6-1982

Variation, heritability, and gain in open-pollinated progeny plantations of Virginia Pine (Pinus virginiana Mill.)

Sammy David Todd

Recommended Citation

Todd, Sammy David, "Variation, heritability, and gain in open-pollinated progeny plantations of Virginia Pine (Pinus virginiana Mill.). " Master's Thesis, University of Tennessee, 1982.
https://trace.tennessee.edu/utk_gradthes/7591

To the Graduate Council:

I am submitting herewith a thesis written by Sammy David Todd entitled "Variation, heritability, and gain in open-pollinated progeny plantations of Virginia Pine (Pinus virginiana Mill.)." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

E. Thor, G. R. Wells, Major Professor

We have read this thesis and recommend its acceptance:

J. B. McLaren, G. Schneider

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

We are submitting herewith a thesis written by Sammy David Todd entitled "Variation, Heritability, and Gain in Open-Pollinated Progeny Plantations of Virginia Pine (*Pinus virginiana* Mill.)." We have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

E. Thor

E. Thor, Major Professor

G. R. Wells

G. R. Wells, Major Professor

We have read this thesis and recommend its acceptance:

G. Schneider

J. B. McLaren

Accepted for the Council:

L. Evans Roth

Vice Chancellor
Graduate Studies and Research

A

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

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Sammy David Todd
June 1982

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. Eyvind Thor of the Department of Forestry, Wildlife, and Fisheries for serving as my major professor, but most for his friendship, guidance, and patience through my graduate studies at The University of Tennessee. I wish to thank Dr. G. R. Wells of the Department of Forestry, Wildlife, and Fisheries for serving as co-chairman of my committee. In addition, thanks go to Dr. J. B. McLaren of the Department of Animal Science and Dr. G. Schneider of the Department of Forestry, Wildlife, and Fisheries for serving on my committee.

I wish to express my appreciation to my fellow graduate students, especially Bob Gall and Safiya Samman, for their help, friendship, and moral support.

Thanks to my parents, John and Ruth Todd, for giving me the opportunity to write this thesis.

Most of all, I wish to thank my wife, Judy, for her patience, understanding, devotion, and encouragement.

ABSTRACT

The objectives of this study were to evaluate the genetic and environmental sources of variation in height, diameter, and volume per tree. Ten-year data from open-pollinated progeny of random trees from 12 natural stands in Tennessee and Kentucky were analyzed. The data were measurements of individual progeny from 128 half-sib families outplanted at three locations in Tennessee.

Individual location analyses indicated that variance components for each source of variation, expressed as a percent of the total variation, were relatively similar from location to location. However, the family-within-stand ($s^2_{F/S}$) variance component was consistently lower at the Camp York location, probably due to the site heterogeneity evident at this location.

Generally, the variance components in the combined location analyses are similar in magnitude to those in the individual analyses. Direct comparisons between the two types of analyses are not strictly valid since the combined analyses are based on different numbers of stands and families-within-stand than those of the individual location analyses.

The two levels of genotype × environment interactions, location by stand and location by family-within-stands accounted for only a small amount of the phenotypic variation; the sum of the interaction components accounted for less than 1.5 percent of the phenotypic variance.

When compared with two- and five-year estimates, ten-year heritability estimates were smaller at Camp York and the Highland Rim locations, and were the same or larger at the Ames Plantation location. Heritability estimates derived from the combined location analyses were in close agreement with the average of estimates derived from the three individual locations; average heritability estimates from the individual location analyses were within a standard error of the heritability estimates from the combined location analyses.

Expected gains were computed on the basis of a hypothetical roguing of each plantation using three selection schemes. Gains from a three-stage system, which include stand, family-within-stands, and within-family selection, ranged from 16.1 to 22.4 percent over mean unselected stem volume. Gains from two-stage selection provided the largest gain in stem volume at all locations. Gains ranged from 22.3 to 30.6 percent over mean unselected stem volume. Mass selection resulted in gains ranging from 6.1 to 10.3 percent.

Two of the plantations, Ames Plantation and Camp York, were actually rogued using the two-stage selection system.

Expected gains above the mean unselected population were 29.9 percent at Ames Plantation and 18.0 percent at Camp York.

TABLE OF CONTENTS

LIST OF TABLES

TABLE PAGE

CHAPTER I

INTRODUCTION

Virginia pine (Pinus virginiana Mill.) possesses two traits that make it a desirable species for management on a large scale. First, Virginia pine generally has high yields of wood per acre on average to poor sites in the mid-south (Thor, 1964). Compared to loblolly pine (Pinus taeda L.) and shortleaf pine (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). Smalley and Pierce (1972) indicated that Virginia pine would probably grow better than loblolly pine on warm south-facing slopes with shallow soils on the Cumberland Plateau and Highland Rim of Alabama and Tennessee. Secondly, the wood fiber is especially desirable for making groundwood pulp and the production of newsprint because of its thin pliable cell walls and low amounts of extractives.

Thousands of acres have been regenerated with Virginia pine; however, most of this regeneration has been done with unimproved stock. For example, of the seed collected within the North Carolina State Tree Improvement Cooperative, less than 1 percent was Virginia pine (NCSU Coop. Report, 1977). If the poor to marginal sites are to be used to their fullest potential, they should be regenerated with genetically improved seedlings. The need to establish more Virginia pine seed orchards is becoming apparent as the demand for Virginia pine seedlings for reclamation of surface mines is growing stronger. Several thousand acres of land in the coal-fields of Kentucky and Tennessee must be reclaimed every year and Virginia pine has proven to be one of the most desirable species for strip mine reclamation.

In 1962 The University of Tennessee and the Kentucky-Tennessee section of the Society of American Foresters initiated a program to study the variation in Virginia pine. There were two main objectives of the study:

(1) to estimate the natural variation of the wood properties of Virginia pine

(2) to estimate the variation of growth characteristics and wood properties in open-pollinated progeny plantations representing populations of Virginia pine in Kentucky and Tennessee.

Portions of these objectives have been realized and results reported (Thor, 1964; Evans, 1971; Evans and Thor, 1971; Rink, 1974; Rink and Thor, 1975).

This thesis presents additional estimates of the variation in open-pollinated progeny. There are three main objectives:

(1) to evaluate the genetic and environmental sources of variation and their interaction for the traits measured

(2) to estimate the degree of inheritance for all traits measured

(3) to estimate the improvement that can be made through a selection breeding program.

CHAPTER II

LITERATURE REVIEW

Description of the Species

Silvical characteristics. Virginia pine often grows in pure stands and usually as a pioneer species following fire or in secondary succession on eroded fields. Like most pioneer species, it is intolerant to competition and requires direct sunlight, especially in its early stages of growth.

Virginia pine does not respond well to thinning if the stands are more than 15-years old. Residual trees of older stands are especially vulnerable to windthrow and breakage by wind, ice, and sleet. Although the species is characterized as being shallow rooted (Fowells, 1965), Kundt (1972) reported that the root system varies greatly. Shallow root systems were observed on shallow soils and relatively long tap roots, eight to ten feet, were observed on deep soils.

Virginia pine grows on a wide variety of soils derived from crystalline rocks, sandstone, and slate; however, it grows best on clay, loam, or sandy loam and generally does poorly on shaly soils and very sandy soils. It will thrive in moderately well-drained soils, but is distinctly less tolerant of wet sites and impeded drainage than loblolly pine (Fowells, 1965).

When compared to loblolly and shortleaf pine in the Virginia Piedmont, site index for Virginia pine was the least sensitive to soil factors. Kormanik (1966) found that of 60 variables investigated to predict site index, thickness of the A horizon and the estimate of the percent water at field capacity of the A_2 and A_3B horizons affected the growth of Virginia pine the most. It was suggested that most woodland sites had a site index between 60 and 70 and that Virginia pine would be superior to either loblolly or shortleaf on the least productive sites. This would especially be true on the drier upland soils and those soils lacking A and/or B horizons.

Taxonomy. Virginia pine has two, sometimes three, needles per fasicle which are 1.5 to 3.5 inches long, pale green, and usually twisted, rigid and sharp-pointed (Genys, 1966). Buds are very resinous (Genys, et al., 1974). Cones are two or three inches long, reddish brown when mature, conic-ovoid to oblong, symmetrical, persistent and found in all portions of the crown. Cone scales are thin and flat, terminating in a prickle. The bark is dark brown and scaly (Genys, 1966).

Species range. Virginia pine grows from sea level to elevations of 2500 feet in the Appalachian Mountains. It grows in 16 states from Southern New York and Central

Pennsylvania to Northern Mississippi, Alabama, Georgia, and South Carolina. The western part of its range extends from Central Pennsylvania through Southwestern Ohio, southwest to parts of Western Kentucky and Tennessee (Fowells, 1965).

Natural Variation

The first suggestion that racial variation patterns might 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, the best growth was found to be in the northern part of the study area. This observation could not be explained by soil or precipitation factors, so it was concluded that it was possibly the result of racial differences.

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

Provenance and Progeny Tests

A provenance test generally is the first step in a tree improvement program. In most cases seed from several parts of the species range are planted in one or more locations to determine which sources will provide the best growth in that region. Genys et al. (1974) reported such a seed source test of Virginia pine with 21 provenances outplanted in Maryland, Michigan, and Tennessee. Thirteenth year results revealed that trees from Tennessee, North Carolina, and Georgia provided the best growth in East Tennessee.

Following provenance testing, phenotypes are sometimes selected from the most promising provenances and their progeny compared to determine their relative breeding values. One way of doing this is to collect open-pollinated seed from random phenotypes and compare growth in replicated progeny tests. However, if superior phenotypes are selected from the best provenances, the resulting variance components and heritability estimates can be applied only to those provenances where collections were made and to the specific population of selected trees (Rink, 1974).

Wright and Bull (1963) suggested an alternative to such an approach. Seed could be collected from random dominant and codominant trees in random stands, maintaining the identity of the stand and mother trees. Since both the stands and mother trees are selected at random, the variance components obtained from the progeny would be applicable to all the population from which collections were made. Also, if the stand collections are thought of as provenances, such a test could serve as both a progeny and provenance test. A similar test was established at The University of Tennessee with Virginia pine (Thor, 1964). This study consisted of wind-pollinated progeny from 128 mother trees from 12 stands in Kentucky and Tennessee. Outplantings were made at six locations in Alabama, Kentucky, and Tennessee. Two- and five-year results indicated that stands from the Great Valley physiographic region of Tennessee provided the best growth at most planting locations (Evans, 1971; Evans and Thor, 1971; Rink, 1974; Rink and Thor, 1975).

Heritability Test

Use of estimates. In a genetic study of quantitative traits, probably the most important function of the heritability estimate is its predictive role for a breeding program. Heritability estimates generally serve as a guide to the degree of correspondence between genotype and phenotype. Specifically, a tree breeder wants to know to what degree the phenotype can be used as a selection guide to predict a genotype's worth (Falconer, 1960). Since measurements on trees are phenotypic measurements, the magnitude of the heritability estimate can indicate:

(1) whether a breeding program will result in improvement of a trait, and if so, approximately how much can be expected

(2) which type of breeding strategy will be most appropriate to obtain the most improvement (Rink, 1974).

Falconer (1960) defined heritability as ". . . the portion of the total variance that is attributable to the average effects of genes." Snyder (1969) defined it as a ". . . measure of the relative degree to which a character (or characteristic) is influenced by heredity as compared to environment." Heritability can be expressed in two ways, either in the broad sense (H) or in the narrow sense (h^2). Broad sense heritability is the ratio of the genetic variance (V_G) to the phenotypic variance (V_P).

$$H = \frac{V_G}{V_P}$$

More specifically, the genetic variance can be partitioned into its components; the additive gene effects (V_A), the dominance gene effects (V_D), and the epistatic gene effects (V_I). Likewise, the phenotypic variance can be partitioned into its components; the variation due to environmental effects (V_E), the variation due to genetic effects (V_G), and the variation due to the interaction of environmental and genetic effects (V_{EG}). Broad sense heritability then becomes:

$$H = \frac{V_A + V_D + V_I}{V_E + V_G + V_{EG}}$$

Narrow sense heritability can be thought of as a subset of broad sense heritability; the ratio of only the additive genetic variance (V_A) to the phenotypic variance (V_P).

$$h^2 = \frac{V_A}{V_P}$$

or

$$h^2 = \frac{V_A}{V_E + V_G + V_{EG}}$$

Toda (1964) indicated when nonadditive effects of individual genotypes cannot be transmitted to their progeny, as in the case of sexual reproduction, then heritability in the narrow sense should be used. When the nonadditive effects are transmitted, as in vegetative propagation, then heritability in the broad sense should be used. Therefore, for breeding purposes, the only portion of the genetic variance that can be exploited is the additive genetic variance (Falconer, 1960).

Ceck (1963) stated that the best selection method can be determined by the magnitude of the narrow sense heritability estimate. If the heritability estimate is high, mass selection will be most productive. Conversely, if the heritability estimate is low with dominance, epistatic, or environmental effects high, then intraspecific hybridization or selection based on family means will be most productive.

Time trends in heritability estimates. There is evidence that there are time trends in heritability estimates. Namkoong et al. (1972) reported that heritabilities for height growth of one-, two-, and three-year old incomplete diallels of eastern white pine (*Pinus strobus* L.) declined with age. Estimates decreased from 0.59 at age one to 0.16 at age three. Two explanations were given; either there was a relative increase or accumulation of environmental sources of error or there was a reduction in the additive genetic variance. A reduction in the additive genetic variance would result from a decrease in nursery and/or seed size effects. It was assumed the lower heritability estimates were due to the increase in environmental variance within and among plots. In Virginia pine heritability estimates generally decreased for height growth from age one to age five. Heritability estimates at age one ranged from 0.17 to 0.44, but ranged from 0.13 to 0.34 at age five (Evans, 1971; Rink, 1974).

In western white pine (*Pinus monticola* Dougl.) Squillace et al. (1967) found that height growth for the first four years was correlated with seed weight. Brown and Goddard (1959) found first year loblolly pine height growth to be correlated with seed size. Snyder (1969), working with longleaf pine (*Pinus palustris* Mill.), indicated that although there was a significant correlation between seed size and one-year old trees, there was no correlation between seed size and eight-year old trees. Kundt (1972) found no evidence of such correlation in Virginia pine, indicating that in this species seed size should not be a significant factor in reducing a heritability estimate the first years following establishment.

