June 8, 1971

157

To the Graduate Council:

I am submitting herewith a thesis written by Richard Martin Evans, entitled "Estimates of Genetic and Environmental Variances and Heritabilities for Natural Populations of Virginia Pine (Pinus Virginiana Mill.)." I recommend that it be accepted for nine quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

Major Professor

We have read this thesis and recommend its acceptance:

Accepted for the Council:

Vice Chancellor for
Graduate Studies and Research

# ESTIMATES OF GENETIC AND ENVIRONMENTAL VARIANCES AND HERITABILITIES FOR NATURAL POPULATIONS OF VIRGINIA PINE (*PINUS VIRGINIANA* MILL.)

---

A Thesis

Presented to

the Graduate Council of

The University of Tennessee

---

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

---

by

Richard Martin Evans

August 1971

ACKNOWLEDGMENTS

The author gratefully expresses appreciation to Dr. Eyvind Thor of the Department of Forestry for his invaluable assistance and counsel as major professor. Appreciation is also extended to Dr. Vernon Reich of the Department of Agronomy and Dr. H. R. DeSelm of the Department of Botany for the critical reading of the manuscript, and serving as committee members.

The writer gratefully acknowledges the help of Mrs. Barbara Bridges of the University of Tennessee Computer Center for her assistance in computer analysis.

Appreciation is extended to the members of the Kentucky-Tennessee Section of the Society of American Foresters who sponsored this study. Special recognition is due the Tennessee Valley Authority and Dr. Kingley Taft for growing the test site seedlings, also to Dr. J. F. Goggans of Auburn University, Jim Hill of Hiwassee Land Company, W. T. Plass of the United States Forest Service, and James Warmbrod, Jim Dring, and P. J. Huffman of the University of Tennessee for their assistance in management of test plantings and collection of data.



984213

## ABSTRACT

The study was undertaken to determine the genetic and environmental variance and narrow sense heritability for the natural population of Virginia pine (Pinus virginiana Mill.) in Kentucky and Tennessee. Open-pollinated progeny from 3 to 13 families each of 13 natural stands were planted in 10 tree row plots at 6 test locations to furnish the test data.

An IBM program was developed to perform an analysis of variance and estimate components of variance. Characteristics analyzed were first-year height and second-year height, branch length, branch diameter, and stem diameter. Each site was analyzed separately.

There was a significant difference in second-year height and stem diameter among stands at all test sites. In second-year stand mean heights at all test sites, stands from the Great Valley physiographic source tended to rank higher than the other physiographic sources.

Variance components values were highly variable among test sites and fluctuated positively with the mean values of each site. Variance components were relatively the same size at each test site for each of the second-year characteristic measured because of the close positive correlation among these characteristics.

Heritability of first-year height and second-year height, branch length, branch diameter, and stem diameter averaged 0.28, 0.28, 0.21, 0.16, and 0.20, respectively, among all test sites. The highest heritability value (0.48) was for second-year height at the Highland Rim test site.

It was estimated that a genetic gain of 25 percent could be made by the selection of the best 45 individual of the best 45 families of the best seven stands at the Highland Rim test site. If stand selection was not practiced, a gain of 21 percent was estimated. Gain from mass selection was estimated to be only 5 percent.

TABLE OF CONTENTS


| CHAPTER | | PAGE |
|---|---|---|
| I. | INTRODUCTION | 1 |
| II. | LITERATURE REVIEW | 5 |
| | Heritability | 5 |
| | The Reliability of Heritability Estimates | 8 |
| | Calculation of Heritabilities | 12 |
| | Experimental Design for Estimating Heritabilities | 23 |
| III. | MATERIALS AND METHODS | 26 |
| | Parent Populations | 26 |
| | Selection of stands | 26 |
| | History and description of stands | 28 |
| | Parent trees | 28 |
| | Planting Material | 28 |
| | Seed collection | 28 |
| | Seedling production | 31 |
| | Descriptions of Test Sites | 33 |
| | Ames Plantation | 34 |
| | Highland Rim | 34 |
| | Camp York | 35 |
| | Decatur Test | 37 |
| | Vina | 38 |
| | Pineville Test Site | 39 |

