S}$	(0.58) 0.0148	(0.66) 0.0633	(0.70) 0.0026	(0.18) 0.0061	(0.50) 0.0030
$\sigma^2_{(RxF)/L,S^2}$	(15.19) 0.3899	(9.83) 0.9408	(9.40) 0.0348	(6.82) 0.2378	(8.36) 0.0500
σ^2_W	(73.44) 1.8851	(81.78) 7.8263	(80.33) 0.2974	(89.97) 3.1356	(86.62) 0.5179
h^2[3]	0.2657	0.1399	0.1944	0.0537	0.0997
S.E.(h^2)[4]	±0.0444	±0.0257	±0.0341	±0.0113	±0.0191

[1] S.E.$(\sigma^2_{F/S})$ = standard error of family-within-stand variance component

$$\sqrt{\frac{2}{k_6^2}\left(\frac{M.S._{F/S}^2}{d.f. + 2} + \frac{M.S._{(LxF)/S}^2}{d.f. + 2}\right)}$$

[2] This component obtained by subtracting the within-plot mean square in Model A (Table 7, page 47) from the mean square for (family x replication)/locations and stands, and dividing the resulting difference by an estimate of k (Model A, Table 7) obtained from the sum and sum of squares of all frequencies of family x

TABLE 35 (continued)

replication in stands and locations in the formula:

$$n = \frac{1}{a-1}\left(N - \frac{n^2}{N}\right).$$

The mean square for (family x replication)/location and stands was obtained by subtracting from the sum of residual sum of squares for all stands in Model C (Table 7) the within-plot sum of squares in Model A (Table 7) and dividing by the appropriate degrees of freedom.

$$^3h^2 = \frac{4s^2_{F/S}}{s^2_W + s^2_{(RxF)/L,S} + s^2_{(LxF)/S} + s^2_{F/S}}$$

^{4}S.E.(h^2) = standard error of heritability

$$\frac{4 \times \text{S.E.}\ (s^2_{F/S})}{s^2_W + s^2_{(RxF)/L,S} + s^2_{(LxF)/S} + s^2_{F/S}}$$

values obtained by the "direct method" of Harvey (1960). A common method of verifying the accuracy of estimates of k values is to compare these estimates with harmonic means of subclass frequencies. Estimates of k values used in computing s^2_{LxS} and $s^2_{(LxF)/S}$ and corresponding harmonic means are presented in Table 36. With one exception, estimates of k values for interaction components are double the harmonic means while estimates of k values for main-effect components are in fairly close agreement with harmonic means. Only for stand 1 is the k value for the interaction of families and locations in close agreement with the harmonic mean. Since stand 1 is the least unbalanced of all stands and, unlike all other stands, has no missing cells in any replications, it appears that the lack of agreement between k values and harmonic means is the result of confounding due to unbalance of experimental design. By using estimates of k values obtained by the "direct method" of Harvey (1960) in calculation of interaction variance components, a conservative estimate of these components is obtained. However, if the harmonic means were used in these calculations, the estimates of interaction variance components would double and thus account for a maximum of only two percent of phenotypic variance.

The estimate of the interaction component $s^2_{(RxF)/L,S}$ (Table 35) corresponds in magnitude to that of $\sigma^2_{(RxF/S)}$ in the individual location analyses. The highest value for this component is for height growth, where it accounts for 15 percent of phenotypic variance. Since this component is a measure of response of families to site heterogeneity in replications within locations, the relative magnitude of this component

TABLE 36. Estimates of k Values Used in Estimating the Interaction Variance Components $\sigma^2_{(LxF)/S}$ and σ^2_{LxS} and Harmonic Means of Corresponding Subclass Frequencies. The Arithmetic Average of k Values of the 11 Stands Was Used in Estimating $\sigma^2_{(LxF)/S}$

Stand Number	k Value for $\sigma^2_{(LxF)}$	Harmonic Mean
1	66.07	66.78
2	191.82	64.31
3	128.37	66.73
4	149.30	69.79
6	148.19	74.40
7	145.34	58.75
8	136.18	71.55
9	142.00	73.64
10	145.71	71.27
11	132.41	61.52
13	141.19	72.68
Average	138.78	68.19
	k Value for σ^2_{LxS}	Harmonic Mean
	1286.38	601.16

for height growth would indicate that this trait is more sensitive to site variability (on the family level) than other traits evaluated.

The single largest source of variance is the within-plot component which accounts for between 73 and 90 percent of phenotypic variance.

Heritability estimates based on variance components from the combined location analyses (Table 35, page 102) are in close agreement with average heritabilities based on six locations; average heritability estimates from individual location analyses are within a standard error of the heritability estimates derived from combined location analyses.