Methods of estimation. There are two methods used to calculate heritability (h^2); the regression method and the variance component method. The regression method estimates heritability as the regression of offspring on parent with heritability expressed as a regression coefficient (b_{po}). Although this method is popular with crop breeders, it is not used much by tree breeders. One major disadvantage of this method is that the parent and offspring must be grown in the same environmental conditions (Rink, 1974). In tree breeding, the progeny must usually be grown in different environments than the parents. Heritability estimates for trees derived from the regression method will be biased due to the confounding of genetic and environmental effects. Additionally, Steinhoff and Hoff (1971) suggested that the differences between a trait measured on juvenile trees and the same trait measured on mature trees may be of such magnitude that it is probably better to consider them two separate traits.

Most estimates of heritability in forest genetics are derived by variance component methods. This method partitions the phenotypic variance into its components, usually using analysis of variance techniques.

Unfortunately, many heritability estimates that have been reported may be biased or erroneous. Several discussions of these errors may be found in the literature (Evans, 1971; Namkoong et al., 1966; Stonecypher, 1966). Probably the most common flaw in published heritability estimates is that these estimates are computed from data representing only one environment. Therefore, no estimate of the genotype × environment interaction can be obtained. Since the interaction is confounded with the additive genetic variance, the resulting heritability may be overestimated when applied to a site other than the test location. Barker (1973) obtained heritability estimates of 0.36 for diameter growth and 0.40 for volume growth at one location and 0.60 for diameter growth and 0.56 for volume growth at another location for ten-year old loblolly pine. Evans (1971) and Rink (1974) found that estimates varied from location to location in Virginia pine.

<u>Heritability of height growth</u>. Evans (1971) obtained variable heritability estimates in Virginia pine from one- and two-year old progeny. Estimates ranged from 0.17 to 0.44 with a mean of 0.28 at age one; at two years estimates ranged from 0.16 to 0.48 with a mean of 0.28. Rink (1974), working with the same material at age five, obtained heritability estimates ranging from 0.13 to 0.34; however, when the data were analyzed across all locations the estimate

was 0.27. Meier and Goggans (1977), working with data from only one location in Alabama, estimated the heritability to be 0.59 at age eight. Kundt (1972) estimated heritability for height of juvenile Virginia pine from a diallel analysis; he obtained heritabilities of 0.09, 0.14, and 0.11 at ages two, seven, and ten months, respectively.

Heritability of diameter growth. Heritability estimates for diameter growth are not commonly reported. Rink (1974) indicated that paucity of data may result from two reasons; the researcher may feel that diameter growth is strongly affected by environmental and spacing factors resulting in difficulty in detecting genetic controls, or he may recognize that there is no standardized method of measuring diameter on trees less than approximately five years old. Kundt (1972) obtained a heritability estimate of 0.03 at age ten months for Virginia pine measured at ground level. Evans (1971) obtained heritability estimates ranging from 0.08 to 0.41 from two-year old Virginia pine at six locations measured at half-height; the mean for the six locations was 0.20. Rink and Thor (1975) estimated the heritability for diameter at half-height of five-year old Virginia pine at the same six locations by combined data analysis to be 0.14. Meier and Goggans (1977) obtained an estimate of heritability for Virginia pine of 0.33 at age eight measured at 4.5 feet (DBH) above the ground.

Heritability of volume growth. Heritability estimates for volume growth are even more scarce in the literature than either height or diameter growth. Since volume growth is usually a composite characteristic computed from height and diameter measurements, few reports would be expected on young planted material. Volume growth heritability estimates would be expected to reflect the magnitude of the variance components of both height and diameter growth. Since diameter measurements are squared and height measurements are of the first power, volume growth variance components and heritabilities should more closely resemble diameter growth variance components and heritability estimates (Rink, 1974). Rink (1974) and Rink and Thor (1975) obtained a combined heritability estimate for volume per tree of 0.19 for five-year old Virginia pine; heritability estimates from six locations ranged from 0.10 to 0.34.

Genotype × Environment Interaction

The interaction of genotype and environment may be defined as ". . . the differential response of genotypes to varied environments" (Owino and Zobel, 1977). Such a response may be manifest in two ways: there may be differences in rank of genotypes in different environments or the relative superiority of the genotypes may differ although the ranking may remain the same (Rink, 1974).

Impact. When genotype × environment interactions occur and are ignored or not realized, predicted heritability or gain estimates may be in error. The impact is that poorly adapted genotypes may be selected for breeding or regeneration purposes, and/or selected genotypes do not perform as predicted.

Crop breeders have used genotype × environment interaction as an indicator of the stability or adaptability of a genotype. Since there is a trend among plant breeders, and especially tree breeders, to breed for varieties adaptable to a broad range of environments, the development of stable varieties or strains requires the consideration of stability parameters as well as productivity data (Reich and Atkins, 1970).

Estimation. To quantify the genotype × environment interaction, several methods have been used. Plaisted and Peterson (1959) and Wricke (1962) have proposed similar methods of partitioning the genotype × environment interaction sum of squares to evaluate stability. Plaisted and Peterson (1959) eliminated individual genotypes one at a time from the general analysis with the reduction of the genotype × environment component being the genotype's proportionate contribution to the interaction. Wricke (1962) partitioned the interaction sum of squares using a series of two-way tables. The yield of each variety at one location is subtracted from the mean yield of all varieties at all locations; the resulting deviations are squared and their sums are subtracted from the total sum of squares for each variety. This result estimates the contribution of each variety to the genotype × environment interaction sum of squares. In both methods, a relatively stable variety will contribute less to the interaction sum of squares than a relatively unstable variety.

A different approach, involving regression analysis, has also been used to rate the stability of a variety. Yates and Cochran (1938) first discussed this method, but it received little attention until Finlay and Wilkenson (1963) and Eberhart and Russell (1966) made actual applications. The genotype × environment interaction is partitioned into the sum of squares due to regression of a variety on the average yield of all varieties in an environment and the sum of squares of the deviation unexplained by regression. The most stable varieties have regression coefficients of approximately 1.0 and a deviation from regression near zero. Morgenstern and Teich (1969) compared the methods of Wricke (1962) and Eberhart and Russell (1966) for evaluating the phenotypic stability of height growth of jack pine (<u>Pinus banksiana</u> Lamb.) provenances at 12 locations. The two methods yielded similar results.

Most genotype × environment interactions have been reported on the provenance level. Wright (1973) reported on a provenance and progeny test of eleven species at age eleven- to twelve-years old. In general, genetic and site effects were greater than the genotype × environment interactions. He indicated that many of the interactions were the result of poor nursery practices or methods of plantation establishment. Wells and Wakely (1966) reported ten-year results of the Southwide Pine Seed Source Study for loblolly pine and concluded that the most surprising aspect of the genotype × environment interactions was that they were of such small magnitude. King (1965), working with Scotch pine (Pinus sylvestris L.), found that seed source × plantation interaction never accounted for more than 6 percent of the total variation for height growth.

Rink (1974) suggested that the small magnitude of the genotype × environment interaction component in provenance studies should not be surprising. If the assumption that most forest trees are heterozygous for most characteristics is true, a seed source collected from random trees in a provenance will probably most closely represent a hybrid blend with considerable diversity. Crop breeders know that either a mixture of heterozygotes or of different genotypes results in a more stable population than a more genetically uniform population (Allard, 1961).

Rink (1974) and Rink and Thor (1975) found that the variance components for genotype × environment interactions in Virginia pine after five growing seasons were so small that, for practical purposes, they could be ignored. However, Campbell (1972) found that these interactions are not necessarily insignificant; in his study with Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), the family × location interaction was a significant part of the total variation for juvenile height growth.

Assumptions Regarding Parent and Progeny Populations

A set of assumptions must be considered in the estimation and interpretation of additive components of variance for the parent and progeny populations. Stonecypher (1966) listed and discussed the validity of these assumptions. Most of the assumptions are based on the Hardy-Weinberg Law of Equilibrium:

(1) There is regular diploid Mendelian inheritance.
(2) Parent populations are in linkage equilibrium.
(3) Parent and progeny are not inbred and are random members of noninbred populations.
(4) Open-pollinated progeny are half-sibs.
(5) There is no epistasis.
(6) There are no maternal effects.

There is little evidence to support the validity of most of these assumptions. With the exception of assumptions (3) and (4), the assumptions are considered reasonable and have not been seriously questioned. The assumption that parents and progeny are not inbred and are random members of a noninbred population is made because there is no way of determining the relationship among random trees in a stand.

The relationship among parent trees is expressed as the coefficient of inbreeding which 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 estimates of inbreeding are not always available, there is no practical way of translating genetic variance from one generation to the next. Franklin (1971a) estimated the average coefficient of inbreeding in loblolly pine parent trees on an old field site to be 0.003. This low inbreeding coefficient was interpreted as being an indicator of the small number of selfed seedlings which reached sexual maturity despite appreciable levels of self-pollination.

Natural selfing has been used as a measure of inbreeding. Fowells (1965) estimated that natural selfing in red pine probably does not exceed 10 percent in closed stands. However, much higher proportions of self-fertilized seed would be expected in small isolated stands. Franklin (1971b) estimated that self-fertilization in loblolly pine could be as much as 34 percent; however, he noted that these estimates varied with crown position. Estimates of selfing based on frequency of mutant forms can be biased because embryonic mortality is not considered (Franklin, 1971a).

Namkoong (1966) suggests that inbreeding is not necessarily linked to self-fertility. Estimates of genetic variance from open-pollinated progeny may be biased due to relationships between the seed parent and its pollinators, relationship among pollinators, or the presence of only a few pollinators.

In an open-pollinated test the family variance component is interpreted as being one-fourth of the additive genetic variance. This is true only if the progeny are all half-sibs. Squillace and Bengston (1961) suggested if all the progeny are not half-sibs, the family variance component should represent between one-fourth and one-half of the additive genetic variance. They indicated that due to synchronized flowering times of some clones, some progeny may be full-sibs. Kundt (1972), working with twenty-two clones of Virginia pine, used a modified diallel to show assortative pollinating mechanisms. Crossability among clones ranged from a high of 86 percent to a low of 19 percent. This high crossability among clones suggests that the degree of relationship among progeny may be closer than half-sibs.

Estimate of Gains

In most selection breeding programs the ultimate goal is to determine the response or gains that can be obtained for a desired trait. The accepted method of computing gains from selection is defined as the product of the selection intensity, the appropriate phenotypic standard deviation, and the heritability for the trait in question (Falconer, 1960). By using this product, the progress that can be obtained through various selection schemes can be evaluated.

Falconer (1960) stated that gains can be made by selecting at different levels of a population. For example, gains can be obtained by phenotypic selection (mass selection), followed by selection of the best families in a progeny test (family selection), and then selecting the best individuals within the best families (within-family selection). Depending on the inheritance patterns of the desired trait, the maximum gain can be obtained either by one or a combination of all levels of selection.

Namkoong et al. (1966) suggested a method for the calculation of genetic gains based upon the initial mass selection of the phenotypes and the selection of families and individuals within families. Evans (1971) modified this approach to estimate gains for one- and two-year old heights of Virginia pine. It was assumed there was no initial genetic gain made in the initial selection because of the random selection of parent trees. The formula for predicting the genetic gain (G) for family and within-family selection is:

$$G = i_1 \frac{\sigma^2_{F/S}}{\sigma_1} + i_2 \frac{3\sigma^2_{F/S}}{\sigma_2}$$

where:

i_1 = family selection intensity

i_2 = within-family selection intensity

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

$\sigma^2_2 = \sigma^2_W + \sigma^2_{R \times F/S}$

N = number of trees in a plot

R = number of replications.

Evans (1971) applied this formula by computing expected gains for two selection schemes to a single two-year old progeny plantation of Virginia pine. In the first approach, expected gains were computed by selecting the tallest stands, then the tallest families, and finally the tallest individuals within the tallest families. Gains from stand selection were estimated by the deviation of the average height of the selected stands and the population mean. This gain was added directly to the gains from family and within-family selection. The second approach involved selecting the tallest families and the tallest individuals within the tallest families, regardless of stand origin. Both schemes resulted in approximately 21 percent gain in height growth. Rink

(1974) predicted volume growth gains using the same formula and selection schemes in the same plantations at age five years. Again the results for the schemes were similar; the estimate of gain was approximately 35 percent for volume growth.

Although the additive methods of Namkoong et al. (1966) and the modification by Evans (1971) work satisfactorily in most cases, there are circumstances when such methods cannot be followed. There are times when all the best individuals for a given characteristic are not selected, especially if a progeny test is to be thinned for seed production. The selection of a particular individual may be precluded by such factors as spacing and/or the effects of other traits. Therefore, a method which predicts the gain (on a more realistic basis) from selection of a specific set of individuals within the test population must be employed.

Falconer (1960) has presented a method to compute gains from multistage selection which can predict gains for any set of individuals within the test population. This method computes heritability in terms of the individual tree heritability:

$$h_F^2 = h_I^2 \cdot \frac{1 + (n-1)r}{1 + (n-1)t}$$

$$h_W^2 = h_I^2 \cdot \frac{1 - r}{1 - t}$$

where:

h_F^2 = heritability of family means

h_I^2 = individual tree heritability

h_W^2 = within-family heritability

n = family size

r = 0.25 for half-sibs or 0.5 for full-sibs

t = intra-class correlation of family members.

Once the appropriate heritability estimates are known, the gains from each stage can be predicted from the product of the appropriate selection differential and the appropriate heritability:

Gains (G) = (selection differential) (appropriate h^2).

The selection differential is the difference between the mean value for the selected set of individuals and the remaining population. By adding the gains from each stage together, the following formula can be used to estimate total genetic gains:

$$G = SD_F h_F^2 + SD_W h_W^2$$

where:

G = total genetic gain

SD_F = selection differential between the selected families and the population mean

SD_W = selection differential between the selected individuals and the mean of the selected families.

This formula can be used to predict gains from the selection of any set of families and/or individuals within a population.