CHAPTER PAGE

Experimental Design. . . . . 41

Measurements . . . . . 42

Statistical Analysis . . . . . 42

Estimates of Components at Variance and Heritability . . . . . 46

IV. RESULTS AND DISCUSSION . . . . . 47

Mean Values. . . . . 47

Analysis of Variance Mean Squares. . . . . 53

Components of Variance . . . . . 62

Estimates of Heritability. . . . . 69

Estimates of Genetic Gains . . . . . 74

V. SUMMARY AND CONCLUSIONS. . . . . 81

LITERATURE CITED . . . . . 84

APPENDIX . . . . . 91

VITA . . . . . 96

LIST OF TABLES


| TABLE | | PAGE |
|---|---|---|
| 1. | Location of Sample Plots, Site Indexes, and Average Values for D.B.H. and Age. Averages are Based on 15 Trees per Stand. . . | 29 |
| 2. | Number of Families per Stand Planted at Each Test Site. . . . . | 32 |
| 3. | Form of Analysis of Variance Used at Each Test Site. . . . . | 44 |
| 4. | Mean Values for First-Year Height and Second-Year Heights, Branch Length, Branch Diameter, and Stem Diameter by Individual Test Sites. . . . . | 48 |
| 5. | Mean Second-Year Height Among Common Families Within Ten Common Stands at All Test Sites. . . . . | 49 |
| 6. | Ranking of Second-Year Mean Height Within Each Test Site. . . . . | 51 |
| 7. | Frequency that any Stand of Each Physiographic Source Ranked in Second-Year Mean Stand Height Across All Test Sites. . . . . | 52 |
| 8. | Mean Squares and Degrees of Freedom for Analysis of Variance of First-Year Heights for the Ames, Highland Rim, and Camp York Test Sites. . . . . | 54 |

TABLE PAGE

9. Mean Squares and Degrees of Freedom for Analysis of Variance of First-Year Heights for the Decatur, Vina, and Pineville Test Sites. . . . . 55

10. Mean Squares and Degrees of Freedom for Analysis of Variance of Second-Year Height, Branch Length, Branch Diameter, and Stem Diameter at the Ames Plantation Test Site. . . . . 56

11. Mean Squares and Degrees of Freedom for Analysis of Variance of Second-Year Height, Branch Length, Branch Diameter, and Stem Diameter at the Highland Rim Test Site . . . . . 57

12. Mean Squares and Degrees of Freedom for Analysis of Variance of Second-Year Height, Branch Length, Branch Diameter and Stem Diameter at the Camp York Test Site . . . . . 58

13. Mean Squares and Degrees of Freedom for Analysis of Variance of Second-Year Height, Branch Length, Branch Diameter, and Stem Diameter at the Decatur Test Site . . . . . 59

TABLE PAGE

14. Mean Squares and Degrees of Freedom for Analysis of Variance of Second-Year Height, Branch Length, Branch Diameter, and Stem Diameter at the Vina Test Site . . . 60

15. Mean Squares and Degrees of Freedom for Analysis of Variance of Second-Year Height, Branch Length, Branch Diameter, and Stem Diameter at the Pineville Test Site . . . . . 61

16. Estimates of Components of Variances and Standard Error of Family Within Stand Variance for First-Year Seedlings Heights by Individual Test Sites. . . . . 63

17. Estimates of Components of Variances and Standard Error of Family Within Stand Variance for Second-Year Seedlings Heights by Individual Test Sites. . . . . 64

18. Estimates of Variances and Standard Error of Family Within Stand Variance for Second-Year Branch Length by Individual Test Sites. . . . . 65

19. Estimates of Components of Variances and Standard Error of Family Within Stand Variance for Second-Year Branch Diameter by Individual Test Sites. . . . . 66

TABLE PAGE

20. Estimates of Variances and Standard Error of Family Within Stand Variance for Second-Year Stem Diameter by Individual Test Sites . . . . . 67

21. Coefficients of Variation for First- and Second-Year Height at Each Test Site. . . . . 69

22. Heritability Estimates of First-Year and Second-Year Height, Second-Year Branch Length and Diameter, and Second-Year Stem Diameter for Each Test Site. . . . . 72

23. Number of Stands, Families, and Individuals Selected and Percent and Selection Intensity for Families and Within Families Selections of Scheme I and Scheme II at the Highland Rim Test Site . . . . . 77