CHAPTER V

APPLICATION OF RESULTS

Since Virginia pine is grown primarily for fiber production, selection for a greater yield of wood per tree would be an appropriate primary selection criterion. One measure of yield is weight of wood per tree (the product of volume of wood per tree and wood specific gravity). However, the results of Rink and Thor (1973) disclosed that gains in weight of wood per tree were at least 10 percent greater when selection was for diameter only than when selection was for a combination of diameter and specific gravity. Since volume of wood per tree was highly correlated with both diameter and height (Table 37), volume was chosen as the primary selection criterion.

The positive correlations between growth variables and branch traits (Table 37) indicate that trees with rapid growth rates tend also to have large limbs. This implies that simultaneous selection for volume and branch traits in juvenile Virginia pine may not be practical. Although some large trees have small branches, a simultaneous selection for volume and small limbs would result in a lower selection intensity and lower gains for volume.

Low stand x location and family-within-stand x location variance components indicate that by selecting only trees in stands and families with high volume growth at all locations, the establishment of one seed orchard to provide improved seed for all locations may be possible.

TABLE 37. Average Coefficients of Correlation Between Characteristics Evaluated; Average is of Estimates at Six Test Locations

Correlation Between:	Correlation Coefficient[1]
Height and diameter	0.698
Height and volume	0.761
Height and branch diameter	0.524
Height and branch length	0.585
Diameter and volume	0.932
Diameter and branch diameter	0.628
Diameter and branch length	0.596
Volume and branch diameter	0.584
Volume and branch length	0.576
Branch diameter and branch length	0.679

[1]For all estimates, $P < 0.0001$.

However, the use of a single orchard would preclude selection of families which do not consistently provide outstanding growth at all locations; although some families provide outstanding growth at some locations, their poor performance at other locations would make them unsuitable for a centralized seed orchard. Selection for stability of performance at all locations may, therefore, result in the sacrifice of some gain in local volume growth.

Results from the combined location analysis (Table 35, page 102) indicate that a combination of stand, family-within-stand, and within-plot selection may be appropriate for a long term breeding program to increase volume yield. Expected gains from such a three-stage selection system will be compared to gains from a two-stage scheme with no stand selection, and from single-stage mass selection.

Stand selection, the first stage of the three-stage system, would be on the basis of a Duncan's New Multiple Range Test for volume (Table 38). Any stand with the poorest growth or not significantly different from the poorest at any plantation would be marked for roguing. Since stand number 12 is represented at only one location, it has not been properly evaluated and must be excluded from stand selection.

Such a selection scheme would result in the selection of four stands: stand 7 from the Cumberland Mountains of south Kentucky, stand 10 from the Great Valley near Etowah, Tennessee, stand 11 from the Great Valley near Vonore, Tennessee, and stand 13 from the Great Valley near Elizabethton, Tennessee. The Duncan tests indicate that trees from stand 10 provide the greatest volume growth at all locations

TABLE 38. Mean Values (Feet^3) for Five-Year Volume of Wood Per Tree of Open-Pollinated Progeny from Parent Stands at Five Planting Locations and Duncan's New Multiple Range Test for Mean Separation

Plantation	Mean Volume Per Tree[1]	Stand Number
Ames	0.103	10
	0.090	11
	0.088	7
	0.082	13
	0.080	4
	0.078	6
	0.077	1
	0.075	9
	0.075	8
	0.072	3
	0.066	2
Camp York	0.111	10
	0.104	7
	0.098	9
	0.093	13
	0.089	8
	0.088	11
	0.087	6
	0.080	4
	0.077	3
	0.060	2
Decatur	0.110	10
	0.103	13
	0.093	11
	0.091	7
	0.090	9
	0.088	8
	0.085	6
	0.083	4
	0.082	3
	0.066	2

TABLE 38 (continued)

Plantation	Mean Volume Per Tree[1]	Stand Number
Highland Rim	0.180	10
	0.167	13
	0.163	12
	0.161	11
	0.160	1
	0.157	7
	0.149	9
	0.148	6
	0.144	4
	0.143	8
	0.134	3
	0.116	2
Vina	0.156	1
	0.144	10
	0.126	13
	0.117	11
	0.116	7
	0.113	6
	0.109	8
	0.109	4
	0.103	3
	0.100	9
	0.093	2

[1]Means connected with the same line are not significantly different from each other, $P > 0.05$.

except Vina where trees from this stand ranked second. This superiority may be a reflection of the fact that trees from stand 10 are open-pollinated progeny of desirable phenotypes since the original stand had been rogued to remove undesirable trees.

Selection of families in these four stands would again be on the basis of good performance at all locations. By rejecting families which did not rank in the upper half of families from the four selected stands in at least five of the six locations, a total of 13 families would be retained.