CHAPTER III

MATERIALS AND METHODS

Parent Population Selection

Method for selecting stands. To develop the plantations for this study, open-pollinated seed was collected from 12 stands in Kentucky and Tennessee. These stands were selected from the three predominant physiographic regions of Kentucky and Tennessee: the Coastal Plain, the Cumberland Plateau and Mountains, and the Great Valley. Due to the distribution of Virginia pine, nine of the stands were selected from Tennessee and four from Kentucky (Figure 1). All stands were essentially even-age of either average or better than average quality established on abandoned fields with site indices ranging from 60 to 87 feet (Thor, 1964). With one exception (stand 10), no stand had received any silvicultural treatment or management; stand 10 was on United States Forest Service land and had been thinned to establish a seed production area. Parent stands ranged from 28 to 53 years old. Stands younger than age 25 were not accepted because parent trees were also used in a wood properties study requiring samples obtained at breast height and representing wood between the tenth and twentieth growth rings. Stands older than 53 years were not used due to difficulty in comparing pruning, branching, and

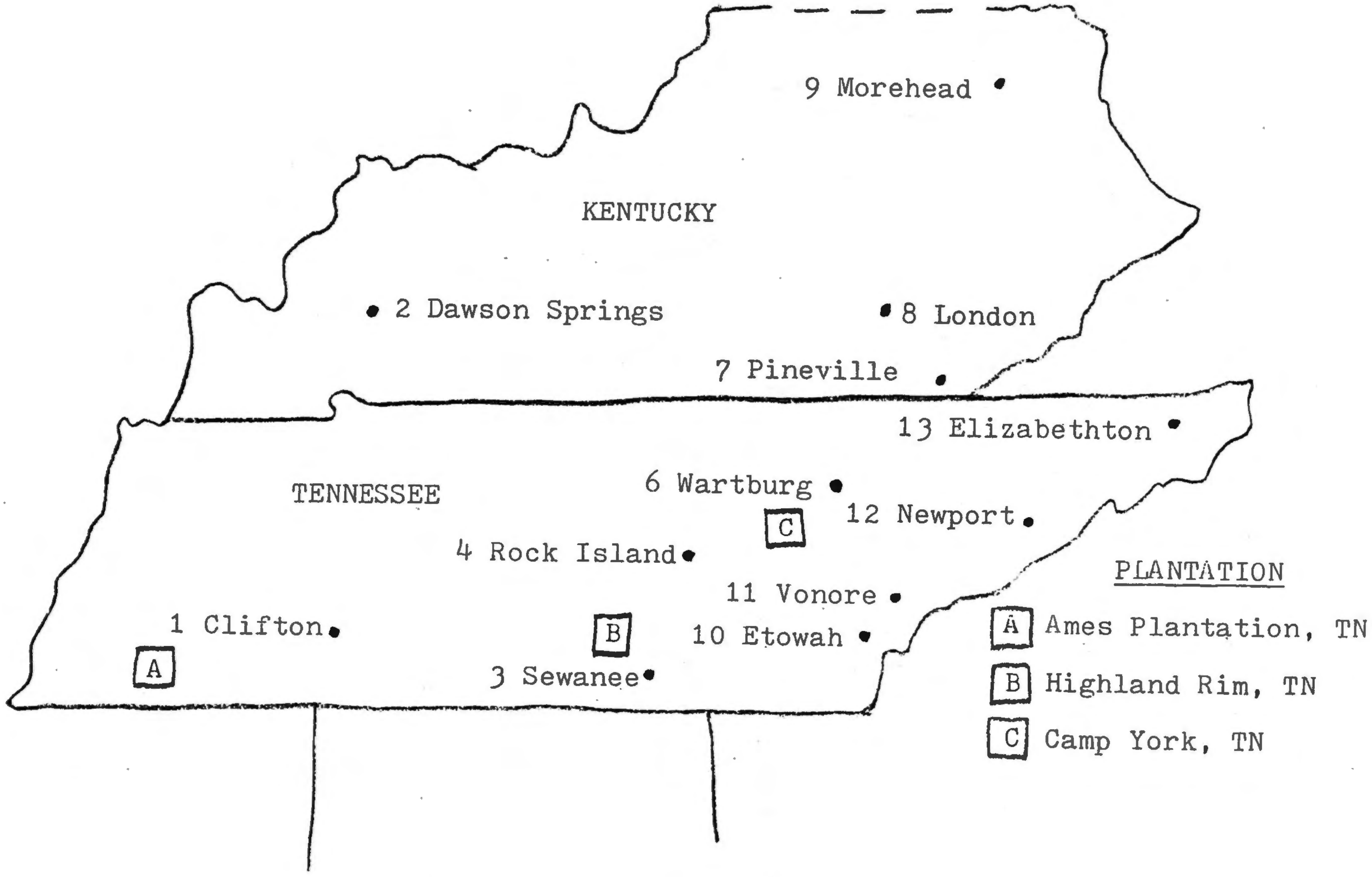

Figure 1. Location of Parent Stands and Plantation Sites.

other characteristics of such stands with younger stands. Site characteristics of the respective stands are summarized in Table 1.

Method of selecting parent trees. From each of the 12 stands, 15 trees were selected. Only dominant or codominant trees that were safe to climb were used. Although poor, average, and excellent genotypes were included, these criteria may have resulted in a slight upward bias toward taller and sturdier trees. Again, stand 10 was an exception; undesirable trees had been removed leaving the remaining trees to be used.

Most abandoned fields in Kentucky and Tennessee are only a few acres in size, therefore, individual trees were selected within a small area; some parent trees were several hundred feet apart while some were adjacent to each other.

Seedling Production

It was estimated that a minimum of 200 cones per tree would be required in order to produce enough seedlings to represent each parent tree at all planting locations. Cones were collected in September and October of 1963, 1964, and 1965 in an effort to obtain sufficient numbers. Even though Virginia pine is characterized as a prolific cone producer, cone production of some stands and individual trees did not meet expectations. However, most parent trees yielded

Table 1. Physiographic Region, Location, Site Index, Diameter Breast Height (DBH), and Age of Parent Stands.[1] (Averages are based on 15 trees per stand.)

Number	Physiographic Region	Location	Site Index (Feet at 50 Years)	DBH (Inches)	Age (Years)
1	Coastal Plain	Clifton, TN	75	9.0	28
2	Coastal Plain	Dawson Springs, KY	69	11.6	52
3	Cumberland Plateau	Sewanee, TN	73	9.7	34
4	Highland Rim	Rock Island, TN	74	10.2	42
6	Cumberland Mountains	Wartburg, TN	87	8.9	35
7	Cumberland Mountains	Pineville, KY	82	9.5	42
8	Cumberland Plateau	London, KY	83	10.9	47
9	Cumberland Plateau	Morehead, KY	69	8.8	32
10	Great Valley	Etowah, TN	81	9.0	34
11	Great Valley	Vonore, TN	60	9.8	53
12	Great Valley	Newport, TN	75	9.7	42
13	Great Valley	Elizabethton, TN	64	11.1	43

---

[1] Thor, E. 1964.

sufficient numbers of cones. Cone production was not a selection criterion.

Cone collection was accomplished by both climbing and cutting down trees. Seeds were extracted from the cones and stored at 10°F in plastic bags until planting (Evans, 1971; Rink, 1974).

Seedlings were grown in the spring of 1966 in unreplicated plots at the Tennessee Valley Authority Nursery at Norris, Tennessee. Seedlings were grown for one growing season, lifted, sorted into bundles of ten seedlings per family, and tagged. Small and deformed seedlings were culled during the process, retaining the healthier ones. Seedlings were packed in damp sphagnum moss and wrapped with seedling wrapper paper for shipment to outplanting locations.

Of the original 195 trees selected as parents, only 128 yielded enough seedlings to be included in the experiment. Since a half-sib family is the open-pollinated progeny of a single mother, a maximum of 128 families could be outplanted. However, because the number of progeny produced by parent trees was so variable, only the Highland Rim location could be planted with all 128 families. Ninety families were outplanted at Ames Plantation and Camp York. The numbers of families from each stand at each location are listed in Table 2.

Table 2. Number of Families per Stand at Each Test Site.[1]

Stand No.	Number of Families Per Test Site Ames Plantation	Camp York	Highland Rim	Total
1	4	0	9	13
2	8	9	10	27
3	8	10	11	29
4	10	10	13	33
6	9	10	12	31
7	10	10	10	30
8	9	9	12	30
9	8	8	11	27
10	9	9	10	28
11	9	8	13	30
12	0	0	7	7
13	6	9	10	25
Total	90	90	128	308

[1] Evans, R. M. 1971 and Rink, G. 1974.

Description of Plantations

Selection of plantation sites. Originally, six open-pollinated progeny plantations were established. However, three plantations were not measured:

(1) Pineville, Kentucky, had been destroyed by strip-mining

(2) Decatur, Tennessee, had poor survival in several replications

(3) Vina, Alabama, would have been too costly due to the lack of local experiment station personnel.

The three plantations that were available to be measured were located at (1) Ames Plantation, (2) Camp York, and (3) the Highland Rim (Figure 1, page 28).

Ames Plantation. Ames Plantation is located in Fayette County near Grand Junction, Tennessee, longitude 89°20' latitude 35°05'. The planting site is on the Coastal Plain physiographic region of West Tennessee (Fenneman, 1938). This region is characterized by loess deposits overlaying a series of sand, clay, and gravel of the Mississippian embayment. The test site is of gently rolling topography of an elevation of 450 feet above sea level. The soil is a deep sandy loam of the Ruston series. The climate is classified as mild. Mean annual precipitation is 53.12 inches with January being the month receiving the most precipitation, 6.28 inches, and October being the month receiving the least, 2.78 inches. Temperatures on the average range from 80.3°F (July) to 42.6°F (January). The average number of frost-free days is 205 (Flowers, 1964). Previous land usage was an upland oak-hickory forest. Prior to planting, the area was clear-cut and mist-blown with 2,4,5,-T (Evans, 1971).

Camp York. Camp York is located in Cumberland County, 12 miles from Crossville, Tennessee, longitude 85°10' latitude 35°55' on the Cumberland Plateau (Fenneman, 1938). The test site is on gently sloping topography at about 1900 feet above sea level on a shallow sandy loam soil of the Hartsell series. The climate is cool in winter and mild in the summer; temperatures range on the average from 37.8°F in January to 73.8°F in July. There are about 176 frost-free days in a year. The average precipitation is 53.53 inches with January being the month receiving the most, 5.97 inches, and October being the month receiving the least, 2.70 inches (Hubbard et al., 1950).

Camp York was used as a World War II prisoner-of-war camp. The planting site is very disrupted with remains of old buildings, foundations for barracks, and roads that are scattered over the area. The replication and planting rows had to be specially arranged to avoid the obstacles, however, seedlings were sometimes planted over hidden structures. More recently the area was a pasture that had been abandoned and grown up in brush. The site was prepared by cutting the brush, mist-blowing it with 2,4,5,-T, and disking (Evans, 1971).

Highland Rim. The Highland Rim Plantation is located on The University of Tennessee Highland Rim Forestry Field Station in Franklin County, near Tullahoma, Tennessee. This location is on the Eastern Highland Rim of Middle Tennessee and is underlain by loess Mississippian cherty limestone. Elevation is 1000 feet above sea level. The soil is a silty loam of the Dickson series with a compact almost impervious fragipan at about 18 inches. This fragipan hinders root development and water movement resulting in wet conditions in winter and dry conditions in summer. Topography is gently sloping. The climate is mild in winter and summer. Temperatures range from 41.5°F in January to 77.6°F in July. There are about 196 frost-free days. Average annual precipitation is 53.48 inches with the largest amount being received in January, 6.19 inches, and the least being received in October, 2.56 inches (Fenneman, 1938).

This site was previously used as pasture land and was disked before planting. The Highland Rim plantation appeared to be the most uniform with respect to soil and site conditions among the test sites (Evans, 1971).

Outplanting Design

The three plantations used in this experiment were arranged in a randomized complete block design with stands and families-within-stands randomized in blocks. Each plantation contains ten replications with half-sib families planted in ten-tree row plots. Spacing was four feet within family-row plots and eight feet between rows. Two border rows, consisting of a mixture of half-sib families, were planted around each plantation. Because of the different number of families represented at each location, the Highland Rim location (128 families) occupied 9.6 acres, while the Ames Plantation and Camp York locations (90 families) occupied 6.6 acres each (Evans, 1971; Rink, 1974).

Measurements

Measurements of individual trees were taken in the latter part of the summer of 1977 through the spring of 1978. Measurements include:

(1) total height to the nearest foot

(2) stem diameter to the nearest tenth of an inch taken at breast height (4.5 feet from the ground).

Total height and stem diameter measurements were used to compute individual tree volumes.

$$V = 0.02056 + (0.021866 \times D^2 \times H)/10$$ (Goebel and Mathews, 1966)

where:

V = volume in cubic feet

D = stem diameter at 4.5 feet (DBH)

H = total height to the nearest foot.

Statistical Analysis

To depict the population two analyses were performed. First, an analysis of variance was performed on data collected at each individual location. Then an analysis of variance was performed combining data collected across all locations. All variables were analyzed on an individual tree basis using the General Linear Models procedure (GLM) of the Statistical Analysis System 1976 version (SAS76) (Barr and Goodnight, 1976). All analyses were performed on the IBM 360/65 computer at The University of Tennessee Computing Center. All effects were assumed to be random.

Individual location analysis. The linear model used for the individual location analysis was:

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

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, $R = 1, \ldots, j$, where j = number of replications

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

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

$R \times F/S_{R \times F/S}$ = effect of interaction of families-within-stand and replication

$E_{R(F/S)W}$ = within-plot (residual) effect, $E = 1, \ldots, k$, where k = number of trees in one family plot.

The form of the analysis of variance along with the expected mean squares is presented in Table 3.

Variance components were obtained by conventional methods of equating expected mean squares to observed values and solving for the appropriate components.

<u>Combined location analysis</u>. The individual and combined location analyses were performed using similar techniques. The form of the analysis for combined locations is presented in Table 4. The linear model used was:

$$Y_{LR(F/S)W} = M + L_L + R/L_{R/L} + S_S + LS_{LS} + S \times R/L_{S \times R/L} + F/S_{F/S} + L \times F/S + (R \times F)/LS_{(R \times F)/LS} + E_{LR(F/S)W}$$

Table 3. Analysis of Variance and Expected Mean Squares for Individual Location Analysis.