24. Estimates of Components of Variances and Mean of Second-Year Heights for All Stands and the Selected Seven Best Stands at the Highland Rim Test Site. . . . . 78

25. Gains from Family and Within Family Selection and Estimated Mean Heights of Two-Year-Old Seedlings at the Highland Rim Test Site . . . . . 79

26. Second-Year Mean Heights and Stand Mean Heights at Each Test Site. . . . . 92

LIST OF FIGURES

FIGURE PAGE

1. Locations of Stands and Test Sites . . . . . 27

2. Excellent Survival and Growth was Obtained Following Two Growing Seasons at the Highland Rim Test Site. This is the Most Homogeneous Site in the Study, With the Tallest Mean First- and Second-Year Height . . . . . 36

3. Poor Growth was Obtained Following Two Growing Seasons at the Pineville Test Site. This planting was Established on Spoils of a Strip Mine. . . . . 40

# CHAPTER I

## INTRODUCTION

In 1962 Dr. Eyvind Thor of the University of Tennessee Forestry Department proposed to the members of the Kentucky-Tennessee Section of the Society of American Foresters a study to determine the natural variation in Virginia pine (Pinus virginiana Mill.). The Section agreed to sponsor the study and several members of the Section pledged assistance in the study.

There were two main objectives in the proposed study: to determine the natural variation in wood properties and to determine the genetic variation in open-pollinated progenies, in the natural populations of Virginia pine found in Kentucky and Tennessee. Results of the first phase have appeared (Thor, 1964). This thesis presents a portion of the results of the second phase of the study which has the following objectives:

1. To develop the analytical methods to calculate genetic variation for this study.
2. To calculate the genetic, environment, and genetic-environment interaction components of variance for characteristics measured in the first and second year after out-planting.
3. To calculate heritabilities for all characteristics measured.

4. To demonstrate methods for estimating gains made from selection of the best stands, families, and individuals.

Of all the southern pines, Virginia pine is the most desirable for pulping by the groundwood (mechanical) processes (Thor, 1964). It gives high yields of fiber per unit volume of wood. The fiber is especially desirable for making newsprint because of thin pliable cell walls and the low amounts of extractives in the wood. Paper companies have already planted thousands of acres of marginal lands to Virginia pine.

Virginia pine, also commonly known as Jersey pine, North Carolina pine, and spruce pine, has needles in twos about two inches long yellow-green, stout, and usually twisted. The bark is usually thin and smooth in younger trees and becomes scaly-plated in the older and slower growing trees. Virginia pine is a small often unkempt-appearing tree with persistent branches and shallow root system (Harlow and Harlow, 1958). It is a very precocious species, often producing cones as early as five years of age, but in dense stands cone production is delayed often a as long as fifty years (Slocum and Miller, 1953).

Virginia pine grows throughout the northern parts of the Piedmont Physiographic Province, the foothills of the Appalachian mountains and at low elevations from central Pennsylvania southward to northeastern Mississippi, Alabama,

and northern Georgia. The species range eastward to the western edges of the Coastal Plain, as far north as Long Island, New York, and extends west into Ohio, southern Indiana, and central and western Kentucky and Tennessee (Sargent, 1935; Fowells, 1965).

Characterized as being an aggressive pioneering species, Virginia pine is typically found growing in pure stands on what were once severely eroded fields. It grows well on a wide variety of soils derived from crystalline rocks, sandstones and shales, and to a lesser extent, from limestone (McIntyre, 1933). The species grows best on clay, loam, or sandy loam soil but generally does poorly on shaly and very sandy soils (Sterrett, 1911). It will thrive in moderately well-drained to well-drained soils, and is tolerant of wet sites and impeded drainage than are pitch pine (Pinus rigida Mill.) and loblolly pine (Pinus taeda L.). Virginia pine generally tolerates soil acidities ranging from a pH of 4.6 to 7.9 (Potzger, 1931) and develop best at 100 feet to 2,500 feet elevation (Sterrett, 1911).