Within-family selection is determined by the need to avoid inbreeding. Only one tree, the one with the greatest volume, in a selected family row plot should be retained.

Expected gains were computed using the method described earlier (see page 23) and originally improvised by Evans (1971). These are gains which can be expected at each location if each plantation were rogued of everything except selected trees.

Selection intensities for family and within-family selection in the three-stage selection scheme are shown in Table 39 along with mean volumes per tree for unselected populations and for the four selected stands. Variance components for analyses of variance in which only these four stands were included are presented in Table 40. Expected gains resulting from the three-stage selection are also listed in Table 40.

The high expected gains resulting from such a three-stage selection scheme are surprising. Percent gain over mean unselected volume

TABLE 39. Mean Volumes (Feet^3) of the Unselected Population and of Trees in Four Selected Stands, Number of Families Selected from Four Stands, and Family and Within-Family Selection Intensities (Phenotypic Standard Deviations) for the Three-Stage Selection

Item	Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
Mean volume unselected population	0.0812	0.0260	0.0889	0.0899	0.1512	0.1139
Mean volume of four selected stands	0.0914	0.0292	0.1007	0.0999	0.1661	0.1262
Total number of families in four selected stands at each location	34	28	34	39	39	36
Number of families selected from four best stands	12	11	12	13	13	13
Family selection[1] intensity	1.050	0.975	1.050	1.100	1.100	1.030
Average number[2] of trees per plot	7.738	7.228	6.841	6.110	9.180	9.234
Within family[1] selection intensity	1.625	1.580	1.550	1.520	1.700	1.700

[1]Namkoong, G., and E. B. Snyder. 1969. Accurate values for selection intensities. Silvae Genetica 18:172-173.

[2]Based on average within-plot survival at each location.

TABLE 40. Expected Gains (Feet^3) at Each Location Resulting from Three Stage Selection. Variance Components (Times 1000) Are Derived from an Analysis of Variance Which Included Only the Four Common Stands with the Highest Volume at Each Location. Numbers in Parentheses Indicate Percent Contribution of Each Stage at Selection

Component	Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
σ^2_W	2.4879	1.1496	3.3469	2.5552	4.1404	4.0391
$\sigma^2_{(FxR)/S}$	0.4103	0.4443	0.5616	0.5216	0.4451	0.5936
$\sigma^2_{F/S}$	0.1095	0.0621	0.3499	0.0651	0.2912	0.3004
h^2	0.146	0.150	0.329	0.083	0.239	0.244
Gain from stand selection	(12.6) 0.0102	(12.3) 0.0032	(13.3) 0.0118	(11.1) 0.0100	(9.9) 0.0149	(10.8) 0.0123
Gain from family selection	(10.5) 0.0085	(20.4) 0.0053	(19.3) 0.0172	(6.3) 0.0057	(10.8) 0.0164	(13.3) 0.0152
Gain from within family selection	(12.2) 0.0099	(28.5) 0.0074	(29.2) 0.0260	(6.0) 0.0054	(14.5) 0.0219	(19.8) 0.0225
Total gain	0.0286	0.0159	0.0550	0.0211	0.0532	0.0500
Estimated mean of new population (feet^3)	0.1098	0.0419	0.1439	0.1110	0.2044	0.1639
Percent gain	35.2	61.2	61.9	23.5	35.2	43.9

ranges from a low of 23.5 at Decatur to a high of 61.9 percent at Camp York. The high expected gain at Camp York is the result of the relatively great family-within-stand variance component at that location. At Pineville the percent gain is 61.2, almost as high as at Camp York, while the family variance component is very low. However, the gain in cubic feet at Pineville is low; expected gains are only high relative to the low unselected mean at that location.

Gains from stand selection range between 10 and 13 percent. Expected gains from both family and within-family selection are more variable. Gains resulting from family selection range between 6.3 and 20.4 percent and from within-family selection between 6.0 and 29.2 percent.

Expected gains resulting from two-stage selection, in which no stand selection would be applied, are shown in Table 41 along with variance components and selection intensities. Two-stage selection results in greater expected gains than three-stage selection at two plantations, Decatur and Highland Rim. However, in terms of absolute expected gain in cubic feet, both selection schemes yield similar results; the increased gains resulting from two-stage selection in two plantations are offset by losses of a similar magnitude in the four remaining plantations.