Source of Variation	d.f.	Expected Mean Squares[1]
Replication	R-1	$\sigma^2_W + W\sigma^2_{R \times F/S} + WF\sigma^2_{R \times S} + WSF\sigma^2_R$
Stands	S-1	$\sigma^2_W + W\sigma^2_{R \times F/S} + WR\sigma^2_{F/S} + WF\sigma^2_{R \times S} + WRF\sigma^2_S$
Replication × Stands	(R-1)(S-1)	$\sigma^2_W + W\sigma^2_{R \times F/S} + WF\sigma^2_{R \times S}$
Families in Stands	(F-1)S	$\sigma^2_W + W\sigma^2_{R \times F/S} + WR\sigma^2_{F/S}$
Replication × Families in Stands	(F-1)(R-1)S	$\sigma^2_W + W\sigma^2_{R \times F/S}$
Within-Plot (residual)	(W-1)RFS	σ^2_W

[1] Expected mean squares were determined in accordance with methods described by Schultz (1955).

Explanation of symbols:

σ^2_W = within-plot variance component.

$\sigma^2_{R \times F/S}$ = variance component for the interaction of replication with families-within-stands.

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

Table 3 (continued)

$\sigma^2_{R \times S}$ = variance component for the interaction of replications with stands.

σ^2_S = among stand variance component.

σ^2_R = among replication variance component.

W = average number of trees per plot =

$$\frac{1}{[(R \times F)/S] - 1}\left[\sum_{R=1}^{j}\sum_{F/S=1}^{p}(t) - \frac{\sum_{R=1}^{j}\sum_{F/S=1}^{p}(t)^2_{F/S}}{\sum_{R=1}^{j}\sum_{F/S=1}^{p}(t)^2_{F/S}}\right],$$

where t = number of trees in each plot (Sokal and Rohlf, 1973).

R = number of replications

F = average number of families-within-stands =

$$\frac{1}{RS - 1}\left[\sum_{R=1}^{j}\sum_{S=1}^{i}(fm) - \frac{\sum_{R=1}^{j}\sum_{S=1}^{i}(fm)^2_S}{\sum_{R=1}^{j}\sum_{S=1}^{i}(fm)_S}\right],$$

Table 3 (continued)

where fm = number of families in each stand (Sokal and Rohlf, 1973).

S = number of stands.

Table 4. 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	$\sigma^2_W + W\sigma^2_{(R \times F)/L,S} + WF\sigma^2_{S \times R/L} + WR\sigma^2_{L \times F/S} + SWF\sigma^2_{R/L} + WRF\sigma^2_{L \times S} + WRFS\sigma^2_L$
2	Replications-within-Locations	(R-1)L	$\sigma^2_W + W\sigma^2_{(R \times F)/L,S} + WF\sigma^2_{S \times R/L} + SWF\sigma^2_{R/L}$
3	Stands	S-1	$\sigma^2_W + W\sigma^2_{(R \times F)/L,S} + WF\sigma^2_{S \times R/L} + WR\sigma^2_{L \times F/S} + WRL\sigma^2_{F/S} + WRF\sigma^2_{L \times S} + WRFL\sigma^2_S$
4	Stands × Locations	(S-1)(L-1)	$\sigma^2_W + W\sigma^2_{(R \times F)/L,S} + WF\sigma^2_{S \times R/L} + WR\sigma^2_{L \times F/S} + WRF\sigma^2_{L \times S}$
5	Stands × Replications-within-Locations	(S-1)(R-1)L	$\sigma^2_W + W\sigma^2_{(R \times F)/L,S} + WF\sigma^2_{S \times R/L}$
6	Families-within-Stands	(F-1)S	$\sigma^2_W + W\sigma^2_{(R \times F)/L,S} + WR\sigma^2_{L \times F/S} + WRL\sigma^2_{F/S}$

Table 4 (continued)

Line Number	Source of Variation	D.F.	Expected Mean Squares[1]
7	Locations × Families-within-Stands	(L-1)(F-1)S	$\sigma^2_W + W\sigma^2_{(R\times F)/L,S} + WR\sigma^2_{L\times F/S}$
8	Replications-within-Locations × Families-within-Stands	(R-1)(F-1)LS	$\sigma^2_W + W\sigma^2_{(R\times F)/L,S}$
9	Residual (Within-Plot)	(W-1)LRF(S)	σ^2_W

[1] Expected mean squares were determined in accordance with methods described by Schultz (1955).

Explanation of symbols:

σ^2_W = within-plot variance component.

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

$\sigma^2_{L\times F/S}$ = variance component for the interaction of location with families-within-stand.

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

$\sigma^2_{S\times R/L}$ = variance component for the interaction of stand and replication-within-location.

Table 4 (continued)

σ^2_S = among stand variance component.

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

σ^2_L = among location variance component.

W = average number of trees per plot =

$$\frac{1}{(R \times F)/LS - 1}\left[\sum_{L=1}^{p}\ \sum_{R/L=1}^{j}\ \sum_{F/S=1}^{i}(t) - \frac{\sum_{L=1}^{p}\ \sum_{R/L=1}^{j}\ \sum_{F/S=1}^{i} t^2_{F/S}}{\sum_{L=1}^{p}\ \sum_{R/L=1}^{j}\ \sum_{F/S=1}^{i} t_{F/S}}\right],$$

where t = number of trees in each plot (Sokal and Rohlf, 1973).

R = number of replications

L = number of locations.

F = average number of families-within-stands =

Table 4 (continued)

$$\frac{1}{LRS - 1}\left[\sum_{L=1}^{p}\ \sum_{R/L=1}^{j}\ \sum_{S=1}^{q}(fm) - \frac{\sum_{L=1}^{p}\ \sum_{R/L=1}^{j}\ \sum_{S=1}^{q}(fm)_S^2}{\sum_{L=1}^{p}\ \sum_{R/L=1}^{j}\ \sum_{S=1}^{q}(fm)_S}\right],$$

where fm = number of families within each stand.

S = number of stands.

where:

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

M = mean

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

$R/L_{R/L}$ = effect of replication-within-location, $R/L = 1, . . ., j$, where j = number of replications per location

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

$S \times R/L_{S \times R/L}$ = interaction effect of stand and replication-within-location

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

$L \times F/S_{L \times F/S}$ = interaction effect of location and family-within-stand

$(R \times F)/LS_{(R \times F)/LS}$ = interaction effect of replication and family-within-location and stand

$E_{LR(F/S)W}$ = within-plot (residual) effect, $W = 1, . . ., m$, where m = number of trees in a family row plot.

However, because of the size of the variance-covariance matrix generated when all data were combined, the complete analysis could not be processed in the computer simultaneously. To arrive at the complete analysis, the model was partitioned into three separate forms (Table 5). The appropriate parts of models A, B, and C were then combined to obtain the complete model.

Sum of squares for lines 1, 3, and 4 were obtained directly from model B. Sum of squares for lines 2, 5, and 8 were obtained by summing the sum of squares from each location for the respective lines in model A. Sum of squares for lines 6 and 7 were obtained by summing the appropriate sum of squares in model C across all parent stands. The sum of squares for line 9 was obtained by summing the corrected sum of squares for all locations (Table 5, Model A).

Coefficients for the expected mean squares were obtained by methods described by Sokal and Rohlf (1973). The difference between the two appropriate mean squares were divided by the coefficient to obtain an estimate of the variance components.

Heritability (h^2) estimates were computed using the following equations:

(1) Individual location,

$$h^2 = \frac{4\sigma^2_{F/S}}{\sigma^2_W + \sigma^2_{R \times F/S} + \sigma^2_{F/S}}$$

Table 5. Analyses of Variance and Expected Mean Squares of the Three Models Used to Construct the Combined Location Analysis of Variance.

Source of Variation	d.f.	Expected Mean Squares[1]
Model A[2]		
Replications	R-1	$\sigma^2_W + W\sigma^2_{R \times F/S} + WF\sigma^2_{R \times S} + WSF\sigma^2_R$
Stands	S-1	$\sigma^2_W + W\sigma^2_{R \times F/S} + WR\sigma^2_{F/S} + WF\sigma^2_{R \times S} + WRF\sigma^2_S$
Replications × Stands	(R-1)(S-1)	$\sigma^2_W + W\sigma^2_{R \times F/S} + WF\sigma^2_{R \times S}$
Families in Stands	(F-1)S	$\sigma^2_W + W\sigma^2_{R \times F/S} + WR\sigma^2_{F/S}$
Replication × Families in Stands	(F-1)(R-1)S	$\sigma^2_W + W\sigma^2_{R \times F/S}$
Within-Plot (residual)	(W-1)RFS	σ^2_W
Model B[3]		
Locations	L-1	$\sigma^2_W + W\sigma^2_{L \times S} + WS\sigma^2_L$
Stands	S-1	$\sigma^2_W + W\sigma^2_{L \times S} + WL\sigma^2_S$
Locations × Stands	(L-1)(S-1)	$\sigma^2_W + W\sigma^2_{L \times S}$
Within-Plot (residual)	(W-1)LS	σ^2_W

Table 5 (continued)

Source of Variation	d.f.	Expected Mean Squares[1]
Model C[4]		
Locations	L-1	$\sigma^2_W + W\sigma^2_{L \times F} + WF\sigma^2_L$
Families	F-1	$\sigma^2_W + W\sigma^2_{L \times F} + WL\sigma^2_F$
Locations × Families	(L-1)(F-1)	$\sigma^2_W + W\sigma^2_{L \times F}$
Within-Plot (residual)	(W-1)LF	σ^2_W

[1] Explanation of symbols:

σ^2_W = within-plot variance component.

$\sigma^2_{(R \times F)/LS}$ = variance component for the interaction of replication-within-location and family-within stand.

$\sigma^2_{L \times F/S}$ = variance component for the interaction of location and family-within-stand.

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

$\sigma^2_{S \times R/L}$ = within location variance component for the interaction of stand and replication.

Table 5 (continued)

$\sigma^2_{L \times S}$ = variance component for the interaction of location and stand.

σ^2_S = among stand variance component.

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

σ^2_L = among location variance component.

W = number of trees per plot.

R = number of replications.

F = number of families.

S = number of stands.

L = number of locations.

[2] Model A was performed for each location.

[3] Model B was performed combining the data across all locations.

[4] Model C was performed for each stand combining the data across all locations.

$$h^2 = \frac{4s^2_{F/S}}{s^2_W + s^2_{R \times F/S} + s^2_{F/S}},$$

each s^2 being an estimate of the corresponding σ^2.

(2) Combined location,

$$h^2 = \frac{4\sigma^2_{F/S}}{\sigma^2_W + \sigma^2_{(R \times F)/LS} + \sigma^2_{L \times F/S} + \sigma^2_{F/S}}$$

$$h^2 = \frac{4s^2_{F/S}}{s^2_W + s^2_{(R \times F)/LS} + s^2_{L \times F/S} + s^2_{F/S}},$$

each s^2 being an estimate of the corresponding σ^2.

CHAPTER IV

RESULTS AND DISCUSSION

Individual Location Analysis

Mean stand and family-within-stand estimates for height, diameter, and volume growth are presented in Tables A-1, A-2, and A-3, respectively (Appendix).

Mean squares, degrees of freedom, and levels of significance for each location and characteristic are presented in Tables 6, 7, and 8. The most important feature of the data is the significance for effects of stands and family-within-stands at all locations. All sources of variation indicated to be significant were so at the 1 percent probability level, except for the effect of family-within-stand for height growth (significant at the 5 percent probability level). The interaction source of variation of stand with replication were nonsignificant (5 percent probability) except for height and volume growth at the Highland Rim location. Interaction of family-within-stand with replication was nonsignificant for volume growth at Camp York and the Highland Rim, and for diameter growth at the Highland Rim location.

Variance components estimates for each location are presented in Tables 9, 10, and 11. Direct comparisons of variance components among locations are not strictly valid

Table 6. Mean Squares and Degrees of Freedom for Height, Diameter, and Volume Growth at Ames Plantation.

Source	d.f.	Height	Diameter	Volume
Replication	9	197.180**[1]	1.388NS[2]	0.551**
Stands	10	204.681**	17.035**	2.681**
Replication × Stands	90	9.222NS	0.701NS	0.080NS
Family-within-Stands	79	42.720**	2.733**	0.380**
Replication × Family-within-Stands	689	9.624**	0.762**	0.081**
Within-Plot	5551	5.369	0.643	0.070

[1] ** = significant at the 1 percent level.

[2] NS = nonsignificant at the 5 percent level.

Table 7. Mean Squares and Degrees of Freedom for Height, Diameter, and Volume Growth at Camp York.

Source	d.f.	Height	Diameter	Volume
Replication	9	348.693**[1]	3.907**	1.642NS[2]
Stand	9	88.078**	17.010**	3.862**
Replication × Stand	81	16.030NS	0.971NS	0.227NS
Family-within-Stand	80	32.269*[3]	2.742**	0.708**
Replication × Family-within-Stand	685	24.982**	1.071**	0.236NS
Within-Plot	4008	6.074	1.033	0.213

[1] ** = Significant at the .01 probability level.

[2] NS = Nonsignificant at the .05 probability level.

[3] * = Significant at the .05 probability level.

Table 8. Mean Squares and Degrees of Freedom for Height, Diameter, and Volume Growth at the Highland Rim Forestry Field Station.

Source	d.f.	Height	Diameter	Volume
Replication	9	273.527**[1]	3.411**	1.478**
Stands	11	191.829**	26.513**	6.928**
Replication × Stands	99	11.706**	0.910NS[2]	0.250**
Family-within-Stands	124	36.724**	3.466**	0.906**
Replication × Family-within-Stands	993	8.003**	0.680NS	0.165NS
Within-Plot	8995	4.992	0.802	0.185

[1] ** = significant at the 1 percent level.

[2] NS = nonsignificant at the 5 percent level.

Table 9. Variance Components for Total Height at Each Location. Numbers in parentheses indicate the percent contribution to the total variance.

Location	σ^2_W	$\sigma^2_{R \times F/S}$	$\sigma^2_{F/S}$	$S.E._{F/S}$[1]	$\sigma^2_{R \times S}$	σ^2_S	σ^2_R
Ames Plantation	5.369 (77.0)	0.587 (8.4)	0.456 (6.5)	0.093	NC[2]	0.274 (3.9)	0.288 (4.1)
Camp York	6.704 (57.8)	3.489 (33.2)	0.134 (1.3)	0.096	NC	0.133 (1.3)	0.682 (6.5)
Highland Rim	4.993 (79.9)	0.399 (6.4)	0.381 (6.1)	0.062	0.043 (0.7)	0.177 (2.8)	0.255 (4.1)
Mean	5.479	1.492	0.324		NC	0.195	0.408

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

[2] NC = negative estimate of component.

Table 10. Variance Components for Stem Diameter at Each Location. Numbers in parentheses indicate the percent contribution to the total variance.