On poor sites in eastern Tennessee, northern Kentucky, and Alabama, Virginia pine and loblolly pine outgrew shortleaf pine (Pinus echinata Mill.) (Allen, 1961). Buckner planted Virginia, loblolly, and shortleaf pines on eroded abandoned field sites in eastern Tennessee; at age two Virginia and loblolly pines had almost twice the height growth

and survival of shortleaf pine.[1] Allen (1961) found that Virginia pine in the northern portion of the Cumberland Plateau of Tennessee grew better on similar sites in northern Alabama and Georgia than the native source. He suggested that the differences may be due in part to racial, or strain, differences and concluded that further study of the genetics of Virginia pine was warranted.

---

[1]E. Buckner, The effect of fertilizer and mulch on six pines planted at two locations for site stabilization. Unpublished manuscript. University of Tennessee. 21 pp.

# CHAPTER II

# LITERATURE REVIEW

## Heritability

The heritability concept was first developed and applied in the field of animal breeding and later extended to plant breeding. The calculation of heritability is one of the first and most important steps in most breeding programs. Armed with an estimate of heritability, a breeder can choose the most effective breeding method to improve a certain characteristic.

Heritability is defined by Falconer (1967) as: "...the proportion of the total variance that is attributable to the average effects of genes and this is what determines the degree of resemblance between relatives." Zoble (1961) defined heritability in these general terms: "...heritability is the relationship of the heritable portion of the variability of a specific characteristic compared to the total variability of that characteristic." The definition in the "Tree Improvement Glossary" (Snyder, 1959) is 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 either broad sense or narrow sense terms. In the broad sense (H) heritability is the ratio of the genetic variance ($V_g$) and the phenotypic

variance ($V_p$); while heritability in the narrow sense ($h^2$) is the ratio of the additive portion of the genetic variance and the phenotypic variance (Allard, 1966). The genetic variance may be broken into components $V_a$, $V_d$, and $V_i$, representing variation due to additive, dominance, and epistatic gene effects, respectively. The phenotypic variance may further be segregated into $V_e$, $V_g$, and $V_{ge}$, representing variation due to environmental, genetic, and genetic-environmental interaction effects, respectively. Hence, broad and narrow sense heritability can be represented as:

$$\text{Broad Sense Heritability} = H = \frac{V_g}{V_p} = \frac{V_a + V_d + V_i}{V_e + V_g + V_{eg}}$$

$$\text{Narrow Sense Heritability} = h^2 = \frac{V_a}{V_p} = \frac{V_a}{V_e + V_g + V_{eg}}$$

Toda (1957) explains a difference between estimations of heritability in the broad and narrow sense. When the non-additive effect of individuals' genotypes cannot be passed on to their progenies, as is the case in which the material is propagated by sexual means, the term heritability must be employed in the narrow sense. When vegetative propagation is used, the effects of dominance and eqistasis are passed on to the next generation because the genotypes of individuals are transferred unchanged and the term heritability may be employed in its broad sense.

According to Stonecypher (1966) broad sense heritabilities are usually obtained on an individual tree basis

while narrow sense estimates usually are derived on an individual or mean basis. Ceck (1963) stated that the best selection method can be determined by the relative amount of broad or narrow sense inheritance. For example, if the narrow sense heritability figure is high, then the mass selection method of breeding will be most productive. Correspondingly, if the dominance or epistatic variation is high, the greatest gain can be accomplished by intra-specific hybridization approach.

In a genetic study of metric characters, as described by Falconer (1967), the most important function of the heritability estimate is its predictive role. Heritability is, therefore, important in expressing the reliability of the phenotypic value as a guide to the breeding value. With the heritability estimate the breeder can predict how much improvement he can make by selecting superior breeding stock based on the phenotype.

Many heritability estimates of forest trees have been published. Hattemer (1963) listed 19 publications with estimates of heritability in tree populations. In another review of heritabilities Namkoong, et al. (1965) listed five additional publications not reviewed by Hattener. Since the review by Namkoong in 1965, several forest geneticists have computed heritability estimates for characteristics such as height, specific gravity, diameter inside bark, percent extractives, volume, fiber length, winter

damages, and flushing of buds (Farmer and Wilcox, 1966; Stonecypher, 1966; Stonecypher, et al., 1966; Toda, 1967; Farmer, 1968; Dietrichson, 1969; Morgenstern, 1969; Snyder, 1969; and Pederick, 1970).