The decision as to which kind of selection to use would depend upon how much improvement in volume growth could be expected by planting seed from a seed orchard established by one of these selection schemes. The three-stage selection scheme provides approximately 10

TABLE 41. Expected Gains (Feet^3) at Each Location Resulting from Two Stage Selection. Variance Components (Times 1000) Are Derived from Original Individual Location Analysis (Table 17, Page 68). Numbers in Parentheses Indicate Percent Contribution at Each Stage of Selection

Component	Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
σ^2_W	1.9623	0.9767	2.7857	2.1788	3.6877	3.5631
$\sigma^2_{(FxR)/S}$	0.2954	0.3361	0.4452	0.3929	0.2255	0.4749
$\sigma^2_{F/S}$	0.0728	0.0323	0.2683	0.1161	0.3645	0.2311
Family selection intensity[1]	1.650	1.425	1.650	1.575	1.750	1.575
Within family selection intensity[2]	1.625	1.580	1,550	1.520	1.700	1.700
Gain from family selection	(13.1) 0.0106	(19.2) 0.0050	(26.5) 0.0236	(14.7) 0.0132	(20.4) 0.0308	(17.6) 0.0201
Gain from within family selection	(9.2) 0.0075	(16.2) 0.0042	(24.6) 0.0219	(11.6) 0.0104	(19.6) 0.0297	(16.2) 0.0185
Total gain	0.0181	0.0092	0.0455	0.0236	0.0605	0.0386

TABLE 41 (continued)

Component	Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
Estimated mean of new population	0.0993	0.0352	0.1344	0.1135	0.2117	0.1525
Percent gain	22.3	35.4	51.2	26.3	40.0	33.9

[1]Namkoong, G., and E. B. Snyder. 1969. Accurate values for selection intensities. Silvae Genetica 18:172-173.

[2]Based on average within plot survival at each location.

percent improvement from stand selection. If stand selection is similar to provenance selection, the bulk of this gain will be transmitted to the progeny. However, only one-quarter of the gain from family and within-family selection can be expected to be transmitted to open-pollinated progeny from trees in a seed orchard. Although the 10 percent improvement from stand selection indicates that the three-stage selection scheme may provide greater improvement from orchard seed, further progeny tests would be necessary to determine the magnitude of this gain.

Gains from mass selection were between 13 and 27 percent of the gains from two-stage selection. Mass selection would, therefore, not be an applicable technique for producing improved seed.

Assuming that the Highland Rim plantation were to be converted into a seed orchard by one of the two selection schemes outlined, one more problem arises. Trees in most seed orchards are planted at a spacing of 30 feet by 30 feet, or between 40 and 48 trees per acre. However, the selection schemes outlined allow for only 13 trees per acre (each replication is approximately one acre). This means that grafted material will have to be interplanted to increase the number of trees per acre in order to maximize seed production per unit of land. However, such a plan assumes that there is time to wait for the orchard to reach full development. If the need for seed is more immediate, selection intensities will have to be lowered enough to permit retention of the number of trees required to produce sufficient seed.

Regardless of which selection scheme is used in the creation of a seed orchard, it is suggested that a progeny test be established to determine the gain realized by using seed orchard seed. It is recommended also that if a central seed orchard is to be established to provide seed for Kentucky and Tennessee, stability parameters be further investigated prior to the final roguing.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The objectives of this study were to evaluate genetic and environmental sources of variation in height, diameter at half-height, volume of wood per tree, branch length and branch diameter in juvenile Virginia pine. Five-year data from open-pollinated progeny of random trees from 12 natural stands in Tennessee and Kentucky were analyzed; data were from measurements of progeny tests outplanted at six locations in Kentucky, Tennessee, and Alabama. In addition, wood samples were obtained from one of the six plantations to estimate the heritability of wood specific gravity. Soil samples were collected from another plantation in an attempt to account for large environmental variation.

Individual location analyses disclosed that variance components for each source of variance, expressed as a percent of total variation, were relatively similar from location to location. Of the five characteristics evaluated, height growth consistently had the highest family-within-stand variance while branch diameter had the lowest.

Since variance components from the combined location analyses are based on numbers of stands and families within stands different from those in the individual location analyses, comparison of variance components from the two types of analyses is not strictly valid. Generally, however, variance components in the combined analyses are similar in magnitude to those in the individual location analyses.

Neither of the two levels of genotype x environment interaction evaluated (the interaction of location with stand and the interaction of location with family within stand) accounted for "appreciable" amounts of phenotypic variance although the corresponding main effects were statistically significant; the sum of these interaction variance components accounted for a maximum of two percent of phenotypic variance.

When compared with two-year estimates, five-year heritability estimates derived from individual location analyses seem to increase in uniformity. Heritability estimates based on variance components from the combined location analyses are in close agreement with averages of estimates from six locations; average heritability estimates from the individual location analyses are within one standard error of the heritability estimate from combined location analyses.

The family-within-stand effect of wood specific gravity was significant at only the 10 percent level of probability while the stand effect was significant at the one percent level, indicating that more improvement in this characteristic may be obtained by stand selection than by family-within-stand selection. There was no evidence of any significant genetic effect on amounts of wood extractives; apparently, this trait is controlled primarily by environmental variables.