Location	σ^2_W	$\sigma^2_{R \times F/S}$	$\sigma^2_{F/S}$	S.E.$_{F/S}$[1]	$\sigma^2_{R \times S}$	σ^2_S	σ^2_R
Ames Plantation	0.643 (91.7)	0.004 (0.6)	0.028 (4.0)	0.006	0.001 (0.1)	0.024 (3.4)	0.001 (0.1)
Camp York	1.033 (93.4)	0.007 (0.6)	0.031 (2.8)	0.008	NC[2]	0.030 (2.7)	0.006 (0.5)
Highland Rim	0.802 (92.1)	NC	0.37 (4.2)	0.006	0.003 (0.3)	0.027 (3.1)	0.002 (0.3)
Mean	0.826	0.004	0.032		0.002	0.027	0.003

---

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

[2] NC = negative estimate of component.

Table 11. Variance Components for Volume per Tree at Each Location. Numbers in parentheses indicate the percent contribution to the total variance.

Location	σ^2_W	$\sigma^2_{R \times F/S}$	$\sigma^2_{F/S}$	$S.E._{F/S}$[1]	$\sigma^2_{R \times S}$	σ^2_S	$^{2}_{R}$
Ames Plantation	0.070 (87.3)	0.001 (1.8)	0.004 (5.1)	0.001	NC[2]	0.004 (4.9)	0.001 (0.9)
Camp York	0.213 (90.5)	0.004 (1.7)	0.009 (3.7)	0.002	NC	0.007 (2.8)	0.003 (1.2)
Highland Rim	0.185 (90.2)	NC	0.010 (4.8)	0.002	0.001 (0.5)	0.007 (3.5)	0.002 (1.0)
Mean	0.156	0.003	0.008		NC	0.005	0.001

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

[2] NC = negative estimate of component.

since each location contains a few families not represented at all locations.

Estimates are more meaningful when presented as a percent of the total variation. The largest source of variation was the within-plot (s_W^2) variance component. The contribution of this component to the total variation ranged from 57.8 to 79.9 percent for height, 91.7 to 93.4 percent for diameter, and 87.3 to 90.5 percent for volume.

Estimates of variance components at Ames Plantation and Highland Rim were similar. However, estimates at Camp York were almost always different and extremely different for height growth. Differences in estimates at Camp York are probably due to site heterogeneity. Remains of World War II prisoner-of-war camp structures were not always recognizable at the time of establishment. The interaction of family-within-stand with replication ($s^2_{R \times F/S}$) is a measure of the consistency of performance of families to site heterogeneity. This component accounted for a large proportion (33.2 percent) of the total variation for height at Camp York. Since height is usually more dependent on site conditions, the magnitude of this component would indicate the site variability at the Camp York location.

Variance components for height growth. In general, the variance components for height were similar at Ames Plantation and the Highland Rim locations (Table 9).

However, for almost all sources of variation the Camp York location was atypical; pure genetic sources of variation were lower and environmental and interaction components were higher compared to the other two locations. The family-within-stand ($s^2_{F/S}$) variance components for Ames Plantation and the Highland Rim were larger for height than for diameter and volume, contributing 6.5 and 6.1 percent to the total variation, respectively; Camp York only contributed 1.3 percent to the total. Assuming family-within-stand ($s^2_{F/S}$) variance component estimates to be one-fourth the additive genetic variance, then the total additive genetic variance for height is approximately 18 to 25 percent of the total genetic variance, depending on the inclusion or exclusion of the Camp York estimate. The stand components (s^2_S) were one-half and two-thirds the magnitude of the family-within-stand ($s^2_{F/S}$) components at Highland Rim and Ames Plantation, respectively. The stand component was essentially the same as the family-within-stand component at Camp York.

The single largest source of variation for height growth was the within-plot (s^2_W) variance component. This component estimated only 57.8 percent of the total variation at Camp York, but 76.9 percent at Ames Plantation and 79.9 percent at the Highland Rim were accounted for by this component. Although Camp York had the lowest percent contribution to the total variation, the absolute value was the largest indicating possible microsite variation exists at this location.

Variance components for interaction of families in stands with replication accounted, as a percent of total variation, for 6.4 percent at the Highland Rim, 8.4 percent at Ames Plantation, and 33.5 percent at Camp York. The magnitude of these components indicate height is more sensitive to site factors than diameter and volume (Tables 10 and 11).

The high within-plot (s_W^2) and interaction component for families in stands with replication ($s_{R \times F/S}^2$) may explain the low family-within-stand ($s_{F/S}^2$) variance component at the Camp York location.

The interaction component for replication with stand ($s_{R \times S}^2$) accounted for less than 1 percent of the total variation for height growth.

Variance components for diameter growth. The largest proportion of total variance for diameter growth was accounted for by the within-plot (s_W^2) component; estimating 91.7 percent at Ames Plantation, 93.3 percent at Highland Rim, and 93.3 percent at Camp York (Table 10). The only important differences among locations appears to be the lower estimates of family-within-stand ($s_{F/S}^2$) and stand (s_S^2)

components at Camp York. These low estimates may be a function of the random site variability at this location. Family-within-stand ($s^2_{F/S}$) components were estimated to be 2.8 percent at Camp York, 4.1 percent at Ames Plantation, and 4.2 percent at the Highland Rim. Stand (s^2_S) variance components were estimated to be 2.7, 3.1, and 3.4 percent of the total variation for Camp York, Highland Rim, and Ames Plantation, respectively. The components of interaction of replication with stand ($s^2_{R \times S}$) and replication with families in stands ($s^2_{R \times F/S}$) were small, each accounting for less than 1 percent of the total variation.

Variance components for volume per tree growth. Since volume growth is a function of height and diameter, the variance components for volume should reflect variation in height and diameter. Since diameter is squared and height used only to the first power in the volume prediction equation, the variation in volume should more closely resemble the variation in diameter growth. In general this was the case.

Variance components for family-within-stand ($s^2_{F/S}$) were 3.7, 4.8, and 5.1 percent of the total variation at Camp York, Highland Rim, and Ames Plantation, respectively (Table 11). The proportion of total variation estimated by the stand (s^2_S) variance component was 2.8 percent at Camp York, 3.5

percent at Highland Rim, and 4.9 percent at Ames Plantation (Table 11).

Combined Location Analysis

Mean squares, degrees of freedom, and levels of significance for height, diameter, and volume per tree growth are presented in Table 12. Sensitivity of the experimental design is evident by the predominance of statistical significance for almost all sources of variation.

Estimates of the variance components for height, diameter, and volume growth are presented in Table 13. Although not directly comparable, the estimates obtained from the combined analysis in general are of the same magnitude as the mean of the individual location estimates. The standard error of the family-within-stand ($s^2_{F/S}$) variance component for each characteristic was approximately 16 percent of the component estimate.

Of the three characteristics measured, height growth was the greatest in relative magnitude for the family-within-stand ($s^2_{F/S}$) variance component. The stand variance components were very similar among the characteristics; estimates ranged between 2 and 3 percent of the phenotypic variation (Table 13).

The two components of interaction of location and stand ($s^2_{L \times S}$) and location and family-within-stand ($s^2_{L \times F/S}$)

Table 12. Mean Squares and Degrees of Freedom for Height, Diameter, and Volume in the Combined Locations Analysis.

Source	d.f.	Height	Diameter	Volume
Locations	2	75,820.093**[1]	432.216**	281.129**
Replication-within-Location	27	273.133**	2.902**	1.223**
Stands	11	352.229**	45.682**	9.811**
Location × Stands	19	39.241NS[2]	3.308**	0.814**
Stand × Replication-within-Location	270	12.176**	0.859**	0.186**
Families-within-Stands	125	67.667**	5.656**	1.337**
Location × Families-within-Stands	159	13.779**	1.127**	0.254**
Replication-within-Location × Families-within-Stands	2367	10.222**	0.791NS	0.161**
Within-Plot	18554	5.339	0.804	0.156

[1] ** = significant at the 1 percent level.

[2] NS = nonsignificant at the 5 percent level.

Table 13. Estimates of Variance Components for Height, Diameter, and Volume per Tree Derived from the Combined Location Analysis. Numbers in parentheses indicate the percent contribution to total variance.

Source	Height	Diameter	Volume
σ^2_L	10.674 (59.5)	0.052 (5.6)	0.039 (18.4)
$\sigma^2_{R/L}$	0.362 (2.0)	0.003 (0.3)	0.001 (0.7)
σ^2_S	0.149 (0.8)	0.021 (2.2)	0.005 (2.4)
$\sigma^2_{L \times S}$	0.039 (0.2)	0.004 (0.4)	NC[2]
$\sigma^2_{S \times R/L}$	0.032 (0.2)	0.001 (0.1)	0.001 (0.2)
$\sigma^2_{F/S}$	0.342 (1.9)	0.029 (3.1)	0.007 (3.2)
S.E.($\sigma^2_{F/S}$)[1]	0.054	0.004	0.001
$\sigma^2_{L \times F/S}$	0.068 (0.4)	0.006 (0.7)	0.002 (0.8)
$\sigma^2_{(R \times F)/L,S}$	0.928 (5.2)	NC	0.001 (0.4)
σ^2_W	5.339 (29.8)	0.804 (87.4)	0.156 (74.0)

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

$$\sqrt{\frac{2}{WRL}\left[\frac{M.S.^2_{F/S}}{d.f. + 2} + \frac{M.S.^2_{L \times F/S}}{d.f. + 2}\right]}$$

where:

W = estimate of the average number of trees per plot
R = number of replications
L = number of locations

[2] NC = negative estimate of component

appear to be too small to be of any practical importance; the combined total accounts for less than 1.5 percent of the phenotypic variation (Table 13).

Five- and ten-year variance component estimates for height, diameter, and volume are presented in Tables 14, 15, and 16. Rink (1974) in his analysis of five-year measurements did not compute either variance components for replication in location ($s^2_{R/L}$) or the interaction of stand with replication in location ($s^2_{S \times R/L}$). Additionally, he assumed the effects of location (s^2_L) to be fixed, therefore no variance components were computed.

Ten-year family-within-stand ($s^2_{F/S}$) variance component estimate for height was about three-fourths the five-year estimate, but diameter and volume estimates were about the same for both analyses. Ten-year stand (s^2_S) variance component estimates for all characteristics were approximately half the five-year estimates. Within-plot (s^2_W) variance component estimate for height growth was about the same for both analyses; however, ten-year estimates for diameter and volume were 11 and 13 percent larger than the five-year estimates, respectively. Increases in the within-plot component estimates were offset by decreases in interaction of replication with families in stands in locations ($s^2_{R \times F/L,S}$) variance components.

Table 14. Five-Year[1] and Ten-Year Variance Components for Height Growth. Numbers in parentheses indicate the percent contribution to phenotypic variance.

Component	Five-Year Estimate	Ten-Year Estimate
σ^2_S	0.108 (4.21)	0.149 (2.16)
$\sigma^2_{L \times S}$	0.006 (0.23)	0.039 (0.56)
$\sigma^2_{S \times R/L}$	--[2]	0.032 (0.46)
$\sigma^2_{F/S}$	0.163 (6.35)	0.342 (4.96)
$\sigma^2_{L \times F/S}$	0.015 (0.58)	0.068 (0.98)
$\sigma^2_{R \times F/L,S}$	0.390 (15.20)	0.928 (13.45)
σ^2_W	1.884 (73.42)	5.339 (77.40)

[1] Rink, G. 1974.

[2] Component not estimated.

Table 15. Five-Year[1] and Ten-Year Variance Components for Diameter Growth. Numbers in parentheses indicate the percent contribution to phenotypic variance.

Component	Five-Year Estimate	Ten-Year Estimate
σ^2_S	0.394 (4.12)	0.021 (2.43)
$\sigma^2_{L \times S}$	0.025 (0.26)	0.003 (0.34)
$\sigma^2_{S \times R/L}$	--[2]	0.001 (0.11)
$\sigma^2_{F/S}$	0.320 (3.34)	0.029 (3.36)
$\sigma^2_{L \times F/S}$	0.063 (0.66)	0.006 (0.69)
$\sigma^2_{R \times F/L,S}$	0.941 (9.83)	NC[3]
σ^2_W	7.826 (81.78)	0.804 (93.05)

[1] Rink, G. 1974.

[2] Component not estimated.

[3] NC = negative estimate of component.

Table 16. Five-Year[1] and Ten-Year Variance Components for Volume Growth. Numbers in parentheses indicate the percent contribution to phenotypic variance.

Component	Five-Year Estimate	Ten-Year Estimate
σ^2_S	0.017 (4.48)	0.005 (2.92)
$\sigma^2_{L \times S}$	0.001 (0.26)	NC[2]
$\sigma^2_{S \times R/L}$	--[3]	0.000 (0.00)
$\sigma^2_{F/S}$	0.017 (4.48)	0.007 (4.09)
$\sigma^2_{L \times F/S}$	0.003 (0.79)	0.002 (1.17)
$\sigma^2_{R \times F/L,S}$	0.044 (11.61)	0.001 (0.58)
σ^2_W	0.297 (78.36)	0.156 (91.22)

[1] Rink, G. 1974.

[2] NC = negative estimate of component.

[3] Component not estimated.

Heritability Estimates

Individual location. Two-year (Evans, 1971), five-year (Rink, 1974), and ten-year heritability estimates for height, diameter, and volume growth are presented in Table 17. At Camp York and the Highland Rim heritabilities have decreased from age two through age ten. This may be the result of a decrease in the family-within-stand ($s^2_{F/S}$) variance and/or an increase in the family-within-stand with replication ($s^2_{R \times F/S}$) component and/or an increase in the within-plot (s^2_W) component. From age two to age five a decrease in the family-within-stand component could be accounted for by a decrease in nursery and seed size effects. From age five to ten the decrease in heritability estimates are more likely the result of increases in the interaction component of family-within-stand with replication and/or within-plot variance components. An increase in the within-plot component would be expected since the growth variables would reflect microsite difference, especially competition effects. Increases in the family-within-stand with replication interaction component would occur as an expression of response of families to site and competition variability within and among replications.

At Ames Plantation the heritability estimates have increased sharply for diameter and volume growth and stayed about the same for height growth and from age five to age

Table 17. Estimates of Heritability[1] for Height, Diameter, and Volume per Tree from Two-, Five-, and Ten-Year Measurements.