## The Reliability of Heritability Estimates

Zobel (1961) emphasizes that scattered throughout the literature are "...many biased, and sometimes questionable, measures of inheritance. Such a situation can be misleading and often dangerous, with the result that published figures may be taken, re-cited subsequently many times, and often given significance which the original author never intended."

Stonecypher (1966) also warned that many published heritabilities should be viewed with caution. He stated that few of the studies were to estimate genetic variance, and the majority were installed as a progeny test of selected material or as provenance experiments, where estimates of genetic variances (from such research plantings) rarely were more than a minor part of the overall goal of the study. As a result these designs impose a variety of restrictions and difficulties when heritability data are sought (Hanover and Barnes, 1962).

Goggans (1962) pointed out that progeny tests and seed source studies were less than satisfactory for estimating genetic and environmental variances, especially when variances were divided into several components. This is because such studies were primarily designed to minimize

variance of a mean. While progeny tests or source studies can give estimates of genetic and environmental variances, experiments designed expressly for estimating variance components will generally provide more reliable variances and useful information to the forest geneticist.

Stonecypher (1966) listed the following points which are characteristic of populations of forest trees from which heritability estimates have been reported:

1. The majority of estimates have been obtained from a very restricted selected sample of the population studied.

2. Most estimates are derived from very young material and may be expected to change with time.

3. Estimates obtained from offspring-parent regressions are difficult to interpret for most characteristics since they are usually based on young progeny and mature parents and a characteristic will often differ with age.

4. Estimates have been obtained for only one environment, and therefore no measure of the effect of the genotype-environment interactions on heritability estimates are available.

Namkoong, et al. (1965) also emphasized that an estimate of the genotype-location interaction has not been made for forest trees, but this interaction component is included in the genetic component of the heritability formula. Therefore, most of the estimated heritabilities are of doubtful value. The authors state that half of the published heritabilities were uninterpretable because the composition of either the numerator or the denominator is unclear. In addition, they cite other errors that can make

heritability estimates unreliable:

1. Incorrect analysis of the mating design. For instance, diallels were analyzed as if the same trees did not often serve as both male and female.
2. Lack of true replication.
3. Intentionally selected populations analyzed for the selected trait.
4. Incorrect estimators or assumptions in the analysis.

Heritability estimates are often biased upward when inadequate environmental sampling causes an overstimation of the numerator and underestimation in the denominator. Since many of the heritabilities reported were from small experiments, they were probably not precise, since the error of estimation depends on the number of individual rametes or seedlings per genotype (Namkoong, et al., 1969).

Trousdell, et al. (1963) in an experiment designed to determine inheritance of branch length in loblolly pine (Pinus tadea L.) selected two groups of trees with good and poor branching characteristics. They stated that because the parent trees were selected, the genetic variance among parent trees as a single group tend to be exaggerated. In this design, heritability calculated using variances among parent trees, ignoring grouping, would be overestimated; heritability calculated using variance among parent trees within groups would be underestimated.

Much has been said about the validity of inferences drawn from progeny tests based on juvenile stock. Van Buijtenen (1969) suggests that meaningful results can be

obtained and sound decisions made from progeny tests of trees half-way through their rotation age, but there is considerable change in ranking before that time. Barber (1964) was of the opinion that progenies which achieve dominance at young ages probably would maintain themselves until a point when the first thinning operation takes place.

Wright (1963a) from a study of a Scotch pine (Pinus sylvestris L.) made the following generalizations from three-year old nursery measurements and parental data:

1. Large and statistically significant genetic improvements could be made from family selection for growth rate.
2. Parent-progeny correlations were too low to justify parental selection.
3. Lack of discernible genetic correlation between traits indicated that selection should be for one or two traits only.
4. The ratio of between-stand to within-stand genetic variance varied by trait. In some, stand selection gives the most gain; in others, family selection.

Open-pollinated progenies of Norway spruce (Picea abies L.) have "good" correlation between height at age four and height at age 11. About 80 percent of the seed lots maintained the same relative rank, above or below average, at both ages (Ruden, 1963). Nilsson (1958), working with Scotch pine, found a significant positive correlation ($r = 0.56$) between mother-tree height/diameter ratio and progeny height at age 10, and a significant negative correlation ($r = -0.43$) between mother-tree volume and progeny height.