Analyses of soil variables at a strip mine site in Kentucky disclosed that 25 percent of total variation in height may be accounted for by three variables (pH, conductivity of soil saturation extract and

and exchangeable aluminum or exchangeable acidity). Inclusion of textural variables in the soil analysis may have resulted in a multiple regression equation accounting for a greater amount of height variation.

Expected gains were computed on the basis of a hypothetical roguing of each plantation using three selection schemes. Gains from a three-stage selection system, which included stand selection, family selection, and within-family selection, ranged from a low of 23.5 to a high of 61.9 percent over mean unselected stem volume. Similar expected gains were obtained with a two-stage selection system (no stand selection); although the two-stage selection resulted in greater gains at two plantations, these greater gains were offset by losses of a similar magnitude at the four remaining plantations. Mass selection, the third selection scheme, resulted in gains of between 13 and 27 percent of the gains from the two-stage selection system.

Expected gains were based on selection of outstanding phenotypes from test plantations. The selected trees were open-pollinated progeny of random (not phenotypically selected) trees from natural stands. Such selections can be applied to any of the existing test plantations to establish a central seed orchard if the need for improved seed is immediate. If such a seed orchard were established, large progeny tests would have to be created to determine the genetic potential of selected trees and provide a sufficient number of progenies for second generation selection.

Since it is generally assumed that greater gains can be obtained

with a combination of phenotypic mass selection and progeny testing, an alternative approach is to apply phenotypic selection to natural stands of Virginia pine. Such mass selection could be confined to the Great Valley Physiographic Province of East Tennessee since, of the four stands selected on the basis of Duncan tests for volume (Table 38, page 110), three were within this region while the fourth was on the northwest limit of the Great Valley. Phenotypic selection may be preceded by a natural variation survey of growth variables since without knowing the range of variation for different site indices in this area, selection criteria would be more difficult to develop. All phenotypic selections would have to be tested and their progeny compared with progeny of unselected trees.

Results from an open-pollinated progeny test of superior phenotypes could be used in selecting one of three approaches to providing improved seed. First, on the basis of progeny-test results, clones of parental grafted material could be interplanted in the existing seed orchard. This would serve to broaden the genetic base of the existing orchard. In addition, such clones could be used to replace existing seed trees in the orchard which are of borderline genetic superiority. This approach would be feasible if the progeny of selected phenotypes did not provide significantly greater gains than progeny of unselected phenotypes. Second, a clonal seed orchard could be established to replace the existing seedling orchard. If progeny of superior phenotypes provided significantly greater gains than progeny in the existing orchard, it may be desirable to replace

the present orchard. Several authors point out that clonal orchards may provide significantly greater gains than seedling orchards (Namkoong, 1965; Toda, 1964). Finally, the open-pollinated progeny test established from seed of superior phenotypes could be rogued to create a seedling orchard to replace the existing orchard. This approach would be more economical than establishing a clonal orchard.

All trees retained as seed trees in a seed orchard should be tested for general combining ability and fecundity.

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APPENDIX

TABLE A-1. Average Five-Year Stand and Family-Within-Stand Height of Virginia Pine Progeny in Each Test Plantation[1]

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
1	1	6.6				9.5	
	2					10.4	
	3					10.5	
	6					10.4	
	7	7.8				10.2	
	9	8.5				10.4	
	12	8.1				9.9	8.5
	13					10.4	
	15					11.0	
Mean stand height		7.8				10.3	8.5
2	1	8.3	4.7	8.5	8.6	10.2	7.5
	3	7.8	4.9	8.6	8.1	10.0	7.7
	6					10.0	
	7	7.3	4.7	7.6	8.5	8.9	7.0
	8	7.4		7.7	7.9	9.1	6.9
	9	7.6		7.1	7.6	9.0	7.2
	10	7.3		7.7	7.4	8.6	7.3
	11	7.6		8.2	7.7	9.3	7.2
	12			7.8	7.9	9.2	7.4
	14	7.4		8.0	8.3	9.2	7.0
Mean stand height		7.6	4.8	7.9	8.0	9.4	7.2
3	2			9.5		10.4	
	4	7.7		8.3	8.0	9.6	6.9
	5			8.7		9.7	7.6
	6	6.7		7.9	7.5	8.9	6.4
	7	7.9		8.4	7.6	9.5	8.0
	8	7.6	4.9	7.5	8.6	9.8	7.3
	9	8.1		8.5	9.0	9.9	7.7
	10	7.7		8.3	9.3	9.4	7.3
	12	8.4	5.6	8.6	9.3	10.4	8.2
	14				9.0	9.7	7.3
	15	7.5	4.8	8.4	8.2	9.5	6.9
Mean stand height		7.7	5.1	8.4	8.5	9.7	7.4

TABLE A-1 (continued)