Location	Two-Year[2] Height	Five-Year[3] Height	Ten-Year Height	Two-Year[2] Diameter	Five-Year[3] Diameter	Ten-Year Diameter	Five-Year[3] Volume	Ten-Year Volume
Ames Plantation	0.16	0.29	0.28	0.08	0.09	0.17	0.12	0.22
Camp York	0.28	0.25	0.06	0.21	0.25	0.12	0.31	0.13
Highland Rim	0.48	0.34	0.26	0.41	0.27	0.18	0.34	0.20

[1] Narrow sense heritability

$$h^2 = \frac{4\sigma^2_{F/S}}{\sigma^2_W + \sigma^2_{R \times F/S} + \sigma^2_{F/S}}$$

[2] Evans, R. M. 1971.

[3] Rink, G. 1974.

ten. This is a result of a proportionally larger family-within-stand ($s^2_{F/S}$) variance component estimate at age ten than at age five. The increase in the family-within-stand component could be the result of decreased sensitivity to site factors. This is evident by the lower interaction of family-within-stand with replication ($s^2_{R \times F/S}$) variance component estimates for diameter and volume growth at age ten than at age five.

Height growth. Estimates of heritability for height growth were 0.05 at Camp York, 0.26 at Highland Rim, and 0.28 at Ames Plantation. The magnitude of these estimates was directly related to the magnitude of the family-within-stand ($s^2_{F/S}$) variance component estimates. The low Camp York estimate resulted from a high family-within-stand by replication interaction component. Compared to five-year heritability estimates, those from Camp York and Highland Rim decreased by age ten while the Ames Plantation estimate remained about the same.

Diameter growth. Heritability estimates for diameter growth were 0.11 at Camp York, 0.17 at Ames Plantation, and 0.18 at the Highland Rim. Camp York and the Highland Rim estimates decreased from age five to ten. The Ames Plantation estimate, however, almost doubled in magnitude during this five-year period.

Volume growth. Since volume is a composite characteristic computed from height and diameter measurements, variation of heritability estimates from location to location would be expected to reflect the size of heritability estimates of height and diameter. Except at Camp York, the volume estimate fell between those for height and diameter heritability estimates. Volume growth heritability estimates were 0.15 at Camp York, 0.20 at Highland Rim, and 0.22 at Ames Plantation.

Combined location. Heritability estimates for each location, mean heritability estimates for the three locations, and heritability estimates for the combined location analysis for height, diameter, and volume growth are presented in Table 18. The combined location estimates in all cases are in agreement with the mean of the three locations heritability estimates. Averages of the three locations are within a standard error of combined location estimates.

Correlation among Characteristics

Knowledge of degree of relationship among various characteristics is needed to avoid or minimize the possibility of eugenic selection for one characteristic and concurrently causing dysgenic selection for another due to negative correlation. Correlation among characteristics is also important when an alternate characteristic is easier to

Table 18. Ten-Year Heritability[1] Estimates for Height, Diameter, and Volume per Tree for the Individual Locations, Mean of the Individual Locations and Combined Location Analyses. Numbers in parentheses indicate the standard error of the estimate.

	Height	Diameter	Volume per Tree
Individual Location			
Ames Plantation	0.284 (0.058)	0.168 (0.035)	0.219 (0.042)
Camp York	0.055 (0.039)	0.115 (0.030)	0.154 (0.035)
Highland Rim	0.264 (0.043)	0.176 (0.027)	0.201 (0.031)
Mean	0.201	0.153	0.141
Combined Location	0.205 (0.032)	0.138 (0.021)	0.166 (0.026)

[1] Narrow sense heritability

Individual Location: $$h^2 = \frac{4s^2_{F/S}}{s^2_W + s^2_{R \times F/S} + s^2_{F/S}}$$

Combined Location: $$h^2 = \frac{4s^2_{F/S}}{s^2_W + s^2_{R \times F/L,S} + s^2_{L \times F/S} + s^2_{F/S}}$$

measure than the desired characteristic. Diameter and volume growth were the most closely related characteristics (r^2 = 0.95) while height and volume were also highly correlated (r^2 = 0.71). Height and diameter growth were only moderately correlated (r^2 = 0.59). Selection for volume growth would appear to be feasible and could be accomplished by selection based on diameter (DBH) measurements.

CHAPTER V

APPLICATIONS OF RESULTS

Virginia pine is mainly grown for fiber production. Thus, selection for greater wood yield per tree may be an appropriate primary selection criterion. Wood fiber yield is the product of volume per tree and wood specific gravity. Rink and Thor (1975) found that gains in wood yield were 10 percent greater when selection was for diameter only than selection for a combination of diameter and specific gravity. Since volume of wood per tree is highly correlated with stem diameter (see page 75) and is generally used as the standard measure of wood fiber yield, volume was chosen as the primary selection criterion.

One consideration of this study was to make suggestions for production of genetically improved Virginia pine seed. The quickest and most cost efficient method to obtain improved seed is to rogue one or more of the open-pollinated progeny tests leaving only the trees that by open-pollination will produce offspring superior in volume growth.

Results of the combined location analysis (Table 13, page 65) indicate that a combination of stand, family-within-stand, and within-plot selection may be an effective technique to increase volume yield. This is possible due to the significant amount of variation found among stands, families-within-stands, and individuals within-plots. Also, the low interaction sources of variation, both location by stand ($s^2_{L \times S}$) and location by family-within-stand ($s^2_{L \times F/S}$), indicate that by selecting progenies of stands and families-within-stands having high volume growth at all locations, the establishment of a single seed orchard may be adequate for Tennessee.

Comparison of Three Selection Schemes

Three selection schemes are proposed:

(1) three-stage selection—based on leaving only the best stands, the best families within the best stands, and the best individuals within the best families

(2) two-stage selection—based on leaving only the best families without regard to stand, and the best individuals within the best families

(3) mass or individual selection—based solely on individual performance regardless of family or stand performance.

Stand selection, the first stage of the three-stage system, will be on the basis of a Duncan's New Multiple Range test (Table 19) and a stand's performance relative to the plantation mean at each location. Only stands that consistently rank best at all locations will be selected.

Table 19. Mean Stand Values for Ten-Year Volume of Wood per Tree of Open-Pollinated Progeny at Three Planting Locations and Duncan's New Multiple Range Test for Mean Separation.

Plantation	Mean Volume per Tree[1]	Stand Number
Ames Plantation	0.697	10
	0.608	11
	0.593	1
	0.570	7
	0.551	4
	0.532	13
	0.520	9
	0.518	6
	0.514	3
	0.494	8
	0.444	2
Camp York	1.093	10
	1.035	7
	1.024	11
	0.974	9
	0.950	6
	0.933	8
	0.923	4
	0.914	13
	0.876	3
	0.765	2
Highland Rim	1.062	10
	0.992	1
	0.951	11
	0.933	12
	0.919	4
	0.886	13
	0.875	7
	0.840	6
	0.808	3
	0.795	8
	0.786	9
	0.775	2

[1] Means connected with the same line are not significantly different from each other, P > .05.

Also, any stand that ranks below the plantation mean at any location will not be selected. Such selection criterion results in the selection of only three stands: stand 10 from the Great Valley near Etowah, Tennessee, stand 11 from the Great Valley near Vonore, Tennessee, and stand 1 from the Coastal Plain near Clifton, Tennessee. Duncan's test indicates that trees from stand 10 provide the greatest volume growth at all locations. This superiority may partly be due to 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. Stand 7, which ranks fourth at Ames Plantation and second at Camp York, will not be selected due to its ranking below the plantation mean at the Highland Rim location. Also, since stand 12 is represented at only one location, proper evaluation cannot be made and this stand must also be excluded from stand selection.

Selection of families in the three selected stands depends on good performance at all locations. By rejecting families which do not rank in the upper half of all families from the three selected stands in at least two of the three locations, a total of 15 families are retained. However, of the 15 families selected only the families which rank in the upper half at a given location are used in estimating gains (Table 20).

Table 20. Mean Volumes (cubic feet per tree) of Unselected Populations and of Trees in Three Selected Stands, Number of Families in Three Selected Stands, and Family and Within-Family Selection Intensities (Phenotypic Standard Deviations) for the Three-Stage Selection.

	Ames	Camp York	Highland Rim
Mean Volume Unselected Population	0.549	0.950	0.881
Mean Volume of Three Selected Stands	0.659	1.059	0.995
Total Number of Families in Three Selected Stands at Each Location	22	17	33
Number of Families Selected from Three Best Stands	15	12	12
Family Selection Intensity[1]	0.750	0.725	1.050
Average Number[2] of Trees per Plot	8.69	3.11	8.16
Within-Family Selection Intensity[1]	1.625	1.125	1.575

[1] Namkoong, G., and E. B. Snyder. 1969.

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

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, is retained.

Expected gains are computed using the methods described earlier by Namkoong et al. (1966) as modified by Evans (1971) (see page 22). These are gains which can be expected at each location if each plantation is hypothetically rogued of all except select trees.

Selection intensities for family and within-family in the three-stage selection scheme are presented in Table 20 along with mean volume per tree for unselected populations and for the three selected stands.

Variance component estimates for family-within-stand ($s^2_{F/S}$), within-plot (s^2_W), and the interaction of replication by family-within-stand ($s^2_{R \times F/S}$) obtained when all stands are included in the analysis of variance (Table 11, page 58) are not appropriate to use in the gains prediction formula once stand selection is accomplished. Therefore, an analysis of variance including only the three selected stands is needed (Table 21). Expected gains resulting from the three-stage selection are also presented in Table 21.

Total gains resulting from the three-stage selection were 22.9 percent at Ames Plantation, 16.1 percent at Camp York, and 22.3 percent at Highland Rim above the mean of the unselected population at each location. Gains from stand

Table 21. Variance Components Derived from An Analysis of Variance which Included Only the Three Selected Stands at Each Location. Expected gains (cubic feet per tree) at each location from three-stage selection. Numbers in parentheses indicate percent contribution at each stage of selection.

Component	Ames	Camp York	Highland Rim
σ^2_W	0.0941	0.2680	0.2242
$\sigma^2_{R \times F/S}$	0.0000	0.0001	NC[1]
$\sigma^2_{F/S}$	0.0005	0.0034	0.0036
Gain from Stand Selection	0.110 (20.0)	0.109 (11.5)	0.114 (12.9)
Gain from Family Selection	0.009 (1.6)	0.022 (2.3)	0.047 (5.3)
Gain from Within-Family Selection	0.007 (1.3)	0.022 (2.3)	0.036 (4.1)
Total Gain	0.126	0.153	0.197
Estimated Mean of New Population	0.670	1.103	1.078
Percent Gain	22.9	16.1	22.3

[1] NC = negative estimate of component.

selection were 20.0 percent at Ames Plantation, 11.5 percent at Camp York, and 12.9 percent at the Highland Rim location. Family selection gains were 1.6 percent at Ames Plantation, 2.3 percent at Camp York, and 5.3 percent at the Highland Rim. Gains from within-family selection were 1.3, 2.3, and 4.1 percent at Ames Plantation, Camp York, and Highland Rim, respectively. Stand selection accounted for most of the gains resulting from the three-stage selection at all locations. The magnitude of gain from stand selection is due to the degree of superiority of the selected stands to the mean of the unselected population. For the three locations the absolute gain in cubic feet per tree at Ames Plantation was the least, but proportionally was the largest. The expected gain is high only relative to the low unselected mean at that location.

Expected gains resulting from two-stage selection, in which no stand selection is applied, are presented in Table 22, along with variance components and selection intensities. Gains were 28.0 percent at Ames Plantation, 22.2 percent at Camp York, and 30.6 percent at Highland Rim. Family selection accounted for 15.1 percent at Ames Plantation, 13.4 percent at Camp York, and 17.8 percent at the Highland Rim. Within-family gains were 12.9, 8.8, and 12.8 percent at Ames Plantation, Camp York, and Highland Rim, respectively.

Table 22. Expected Gains (cubic feet per tree) at Each Location from Two-Stage Selection. Variance components are derived from the original individual location analysis (Table 11, page 58). Numbers in parentheses indicate percent contribution at each stage of selection.

Component	Ames	Camp York	Highland Rim
σ^2_W	0.070	0.213	0.185
$\sigma^2_{R \times F/S}$	0.001	0.004	NC[1]
$\sigma^2_{F/S}$	0.004	0.009	0.010
Family Selection Intensity[2]	1.475	1.625	1.750
Within-Family Selection Intensity[3]	1.575	1.450	1.625
Gain from Family Selection	0.083 (15.1)	0.127 (13.4)	0.157 (17.8)
Gain from Within-Family Selection	0.071 (12.9)	0.084 (8.8)	0.113 (12.8)
Total Gain	0.154	0.211	0.270
Estimated Mean of New Population	0.703	1.161	1.151
Percent Gain	28.0	22.2	30.6

[1] NC = negative estimate of component.

[2] Namkoong, G., and E. B. Snyder. 1969.

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

Gains from mass selection were 6.6, 6.1, and 10.3 percent at Ames Plantation, Camp York, and Highland Rim, respectively.

Two-stage selection resulted in greater gains than three-stage selection at all three locations: 22.2 percent greater at Ames Plantation, 37.9 percent greater at Camp York, and 37.0 percent greater at the Highland Rim. Two-stage selection appears to be the most desirable selection scheme and mass selection appears to be the least desirable as methods for producing improved seed.

Rink (1974) estimated gains using the three-stage and two-stage selection schemes based on five-year data. Estimated gains for three-stage selection at that age were 35.2 percent at Ames Plantation, 61.9 percent at Camp York, and 35.2 percent at the Highland Rim. Gains for two-stage selection were 22.3, 51.2, and 40.0 percent at Ames Plantation, Camp York, and Highland Rim, respectively. In general, gains estimates have decreased from age five to age ten. This would be expected since the size of the trees are larger and the proportion of added volume relative to tree size is less. The magnitude of the gains estimates correspond roughly to the magnitude of the heritability estimates. However, this correspondence is modified by the selection intensity and the mean of the unselected population at a given location. Estimates of gains at Camp York at ten years, both for three-stage and two-stage selection, were much lower than estimates at age five years. These low estimates could partly be due to the low family-within-stand variance component, which resulted in low heritability estimates obtained at ten years.