An analysis of height growth in two plantings of Douglas fir (Pseudotsuga menziesii Mirb.) indicated the existence of time trends in genetic variation among sources (Namkoong, et al., 1970). In the seedling stage (0 to 15-years-old), moderate levels of genetic variation among families within populations existed. However, as the trees entered the grand period of growth (15-years-old) the within population genetic variance declined to zero while between population genetic variance became strongly established. This effect was also noticed in ponderosa pine (Pinus ponderosa Laws.). During the first 25 years family variation decreased from 21 percent to 11 percent while in Douglas fir family variation decreased from 11 percent to five percent in 28 years. The variance among populations of ponderosa pines increased from eight to 38 percent at 25 years while in Douglas fir this variance increased from 6 to 20 percent in 28 years.

Barber, et al. (1955) noted that crown width of 3-year-old slash pine (Pinus elliottii Engelm.) in 1-parent progeny tests showed strong correlation with crown width of mother tree. This relationship held true for both wide-crown and narrow-crown trees.

## Calculation of Heritabilities

There are two general methods used to calculate heritabilities, the regression method and the component method. The regression method expresses the heritability as a

regression coefficient ($b_{po}$). Falconer (1967) presents the regression coefficient as the ratio of the covariance between the parents and the offspring (Cov(P,O)) and the variance of the mid-parents (Var(P)), if both parents are known. The relationship of heritability and the regression coefficient is expressed mathematically as:

$$h^2 = \frac{Cov(P,O)}{Var(P)} = b_{po}$$

The regression method is not very useful for obtaining estimates in forest trees. The difficulty in using this method is that the parent and offspring must be grown under the same environmental conditions. Because of the time required to raise trees to maturity it would be impractical to attempt to raise two generations to maturity for heritability estimates. If one attempts to calculate heritability by regressing field selected parents on their progeny which were grown on a different site, an environmental-genetic interaction effect would be confounded in the covariance component of the regression equation.

Snyder (1969) calculated heritabilities of height growth of long-leaf pine (Pinus palustris Mill.) by the regression method. He adjusted for the difference in environment and age prior to correlation computations. The formula

$$h^2 = 2b \frac{\sigma_x}{\sigma_y} = 2r$$

was used to equate the correlation coefficient (r) to heritability for full sibs. This is a formula equal to that of Falconer's stated earlier (page 13). But as Falconer (1967) indicated the covariance is not a valid measure of Va, moreover, the correlation and regression coefficients are not equal.

Heritabilities as calculated by the component method are the most applicable for forest trees. The basis of the component method is separating the total or phenotypic variance into its components. It is convenient to describe the phenotypic variance in a linear fashion so the expression of any particular character, say yield or height, denoted by A, can be represented as:

$$A = u + a + e + (ae)$$

In the expression the numerical value of the phenotype is visualized as the sum of a general population mean (u), a genotypic effect (a), an environmental effect (e), and an interaction effect (ae) (Allard, 1966).

From the view point of the tree breeder, genotypes must be measured with reference to some particular group of environments, usually the one occurring over a number of locations within some geographical area. Allard (1966) pointed out that experimental measurements of genotypic values, no matter how extensive within practical limits, can only sample the population of environments occuring

within this geographical area. Hence, the plant breeder must usually be satisfied with an attempt to identify the effects of the environmental components that are likely to be important in determining the commercial value of genotypes, for example, geographical location, soil, and disease or other environmental conditions.

Zobel (1961) emphasizes that the estimates apply specifically to conditions existing in the experiment in which they were obtained. In practice, environmental conditions are usually identified with locations. If the analysis is conducted in terms of different locations the phenotypic variance model can be expanded to:

$$A = u + a + r + l + rl + al + ar + arl + e$$

In this expression, u and a remain the population mean and the genotypic effect (Allard, 1966), r and l are direct effects of replication and location, respectively, and e is a composite error term of the remaining effect (including the effect of the plot compared to others in the same replication, error due to sampling among plants within the same family, and errors of measurement). Combination of symbols indicate interactions between or among these main factors; al for example represents the effect of interaction between a specific genotype and location.

A variety of methods and procedures have been published in the forestry literature for obtaining estimates of the

variance components and calculating heritability of forest trees. Depending on the characteristics of the species and the goal and resources of the forest geneticists certain of these methods are more applicable than others. But as pointed out earlier in this chapter, many of the heritabilities published were based on faulty or inaccurate procedures or assumptions.