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
4	1	8.4	4.4	8.6	8.5	9.7	7.5
	2	7.9	5.5	8.6	9.0	10.0	7.7
	3					10.4	
	4	7.8	4.6	8.2	8.5	9.6	7.5
	5	7.8	4.3	8.6	7.2	10.3	7.5
	6	7.7	4.5	8.6	7.5	9.5	7.0
	7					11.1	
	8	8.7	5.2	8.9	9.8	10.9	8.5
	9				9.2	10.4	7.9
	10	8.1		8.5	8.7	9.8	7.2
	12	8.1	4.5	7.8	9.0	10.1	7.7
	13	8.2	4.8	8.7	8.3	9.9	
	14	8.7	5.2	9.3	—	10.6	8.4
Mean stand height		8.1	4.8	8.6	8.6	10.2	7.7
6	2			9.0		10.5	
	3	8.0		8.0	8.4	9.5	7.1
	4	7.7	5.1	8.3	8.1	9.5	7.6
	6	8.0		8.7	7.8	9.7	7.3
	7	7.1		8.1	7.6	9.4	6.8
	8	8.2	5.1	8.2	9.0	9.9	8.1
	9			9.0		10.0	7.3
	10	8.1	3.9	8.2	8.6	9.6	7.2
	11	7.7	4.6	8.0	8.6	9.3	7.2
	12	8.6		9.3	9.1	10.8	8.2
	14	8.7				11.2	8.3
	15	—	—	—	—	9.6	—
Mean stand height		8.0	4.7	8.5	8.4	9.9	7.5
7	1	7.5	5.0	8.4	8.6	9.6	7.0
	4	8.4	5.8	9.8	9.2	10.0	8.0
	5	7.3	4.8	8.8	7.6	9.5	7.0
	6	8.0	4.7	9.5	8.7	9.2	7.3
	8	7.9	5.5	9.0	9.2	10.2	7.6
	10	8.1	5.0	8.8	8.2	9.5	6.9
	11	8.1	4.8	8.8	8.3	10.3	7.7
	13	8.5	5.0	8.7	10.4	10.1	8.0

TABLE A-1 (continued)

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
7	14	9.4	5.3	10.0	9,4	10.8	8.7
	15	8.7	5.6	9.1	8.4	10.6	8.3
Mean stand height		8.2	5.2	9.1	8.8	10.0	7.7
8	3	7.7	4.1	8.7	7.6	9.6	7.2
	4			9.4		10.2	
	5	8.2	5.4	9.4	9.5	10.4	7.8
	6	7.9		8.7	9.0	9.4	7.7
	8			9.1		10.5	
	9	8.1	4.7	8.5	8.3	9.7	7.2
	10	7.5		8.6	8.5	9.6	7.6
	11					10.2	
	12	8.2				9.4	
	13	8.1		9.3	9.7	9.8	8.3
	14	7.5	4.3	7.3	8.3	8.8	7.5
	15	8.2	—	—	9.0	9.9	—
Mean stand height		7.9	4.6	8.8	8.7	9.8	7.6
9	1	8.0	5.1	8.8	9.4	10.8	8.5
	3					10.0	
	4	8.3	5.2	9.2	9.1	9.7	7.6
	5	7.7	4.8	9.8	8.6	10.1	7.6
	6	7.3	5.4	8.9	7.8	9.8	7.2
	7	7.9	4.5	8.6	8.2	9.2	7.2
	9	6.9		7.6	8.6	9.5	6.5
	10	7.7	5.4	8.4	9.3	9.6	7.4
	11					9.7	
	12	8.6		10.0		11.1	
	13	—	—	—	—	10.1	—
Mean stand height		7.8	5.1	8.9	8.7	10.0	7.4
10	2	9.5	5.4	10.0	9.8	10.5	9.2
	3	8.6	5.5	9.1	9.4	10.5	7.9
	4	9.5	6.6	9.1	9.4	10.6	8.3
	5	9.1	4.7	9.2	8.8	10.4	8.3
	6	8.7	6.3	8.3	9.5	10.2	8.6
	9	8.6	5.1	9.4	9.4	10.5	8.8
	10	8.5	5.5	9.4	9.0	10.0	8.3

TABLE A-1 (continued)