Gains from Rogued Progeny Plantations

Two of the progeny plantations, Ames Plantation and Camp York, were actually rogued for the production of genetically improved seed. Two-stage selection schemes were used to determine which trees to retain to produce improved open-pollinated seed. Families were selected based on their performance across all locations. The number of families to be retained was increased compared to the hypothetical roguing in order to have approximately 40 to 45 trees per acre for maximum seed production per acre. Although volume growth was the main selection criterion, individuals with poor stem form were not accepted. Therefore, the greatest volume producing tree in a family-row plot may not always be retained, thereby possibly sacrificing some volume gain.

Since the actual trees selected were known and were not necessarily the largest volume trees in the family-row plots, gains were computed using Falconer's (1960) method of multi-stage selection (see page 24). Falconer's (1960) method should result in more realistic estimates of volume growth gain since gains from any given set of selected trees can be estimated.

Falconer's (1960) method of computing gains resulting from family and within-family selection computes heritability for family means (h_F^2) and heritability for individuals within-family (h_W^2) in terms of individual tree heritability (h_I^2):

$$h_F^2 = h_I^2 \cdot \frac{1 + (n-1)r}{1 + (n-1)r}$$

$$h_W^2 = h_I^2 \cdot \frac{1 - r}{1 - r}$$

where:

n = family size

r = 0.25 for half-sibs

t = intraclass correlation of family members.

Expected gains from both plantations are presented in Table 23. The selection differential (SD_F) between selected families and the location mean was multiplied by the family mean heritability (h_F^2) to obtain an estimate of gain (G_F) from family selection.

$$G_F = SD_F h_F^2$$

Likewise, the selection differential (SD_W) between the mean of the individuals selected within selected families and the mean of all selected families was multiplied by the within-family heritability (h_W^2) to obtain an estimate of gain (G_W) from within-family selection.

Table 23. Expected Gains in Volume Growth (cubic feet per tree) by Roguing Ames Plantation and Camp York Using Two-Stage Selection. Numbers in parentheses indicate percent contribution for each stage of selection.

Item	Ames	Camp York
Location Mean Volume	0.549	0.950
Mean Tree Volume of the Selected Families	0.660	1.090
Mean Tree Volume of the Selected Trees within the Selected Families	1.075	1.691
Selection Differential for Selected Families	0.111	0.140
Selection Differential for Selected Trees within Families	0.415	0.601
Number of Families Selected	27 of 90	28 of 90
Volume Gain for Family Selection	0.092 (16.8)	0.100 (10.5)
Volume Gain for Within-Family Selection	0.072 (13.1)	0.072 (7.6)
Total Volume Gain	0.164 (29.9)	0.172 (18.0)

$$G_W = SD_W h_W^2$$

The total gain is the sum of the gain obtained from each stage of selection. By using the two-stage selection system, the expected volume per tree growth gain at Ames Plantation and Camp York was 0.164 and 0.172 cubic feet, respectively. Proportionally, the gains were 29.9 percent at Ames Plantation and 18.0 percent at Camp York above the unselected population mean (Table 23).

CHAPTER VI

SUMMARY

The objectives of this study were to evaluate the genetic and environmental sources of variation in height, diameter, and volume per tree. Ten-year data from open-pollinated progeny of random trees from 12 natural stands in Tennessee and Kentucky were analyzed. The data were measurements of individual progeny from 128 half-sib families outplanted at three locations in Tennessee.

Individual location analyses indicated that variance components for each source of variation, expressed as a percent of the total variation, were relatively similar from location to location. However, the family-within-stand ($s^2_{F/S}$) variance component was consistently lower at the Camp York location, probably due to the site heterogeneity evident at this location.

Generally, the variance component in the combined location analyses are similar in magnitude to those in the individual analyses. Direct comparisons between the two types of analyses are not strictly valid since the combined analyses are based on different number of stands and families-within-stands than those of the individual location analyses.

The two levels of genotype × environment interactions, location by stand and location by family-within-stands accounted for only a small amount of the phenotypic variation; the sum of the interaction components accounted for less than 1.5 percent of the phenotypic variance.

When compared with two- and five-year estimates, ten-year heritability estimates decreased at Camp York and the Highland Rim locations, and have stayed the same or increased at the Ames Plantation location. Heritability estimates derived from the combined location analyses are in close agreement with the average of estimates derived from the three individual locations; average heritability estimates from the individual location analyses are within a standard error of the heritability estimate from the combined location analyses.

Expected gains were computed on the basis of a hypothetical roguing of each plantation using three selection schemes. Gains from a three-stage system, which include stand, family-within-stand, and within-family selection, ranged from 16.1 to 22.4 percent over mean unselected stem volume. Gains from two-stage selection provided the most gain at all locations. Gains ranged from 22.2 to 30.6 percent over mean unselected stem volume. Mass selection resulted in gains ranging from 6.1 to 10.3 percent.

Two of the plantations, Ames Plantation and Camp York, were rogued using the two-stage selection system. Expected gains were 29.9 percent at Ames Plantation and 18.0 percent at Camp York above the mean unselected population.

Recommendations for future breeding efforts would be to establish progeny tests from either control-pollination or open-pollination of trees remaining at Ames Plantation and Camp York. The control-pollinated progeny would be the most desirable since information about specific combining ability can be obtained. Also control-pollinated progeny would provide trees for selection in second generation orchards of known pedigree. This information would be valuable in order to avoid inbreeding in future generations. However, control-pollination requires extra expense and time to accomplish. Although less desirable, open-pollinated progeny could be used to obtain information concerning general combining ability and provide material for future generations of seed orchards.

Future efforts should examine other traits, such as tree form, straightness, and branching habit, that would make Virginia pine a more desirable species for commercial and strip-mine reclamation applications.

LITERATURE CITED

LITERATURE CITED

Allard, R. W. 1961. Relationship between genetic diversity and consistency of performance in different environments. Crop Sci., 1:127-133.

Allen, J. C. 1961. Site index relationships of loblolly, shortleaf, and Virginia pines of the Cumberland Plateau and Sand Mountain. Unpublished report by Tenn. Valley Auth. Div. For. Rel. Norris, Tennessee. 15 pp.

Barker, J. A. 1973. Location differences and their influence on heritability estimates and gain predictions for 10-year-old loblolly pine. Proc. 12th South. Conf. For. Tree Imp. pp. 38-45.

Barr, A. J., and J. H. Goodnight. 1976. A guide to the supplementary procedure library for the statistical analysis system 1976 version. Student Supply Stores, North Carolina State University, Raleigh, North Carolina.

Brown, C. L., and R. E. Goddard. 1959. Variation in nursery-grown seedlings from individual mother trees in a seed-producing area. Proc. 5th South. Conf. For. Tree Imp. pp. 68-76.

Campbell, R. K. 1972. Genetic variability in juvenile height-growth of Douglas fir. Silvae Genetica 21:126-129.

Ceck, F. C. 1963. Breeding methods in tree improvement. Proc. 7th South. Conf. For. Tree Imp. pp. 27-30.

Eberhart, S. A., and W. A. Russell. 1966. Stability parameters for comparing varieties. Crop Sci. 6:36-40.

Evans, R. M. 1971. Estimates of genetic and environmental variances and heritabilities for natural populations of Virginia pine (Pinus virginiana Mill.). Master's thesis The University of Tennessee, Knoxville, Tennessee. 96 pp.

Evans, R. M., and E. Thor. 1971. Estimates of heritabilities and genetic gains for populations of Virginia pine. Proc. 11th South. Conf. For. Tree Imp. pp. 133-141.

Falconer, D. S. 1960. Introduction to Quantitative Genetics. The Ronald Press Company, New York. 365 pp.

Fenneman, N. M. 1938. Physiography of Eastern United States. McGraw Hill Book Company, New York. 714 pp.

Finlay, K. W., and G. N. Wilkenson. 1963. The analysis of adaptation in a plant breeding program. Australia Jour. Agri. Res. 14:742-754.

Flowers, R. L. 1964. Soil Survey of Fayette County, Tennessee. USDA Series 1960, No. 13. 98 pp.

Fowells, H. A. 1965. Silvics of Forest Trees of the United States. USDA For. Ser. Handbook 271. 762 pp.

Franklin, E. C. 1971a. Estimating frequency of natural selfing based on segregating mutant forms. Silvae Genetica 20:193-194.

Franklin, E. C. 1971b. Estimates of frequency of natural selfing and of inbreeding coefficients in loblolly pine. Silvae Genetica 20:194-195.

Genys, J. B. 1966. Geographic variation in Virginia pine. Silvae Genetica 15:72-76.

Genys, J. B., J. W. Wright, and D. C. Forbes. 1974. Intraspecific variation in Virginia pine, results of a provenance trail in Maryland, Michigan, and Tennessee. Silvae Genetica 23:99-104.

Goebel, N. B., and R. M. Mathews. 1966. Volume tables for small diameter loblolly, shortleaf, and Virginia pine in the upper South Carolina Piedmont. Clemson Univ. For. Res. Series 7.

Hubbard, E. H., B. L. Matzer, and M. E. Austin. 1950. Soil Survey of Cumberland County, Tennessee. USDA Series 1938, No. 25. 107 pp.

King, J. P. 1965. Seed source × environment interactions in Scotch pine. I. Height growth. Silvae Genetica 14:105-115.

Kormanik, P. P. 1966. Predicting site index of Virginia, loblolly, and shortleaf pine in the Virginia Piedmont. USDA For. Ser. Res. Paper SE-20. 14 pp.

Kundt, J. F. 1972. A diallel analysis in Virginia pine (Pinus virginiana Mill.). Ph.D. dissertation. North Carolina State University, Raleigh, North Carolina. 86 pp.

Meier, R. J., and J. F. Goggans. 1977. Heritabilities of height, diameter, and specific gravity of young Virginia pine. For. Sci. 23:450-456.

Morgenstern, E. K., and A. H. Teich. 1969. Phenotypic stability of height growth of jack pine provenances. Can. Jour. Genet. Cytol. 11:110-117.

Namkoong, G. 1966. Inbreeding effects on estimation of genetic additive variance. For. Sci. 12:8-13.

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

Namkoong, G., E. B. Snyder, and R. W. Stonecypher. 1966. Heritability and gains concepts for evaluating breeding systems such as seedling orchards. Silvae Genetica 15:76-83.

Namkoong, G., R. A. Uranis, and R. R. Silen. 1972. Age-related variation in genetic control of height growth in Douglas fir. Theoretical and Applied Genetics 42:151-159.

North Carolina State University-Industry Cooperative Tree Improvement Program. 1977. 22nd Annual Report. North Carolina State University, Raleigh, North Carolina. 72 pp.

Owino, F., and B. J. Zobel. 1977. Genotype × environment interaction and genotypic stability in loblolly pine. I. General introduction and description of the experiment. Silvae Genetica 26:18-21.

Plaisted, R. L., and L. C. Peterson. 1959. A technique of evaluating the ability of selections to yield consistently in different seasons or locations. Amer. Potato Jour. 36:381-385.

Reich, V. H., and R. E. Atkins. 1970. Yield stability of four population types of grain sorghum, *Sorghum bicolor* (L.) Moench, in different environments. Crop Sci. 10:511-517.

Rink, G. 1974. Variation in open-pollinated progeny plantations of Virginia pine (*Pinus virginiana* Mill.). Ph.D. dissertation. The University of Tennessee, Knoxville, Tennessee. 143 pp.

Rink, G., and E. Thor. 1975. Variance components and gains in volume growth of Virginia pine (Pinus virginiana Mill.). Silvae Genetica 25:17-22.

Schultz, E. F., Jr. 1955. Rules of thumb for determining expectations of mean squares in analysis of variance. Biometrics 11:123-135.

Smalley, G. W., and K. Pierce. 1972. Yellow-poplar, loblolly pine, and Virginia pine compared in Cumberland Plateau plantations. USDA For. Ser. Res. Note SO-141.

Snyder, E. B. 1969. Parental selection versus half-sib selection of longleaf pine. Proc. 10th South. Conf. For. Tree Imp. pp. 84-88.

Sokal, R. R., and F. J. Rohlf. 1973. Introduction to Biostatics. W. H. Freeman and Company, San Francisco. 368 pp.

Squillace, A. E., and G. W. Bengston. 1961. Inheritance of gum yield and other characteristics of slash pine. Proc. 6th South. Conf. For. Tree Imp. pp. 85-96.

Squillace, A. E., R. T. Bingham, G. Namkoong, and H. F. Robinson. 1967. Heritability of juvenile growth rate and expected gain from selection in western white pine. Silvae Genetica 16:1-6.

Steinhoff, R. J., and R. J. Hoff. 1971. Estimates of the heritability of height growth in western white pine based on parent-progeny relationships. Silvae Genetica 20:5-6.

Stonecypher, R. W. 1966. Estimates of genetic and environmental variance and covariance in a natural population of loblolly pine (Pinus taeda L.). International Paper Company Tech. Bull. 5. 128 pp.

Thor, E. 1964. Variation of Virginia pine. Part I. Natural variation in wood properties. Jour. Forestry 62:258-262.

Toda, R. 1964. A brief review and conclusions of the discussion on seed orchards. Silvae Genetica 13:1-3.

Wells, O. O., and P. C. Wakeley. 1966. Geographic variation in survival, growth and fusiform rust infection of planted loblolly pine. For. Sci. Monograph 11. 40 pp.

Wricke, G. 1962. Über eine Methode zur Erfassung der Öklogischen Streubreite in Feldversuchen. Zeitschrift fur Pflanzenzuchtung. 47:92-96.

Wright, J. W. 1973. Genotype-environment interaction in north central United States. For. Sci. 19:113-123.

Wright, J. W., and W. I. Bull. 1963. A one-parent progeny test and seed orchard for the improvement of red pine. Jour. Forestry 61:747-750.

Yates, F., and W. G. Cochran. 1938. The analysis of groups of experiments. Jour. Agri. Sci. Camb. 28:556-580.

APPENDIX

Table A-1. Average Stand and Family-Within-Stand Height (feet) at Ten Years for Virginia Pine in Three Test Plantations.