There are essentially three types of mating designs used in genetic variation studies of forest trees, i.e., clonal, full-sib, and half-sib (Stonecypher, 1967). The half-sib method is the one most predominantly used. Goddard and Brown (1961) and Wright (1962) state that half-sib progeny tests can function as a seedling seed orchard and it is often cheaper and "better" than a clonal orchard. Moreover, a large test may be started in a single season (Wright, 1963b). A half-sib method gives a measure of narrow sense heritability and an estimate of general combining ability, while the clonal method will give only broad sense heritability and an estimate of cloning value.

When a full-sib mating design is used, an estimate of narrow sense heritability is obtainable as well as an estimate of non-additive genetic variation. General and specific combining ability can be estimated with a full-sib progeny test. A large full-sib progeny can also function as a seed orchard. As compared with a half-sib test, a full-sib test generally provides more information per

parent but information about fewer parents. Half-sib tests are more practical if controlled pollinations are very time consuming (Wright, 1963b).

The majority of heritability estimates published for forest trees have been calculated from half-sib mating designs by the component method. Surprisingly, there are numerous variations in formulas used to estimate heritability.

To translate components of variance and covariance to genetic components of variance and covariance, certain assumptions must be made about the material under study. Stonecypher, et al. (1964) lists some of the most important of these assumptions:

1. Inheritance is of a normal diploid type.
2. The progenies from which the heritability estimates are made are not inbred.
3. There is no epistasis.
4. Each seedling from one maternal parent has a different paternal parent, i.e., they are half-sibs.
5. There are no maternal effects.

Half-sib heritabilities formula can generally be divided into two groups; formulas with or without the family variance component ($\sigma_f^2$) multiplied by four. Falconer (1967), Allard (1966), and Stonecypher, et al. (1964) demonstrated that a variance component for half-sib families is equal to one-quarter of the additive genetic variation [$1/4(V_a)$], i.e., $\sigma_f^2 = 1/4(V_a)$. Founded on this

concept, most narrow sense half-sib heritability formulas are represented as

$$h^2 = \frac{4\sigma_a^2}{\sigma_p^2}$$

where $\sigma_p^2$ is the phenotypic variance.

Squillace and Bengton (1961) maintains that the true value to multiply the additive variance by is a number between two and four. Ordinarily, they state, one assumes that the wind-borne pollen is genetically uniform and equally effective for all seed parents. Under this assumption one multiplies the additive genetic variance by four to estimate heritability. However, the parents may be growing in different areas in which case the wind-borne pollen may be genetically different because of racial effects. A similar situation may be true even for trees within the same stand; that is, pollen in the immediate neighborhood of one mother tree may be genetically superior to that surrounding another. There is also a chance that a mother tree is primarily pollinated by one or two trees. This may often be the case because of differences in phenology. Finally, individual trees may have different degrees of selfing or other types of inbreeding. All these factors, they concluded, tend to exaggerate the estimate of additive genetic differences. If one assumes that the wind-borne pollen effective on each tree are completely different,

the computed additive genetic variance should be multiplied by two instead of four. Heritability may be presented as a range between the two values representing the two extreme cases discussed.

If genotypes are tested and compared on a single site, the interaction of genotypes and environments ($\sigma^2_{ae}$) is inseparable from the genetic effect (Namkoong, et al., 1965). Thus, for heritability estimates on a single site, the heritability formula should be revised to:

$$h^2 = \frac{4(\sigma^2_a + \sigma^2_{ae})}{\sigma^2_p} \quad .$$

Stonecypher (1966) uses this method for calculating a heritability value. His heritability formula

$$h^2 = \frac{4(\sigma^2_f)}{\sigma^2_w/k + \sigma^2_p + \sigma^2_f}$$

was used for estimates by separate locations, and the formula

$$h^{2'} = \frac{4(\sigma^{2'}_f)}{\sigma^2_w/k + \sigma^2_p + \sigma^{2'}_{lf} + \sigma^{2'}_f}$$

(Prime (') is used to denote variances across locations) for estimates for combined locations, where

$\sigma_f^2$ = variance due to differences among families

$\sigma_p^2$ = plot to plot variance or the component for family by replication interaction

$\sigma_{lf}^2$ = variance due to family by location interaction

$\sigma_w^2/k$ = an estimate of the within plot variance that consist of the within plot differences plus the remaining genetic variability among individual within plot

k = harmonic mean of number of trees per plot.