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
10	11		5.0		9.7	10.7	8.4
	14	9.1	5.0	9.4	9.6	11.0	8.5
	15	8.6	5.5	8.8	9.0	10.5	8.0
Mean stand height		8.9	5.5	9.2	9.4	10.5	8.4
11	1					10.8	
	2	8.6			8.6	9.8	7.6
	3	8.8	4.8	7.7	8.8	10,1	8.0
	4				8.9	10.6	
	5	8.4	5.2	8.0	8.3	9.8	8.2
	6	8.1	6.2	9.8	8.8	10.3	8.2
	7					11.0	
	8					10.6	
	9	8.5		9.0	9.1	9.9	8.0
	10	7.9		8.2	8.1	9.6	7.3
	11	7.9		8.7	8.4	10.0	7.6
	14	8.3		9.1	9.3	10.0	7.7
	15	7.8		8.0	8.3	9.7	6.7
Mean stand height		8.3	5.4	8.6	8.7	10.2	7.7
12	5					11.1	
	6					10.0	
	7					10.7	
	10					10.0	
	12					10.4	
	14					9.8	
	15					9.5	
Mean stand height						10.2	
13	1	8.7	5.3	8.4	9.0	10,2	8.3
	2	8.4	6.3	8.5	8.6	10.3	7.9
	3	8.9		9.4	9.9	10.5	7.9
	4	8.3		9.7	9.1	10.4	8.7
	6	7.5	4.2	8.6	8.8	9.8	7.4
	7		5.2		9.0	10.1	
	9			8.9	9.8	10.4	7.8
	11	7.9	5.1	8.1	8.7	10.1	8.0

TABLE A-1 (continued)

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
13	14					10.7	
	15				9.7	10.2	
Mean stand height		8.3	5.2	8.8	9.2	10.3	8.0

[1]All measurements in feet.

TABLE A-2. Average Five-Year Stand and Family-Within-Stand Diameter at Half-Height of Virginia Pine Progeny in Each Test Plantation[1]

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
1	1	1.05				1.39	
	2					1.46	
	3					1.50	
	6					1.57	
	7	1.24				1.57	
	9	1.24				1.68	
	12	1.17				1.49	1.64
	13					1.61	
	15	____				1.61	____
Mean stand diameter		1.18				1.54	1.64
2	1	1.13	0.69	1.06	1.05	1.46	1.40
	3	1.16	0.73	1.09	1.09	1.44	1.43
	4					1.48	
	7	1.12	0.77	0.85	1.09	1.27	1.33
	8	1.11		0.95	1.03	1.25	1.27
	9	1.12		0.90	1.07	1.30	1.39
	10	1.12		0.95	1.00	1.31	1.39
	11	1.17		1.11	1.11	1.40	1.37
	12			0.99	1.04	1.38	1.39
	14	1.08	____	1.02	1.05	1.39	1.37
Mean stand diameter		1.13	0.73	0.99	1.06	1.37	1.37
3	2			1.28		1.53	
	4	1.17		1.12	1.04	1.40	1.35
	5			1.17		1.51	1.47
	6	1.07		1.04	1.09	1.39	1.30
	7	1.16		1.08	1.04	1.41	1.50
	8	1.20	0.79	0.96	1.19	1.44	1.46
	9	1.19		1.07	1.16	1.46	1.45
	10	1.13		1.02	1.24	1.38	1.47
	12	1.26	0.88	1.15	1.23	1.57	1.56
	14				1.28	1.44	1.42
	15	1.17	0.76	1.05	1.09	1.39	1.32
Mean stand diameter		1.17	0.81	1.09	1.15	1.45	1.43

TABLE A-2 (continued)

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
4	1	1.22	0.66	1.08	1.06	1.34	1.35
	2	1.16	0.81	1.09	1.27	1.42	1.41
	3					1.45	
	4	1.15	0.70	1.07	1.17	1.42	1.42
	5	1.15	0.67	1.12	1.03	1.52	1.43
	6	1.14	0.65	1.13	0.98	1.35	1.32
	7					1.67	
	8	1.24	0.76	1.24	1.29	1.61	1.60
	9				1.23	1.49	1.38
	10	1.23		1.12	1.23	1.42	1.42
	12	1.23	0.65	0.95	1.24	1.51	1.43
	13	1.14	0.71	1.15	1.13	1.40	
	14	1.23	0.81	1.22		1.50	1.55
Mean stand diameter		1.19	0.71	1.12	1.16	1.47	1.43
6	2			1.24		1.57	
	3	1.23		1.12	1.12	1.49	1.43
	4	1.17	0.84	1.13	1.14	1.52	1.47
	6	1.23		1.26	1.12	1.48	1.47
	7	1.21		1.13	1.21	1,49	1.37
	8	1.17	0.73	1.05	1.18	1.42	1.50
	9			1.31		1.59	1.48
	10	1.12	0.65	1.09	1.23	1.46	1.45
	11	1.30	0.74	0.15	1.32	1.49	1.50
	12	1.27		1.31	1.32	1.70	1.57
	14	1.21				1.52	1.61
	15					1.46	
Mean stand diameter		1.21	0.74	1.18	1.21	1.52	1.49
7	1	1.12	0.77	1.18	1.23	1.45	1.41
	4	1.31	0.89	1.38	1.29	1.56	1.54
	5	1.17	0.75	1.23	1.02	1.42	1.36
	6	1.29	0.79	1.38	1.32	1.54	1.50
	8	1.21	0.85	1.24	1.22	1.57	1.49
	10	1.25	0.74	1.18	1.14	1.47	1.33
	11	1.21	0.75	1.22	1.17	1.72	1.51