Stand	Family	Plantations Ames	 Camp York	 Highland Rim
1	1	16		23
	2			24
	3			24
	4			24
	6			24
	7	17		24
	9	19		25
	12	18		24
	13			25
	15			26
Mean Stand Height		18		24
2	1	18	24	24
	3	18	23	24
	4			24
	5			23
	7	16	21	23
	8	16	23	22
	9	16	21	23
	10	16	21	22
	11	16	23	23
	12		23	23
	14	16	22	24
Mean Stand Height		17	22	23
3	2		25	24
	3			25
	4	16	22	23
	5		23	23
	6	17	22	22
	7	18	24	23
	8	17	22	23
	9	17	23	24
	10	18	24	24
	12	19	24	25
	14			24
	15	17	24	24
Mean Stand Height		17	23	24

Table A-1 (continued)

			Plantations	
Stand	Family	Ames	Camp York	Highland Rim
4	1	18	24	24
	2	17	23	24
	3			24
	4	17	23	23
	5	18	23	24
	6	17	24	24
	7			24
	8	19	25	25
	9			25
	10	17	23	24
	12	18	23	25
	13	18	24	24
	14	19	24	24
Mean Stand Height		18	24	24
6	1			21
	2		24	24
	3	17	23	23
	4	17	23	23
	5	16		
	6	18	23	23
	7	16	23	22
	8	18	23	24
	9		23	23
	10	17	23	24
	11	17	23	22
	12	19	24	25
	14	18		24
	15			23
Mean Stand Height		17	23	23
7	1	17	24	23
	4	19	24	24
	5		23	22
	6	18	24	22
	8	17	23	24
	10	18	24	24
	11	18	24	24
	13	19	24	24
	14	20	26	25
	15	18	24	24
Mean Stand Height		18	24	24

Table A-1 (continued)

Stand	Family	Plantations		
		Ames	Camp York	Highland Rim
8	1			24
	3	17	23	23
	4		24	24
	5	18	24	24
	6	18	24	23
	8		24	24
	9	17	23	23
	10	17	23	23
	11			24
	12	18		23
	13	18	24	23
	14	17	22	22
	15	18	—	24
Mean Stand Height		18	23	24
9	1	18	24	25
	3			23
	4	18	24	23
	5	18	25	24
	6	17	24	24
	7		23	22
	8			22
	9	16	22	23
	10	17	23	23
	11			22
	12	18	24	24
	13	—	24	24
Mean Stand Height		18	24	23
10	2	19	25	25
	3	19	23	24
	4	20	24	25
	5	19	24	24
	6	19	23	25
	9	19	25	25
	10	18	24	24
	11			25
	14	19	24	25
	15	19	23	25
Mean Stand Height		19	24	25

Table A-1 (continued)

Stand	Family	Ames	Plantations Camp York	Highland Rim
11	1			25
	2	18		24
	3	19	23	25
	4			24
	5	18	22	23
	6	18	24	24
	7			25
	8			25
	9	18		24
	10	18	23	23
	11	17	24	24
	14	19	25	24
	15	17	23	24
Mean Stand Height		18	24	24
12	5			25
	6			24
	7			25
	10			24
	12			24
	14			24
	15			24
Mean Stand Height				24
13	1	19	23	24
	2	19	24	24
	3	18	24	24
	4	18	24	25
	6	17	22	[illegible]
	7			
	9			
	11	17	22	
	13			
	14			
	15			
Mean Stand Height		18		

Table A-2. Average Stand and Family-Within-Stand Diameter at Breast Height (inches) at Ten Years for Virginia Pine Progeny in Three Test Plantations.

Stand	Family	Ames	Plantations Camp York	Highland Rim
1	1	3.0		3.7
	2			3.8
	3			3.8
	4			4.2
	6			4.0
	7	3.6		4.2
	9	3.9		4.3
	12	3.6		4.1
	13			4.5
	15			4.4
Mean Stand Diameter		3.6		4.1
2	1	3.3	4.0	4.0
	3	3.2	3.6	3.7
	4			4.0
	5			3.4
	7	3.3	3.3	3.6
	8	3.1		3.3
	9	3.4	3.5	3.6
	10	3.1	3.4	3.5
	11	3.0	3.9	3.5
	12		3.8	3.6
	14	3.3		3.7
Mean Stand Diameter		3.2	3.6	3.6
3	2		4.4	[illegible]
	3			[illegible]
	4	3.1	3.7	[illegible]
	5		4.0	[illegible]
	6	3.2	[illegible]	[illegible]
	7	3.6	[illegible]	[illegible]
	8	3.4	[illegible]	[illegible]
	9	3.4	[illegible]	[illegible]
	10	[illegible]	[illegible]	[illegible]
	12	[illegible]	[illegible]	[illegible]
	14	[illegible]	[illegible]	[illegible]
	15	3.[illegible]	[illegible]	[illegible]
Mean Stand Diameter		3.4	[illegible]	[illegible]

Table A-2 (continued)

Stand	Family	Ames	Plantations Camp York	Highland Rim
4	1	3.6	3.9	3.8
	2	3.3	3.8	3.8
	3			4.2
	4	3.2	3.6	3.6
	5	3.5	3.9	4.1
	6	3.2	3.9	4.1
	7			4.2
	8	3.9	4.7	4.5
	9			3.9
	10	3.4	4.0	3.7
	12	3.7	3.9	4.0
	13	3.4	4.0	3.7
	14	3.6	4.1	3.9
Mean Stand Diameter		3.5	4.0	4.0
6	1			3.7
	2		4.2	4.0
	3	3.4	4.0	7.8
	4	3.3	3.8	3.6
	6	3.7	4.2	3.8
	7	3.3	3.8	3.5
	8	3.6	4.1	3.8
	9		4.4	3.9
	10	3.4	3.8	3.9
	11	3.5	4.1	3.8
	12	3.6	4.3	4.3
	14	3.6		3.8
	15			3.8
Mean Stand Diameter		3.5	4.1	4.1
7	1	3.5	4.2	3.8
	4	3.7	4.3	3.
	5	3.1	3.9	[illegible]
	6	3.5	4.4	[illegible]
	8	3.3	4.2	[illegible]
	10	3.6	3.8	[illegible]
	11	3.5	4.3	[illegible]
	12			[illegible]
	13	3.7	4	[illegible]
	14	4.1	[illegible]	[illegible]
	15	3.8	[illegible]	[illegible]
Mean Stand Diameter		3.6	[illegible]	[illegible]

Table A-2 (continute)

Stand	Family		Plantations	
		Ames	Camp York	Highland Rim
8	1			3.4
	3	3.3	4.0	3.7
	4		4.4	3.9
	5	3.6	4.1	3.8
	6	3.4	4.1	3.8
	8		4.4	4.0
	9	3.3	3.8	3.6
	10	3.3	3.7	3.5
	11			4.1
	12	3.4		
	13	3.4	4.1	3.5
	14	3.2	3.5	3.3
	15	3.4		3.8
Mean Stand Diameter		3.4	4.0	3.7
9	1	3.5	4.1	4.0
	3			3.6
	4	3.6	4.2	3.8
	5	3.3	4.4	3.7
	6	3.3	4.0	3.8
	7	3.6	4.0	3.5
	8			3.9
	9	3.3	4.0	3.7
	10	3.2	3.9	3.4
	11			3.4
	12	3.8	4.2	4.1
	13			3.7
Mean Stand Diameter		3.4	4.1	3.7
10	2	4.0	4.6	4.3
	3	3.7	4.0	4.1
	4	4.2	4.4	4.3
	5	3.8	4.2	4.1
	6	3.8	4.0	4.2
	9	3.6	4.4	4.
	10	3.8	4.3	
	11			
	14	3.8	4.4	
	15	4.0	4.4	
Mean Stand Diameter		3.9	4.3	

Table A-2 (continued)

			Plantations	
Stand	Family	Ames	Camp York	Highland Rim
11	1			4.2
	2	3.7		3.9
	3	3.9	4.1	4.4
	4			4.1
	5	3.7	4.1	3.9
	6	3.8	4.4	4.1
	7			4.1
	8			4.2
	9	3.9	4.5	4.1
	10	3.6	4.2	3.8
	11	3.5	4.4	4.0
	14	3.8	4.2	4.1
	15	3.5	3.8	3.9
Mean Stand Diameter		3.7	4.2	3.8
12	5			4.3
	6			4.0
	7			4.1
	10			3.9
	12			4.0
	14			4.0
	15			3.7
Mean Stand Diameter				4.0
13	1	3.6		4.0
	2	3.6	4.0	3.9
	3	3.5	4.1	3.7
	4	3.6	4.3	4.2
	6	3.2	3.5	3.6
	7			3.9
	9		4.2	3.8
	11	3.2	3.6	3.8
	13			3.9
	14			4.0
	15			3.9
Mean Stand Diameter		3.5	3.9	3.9

Table A-3. Average Stand and Family-Within-Stand Volume Growth (cubic feet per tree) at Ten Years for Virginia Pine Progeny in Three Test Plantations.

			Plantations	
Stand	Family	Ames	Camp York	Highland Rim
1	1	0.387		0.640
	2			0.844
	3			0.851
	4			0.993
	6			0.932
	7	0.563		0.914
	9	0.702		0.917
	12	0.604		0.812
	13			1.171
	15			1.182
Mean Stand Volume		0.623		0.926
2	1			0.772
	2	0.491		
	3	0.471	0.805	0.683
	4		0.910	0.910
	5			0.680
	7	0.470	0.599	0.615
	8	0.404	0.677	0.564
	9	0.467	0.693	0.631
	10	0.388	0.660	0.591
	11	0.390	0.889	0.673
	12		0.820	0.783
	14	0.443	0.741	0.679
Mean Stand Volume		0.440	0.755	0.681
3	2		1.123	1.002
	3			1.108
	4	0.402	0.757	0.599
	5		0.912	0.862
	6	0.432	0.729	0.554
	7	0.567	0.903	0.731
	8	0.504	0.853	0.741
	9	0.491	0.807	0.678
	10	0.528	0.774	0.695
	12	0.686	0.957	0.901
	14			0.835
	15	0.491	0.988	0.713
Mean Stand Volume		0.512	0.880	0.785

Table A-3 (continued)

Stand	Family		Plantations	
		Ames	Camp York	Highland Rim
4	1	0.597	0.883	0.748
	2	0.467	0.810	0.710
	3			1.045
	4	0.450	0.756	0.659
	5	0.540	0.887	0.824
	6	0.467	0.912	0.788
	7			1.031
	8	0.723	1.268	1.063
	9			0.905
	10	0.495	0.909	0.725
	12	0.617	0.897	0.809
	13	0.535	0.968	0.764
	14	0.614	1.003	0.845
Mean Stand Volume		0.550	0.929	0.840
6	1			0.748
	2		1.039	0.968
	3	0.491	0.935	0.736
	4	0.542	0.824	0.618
	6	0.578	1.002	0.782
	7	0.458	0.827	0.646
	8	0.564	0.932	0.769
	9		1.110	0.977
	10	0.491	0.814	0.716
	11	0.503	0.936	0.728
	12	0.593	1.076	0.917
	14	0.578		0.710
	15			0.779
Mean Stand Volume		0.523	0.950	0.776
7	1	0.508	1.027	0.776
	4	0.635	1.054	0.830
	5	0.403	0.858	0.617
	6	0.527	1.101	0.763
	8	0.487	1.010	0.778
	10	0.565	0.829	0.735
	11	0.555	1.055	0.807
	13	0.629	1.081	0.855
	14	0.781	1.316	1.070
	15	0.620	1.061	0.858
Mean Stand Volume		0.571	1.039	0.809

Table A-3 (continued)

Stand	Family	Plantations Ames	 Camp York	 Highland Rim
8	1			0.741
	3	0.466	0.907	0.700
	4		1.126	0.978
	5	0.549	0.996	0.812
	6	0.518	0.958	0.752
	8		1.109	0.986
	9	0.459	0.839	0.652
	10	0.450	0.769	0.617
	11			0.965
	12	0.534		0.636
	13	0.528	0.954	0.711
	14	0.437	0.681	0.565
	15	0.521		0.686
Mean Stand Volume		0.496	0.926	0.754
9	1	0.558	0.934	0.817
	3			0.692
	4	0.561	1.038	0.776
	5	0.486	1.118	0.795
	6	0.477	0.921	0.746
	7	0.545	0.930	0.720
	8			0.819
	9	0.451	0.897	0.700
	10	0.438	0.876	0.630
	11			0.638
	12	0.620	1.031	0.877
	13			0.765
Mean Stand Volume		0.517	0.968	0.748
10	2	0.737	1.232	0.997
	3	0.640	0.911	0.845
	4	0.824	1.222	1.049
	5	0.682	1.030	0.909
	6	0.656	0.913	0.878
	9	0.617	1.142	0.909
	10	0.677	1.061	0.871
	11			1.124
	14	0.696	1.123	1.024
	15	0.724	1.123	0.989
Mean Stand Volume		0.695	1.084	0.960

Table A-3 (continued)

Stand	Family		Plantations	
		Ames	Camp York	Highland Rim
11	1			1.011
	2	0.618		0.742
	3	0.687	0.989	0.931
	4			0.988
	5	0.605	0.929	0.787
	6	0.621	1.147	0.877
	7		0	0.966
	8			1.034
	9	0.698	1.195	0.906
	10	0.558	0.995	0.744
	11	0.521	1.092	0.788
	14	0.633	1.066	0.865
	15	0.534	0.849	0.754
Mean Stand Volume		0.608	1.033	0.876
12	5			1.116
	6			0.947
	7			1.018
	10			0.867
	12			0.906
	14			0.926
	15			0.791
Mean Stand Volume				0.938
13	1	0.594	0.870	0.802
	2	0.582	0.914	0.805
	3	0.570	0.978	0.747
	4	0.584	1.102	0.900
	6	0.435	0.700	0.614
	7			0.900
	9		0.997	0.892
	11	0.432	0.754	0.650
	13			0.866
	14			0.946
	15			0.864
Mean Stand Volume		0.533	0.902	0.817

VITA

The author was born in Waynesboro, Tennessee, on May 27, 1954. In 1960 he moved with his parents to Nashville, Tennessee, where he attended elementary school and graduated from McGavock Comprehensive High School in 1972. He entered The University of Tennessee at Martin in 1972, transferred to The University of Tennessee at Knoxville in 1974, and received the degree of Bachelor of Science in Forestry in 1976.

In the fall of 1976 he entered The University of Tennessee Graduate School to begin work towards a Master's Degree in Forestry, specializing in tree improvement.

In December of 1977, he accepted the position of Seed Orchard Supervisor for Champion International Corporation. Presently, he is Research and Development Supervisor for Champion.

David Todd is married to the Former Judy Rainwater and they have one daughter, Carrie Elizabeth.

He is a member of the Society of American Foresters, North Carolina Forestry Association, and Xi Sigma Pi.