TABLE A-2 (continued)

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
7	13	1.25	0.70	1.11	1.39	1.54	1.54
	14	1.34	0.73	1.39	1.23	1.61	1.65
	15	1.31	0.77	1.22	1.21	1.64	1.60
Mean stand diameter		1.25	0.77	1.25	1.22	1.55	1.49
8	3	1.18	0.70	1.19	1.04	1.38	1.46
	4			1.36		1.62	
	5	1.18	0.79	1.24	1.29	1.56	1.49
	6	1.23		1.13	1.31	1.44	1.49
	8			1.26		1.63	
	9	1.21	0.68	1.14	1.11	1.46	1.35
	10	1.13		1.12	1.17	1.40	1.45
	11					1.55	
	12	1.13				1.48	
	13	1.25		1.32	1.40	1.54	1.54
	14	1.14	0.68	0.89	1.12	1.26	1.46
	15	1.19			1.22	1.58	
Mean stand diameter		1.18	0.71	1.18	1.21	1.49	1.46
9	1	1.16	0.81	1.27	1.26	1.61	1.55
	3					1.49	
	4	1.30	0.79	1.25	1.33	1.56	1.46
	5	1.16	0.71	1.34	1.25	1.57	1.42
	6	1.14	0.78	1.23	1.07	1.43	1.34
	7	1.21	0.69	1.23	1.18	1.50	1.37
	9	1.11		1.01	1.26	1.48	1.35
	10	1.14	0.80	1.09	1.26	1.43	1.41
	11					1.51	
	12	1.29		1.40		1.67	
	13					1.48	
Mean stand diameter		1.19	0.76	1.23	1.23	1.52	1.41

TABLE A-2 (continued)

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
10	2	1.36	0.77	1.46	1.26	1.69	1.66
	3	1.25	0.82	1.24	1.33	1.57	1.48
	4	1.39	0.98	1.24	1.31	1.70	1.65
	5	1.34	0.72	1.25	1.24	1.58	1.66
	6	1.24	0.94	1.13	1.33	1.53	1.60
	9	1.24	0.75	1.33	1.28	1.58	1.59
	10	1.28	0.83	1.42	1.23	1.59	1.51
	11		0.79		1.34	1.70	1.57
	14	1.26	0.74	1.30	1.31	1.67	1.56
	15	1.30	0.83	1.17	1.31	1.60	1.47
Mean stand diameter		1.30	0.82	1.28	1.29	1.62	1.58
11	1					1.66	
	2	1.31			1.26	1.56	1.45
	3	1.39	0.75	1.00	1.09	1.53	1.59
	4				1.24	1.72	
	5	1.25	0.79	1.15	1.18	1.52	1.54
	6	1.23	0.91	1.37	1.24	1.61	1.56
	7					1.50	
	8					1.59	
	9	1.37		1.21	1.34	1.61	1.56
	10	1.18		1.07	1.25	1.46	1.41
	11	1.22		1.23	1.28	1.51	1.52
	14	1.24		1.18	1.28	1.52	1.49
	15	1.17	____	0.99	1.16	1.37	1.39
Mean stand diameter		1.26	0.82	1.15	1.23	1.55	1.50
12	5					1.71	
	6					1.50	
	7					1.69	
	10					1.54	
	12					1.55	
	14					1.56	
	15					1.47	
Mean stand diameter						1.57	

TABLE A-2 (continued)

Stand	Family	Plantation					
		Ames	Pineville	Camp York	Decatur	Highland Rim	Vina
13	1	1.21	0.75	1.11	1.22	1.56	1.57
	2	1.24	0.98	1.17	1.22	1.54	1.51
	3	1.26		1.25	1.30	1.54	1.39
	4	1.26		1.40	1.27	1.66	1.65
	6	1.18	0.67	1.23	1.29	1.57	1.46
	7		0.73		1.22	1.58	
	9			1.22	1.39	1.63	1.51
	11	1.17	0.69	1.06	1.22	1.52	1.57
	14					1.67	
	15	———	———	———	1.37	1.63	———
Mean stand diameter		1.22	0.76	1.21	1.28	1.59	1.52

[1]All measurements in inches.

VITA

The author was born in Riga, Latvia, on January 17, 1942. In 1949 he emigrated to New York City, New York, where he graduated from Long Island City High School in 1959 and from New York University in 1963 with a Bachelor of Arts degree in Geology.

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