The variance for within plots was calculated from individual tree measurements, while the other variances were calculated from plot means. (To get the within plot variance, $\sigma_w^2$ was divided by the harmonic mean of the number of trees in each plot.) Snyder (1969) also used this general method but with one exception: He multiplied $\sigma_p^2$ and $\sigma_f^2$ by the harmonic mean of the number of trees per plot. The use of harmonic means as in the method above, is outlined in Snedecor (1956) and Steel and Torrie (1960).

Stonecypher's family variance component ($\sigma_f^2$), in the formula for heritability at separate locations, which is equivalent to $\sigma_a^2$, also contains some genetic-environmental interaction ($\sigma_{ae}^2$), therefore, $\sigma_f^2$ is actually $\sigma_a^2 + \sigma_{ae}^2$. Namkoong, et al. (1965) maintains that $\sigma_{ae}^2$, if large, appreciably reduced the accuracy with which the genotypes can be compared and causes an overestimation of expected gains. He concludes that any interaction between particular genotypes on special sites will be lost when genotypes are

planted elsewhere. Therefore, any interaction should be estimated and separated from the purely genetic effects. Barber (1964), Farmer and Wilcox (1966), and Pederick (1970) published heritabilities calculated similarly to Stonecypher's and also show the family variance component as $\sigma_a^2$.

Snyder (1969) calculated heritability based on plot means with no estimate of within plot variance obtained in the denominator. His heritability formula is:

$$h^2 = \frac{4\sigma_f^2}{\sigma_e^2 + \sigma_f^2} \quad .$$

Formulas for calculating the inheritance of survival have been published in the literature in two different forms. Stonecypher (1966) and Snyder (1969) both calculated heritabilities on a plot mean basis:

$$h^2 = \frac{\sigma_f^2}{\frac{\sigma_{fr}^2}{r} + \sigma_f^2} \qquad \text{(Stonecypher, 1966)}$$

$$h^2 = \frac{4\sigma_f^2}{\sigma_{fr}^2 + \sigma_f^2} \qquad \text{(Snyder, 1969)}$$

Snyder multiplied the family variance component ($\sigma_f^2$) by four; Stonecypher did not. Stonecypher estimated his heritability per replication by dividing the variance component for replication-family interaction by the number of

replications (r). The use of the quantity $\sigma^2_{fr/r}$ in the denominator makes the estimate applicable to selection based upon family means (Wright, 1963a).

A number of heritability formulas found in the literature do not multiply the family variance by four. Wright (1963b) states that only 1/4 of the additive genetic variance is recovered in a half-sib progeny test and the numerator should properly contain the quantity $4\sigma^2_f$ rather than $\sigma^2_f$, but heritability estimates must be divided by four to be applicable to the next generation in a half-sib breeding program. He rationalized that it is easiest to omit the four altogether.

Namkoong, et al. (1965) reconstructed the heritability formulas in 18 publications that estimated heritability. Ten of the heritability formulas were for half-sib mating designs, and in every case, they showed the genetic variance to contain some genetic-environmental interaction; the genetic variance component in reality estimated $\sigma^2_a + \sigma^2_{ae}$. It would be expected that this genetic variance component would also be represented as part of the phenotypic variance in the denominator. However, in two cases (Nicholls, et al., 1964 and Stonecypher, et al., 1964) Namkoong showed the denominator having estimated the total genetic variance component and total genetic-gross environment interaction, i.e., $\sigma^2_g + \sigma^2_{ge}$. Namkoong showed the heritabilities estimated by Nicholls, et al. and Stonecypher,

et al., mathematically as:

$$h^2 = \frac{\sigma_a + \sigma^2_{ae}}{\sigma^2_w + \sigma^2_p + \sigma^2_{ge} + \sigma^2_g} \cdot$$

Experimental Design for Estimating Heritabilities

Stonecypher (1967) states that, "The choice of the experimental design, will like a mating design, depend upon the objectives of the study, the resources available, and the degree of precision desired." Basic to any valid experimental design are the conditions of randomization and replication which determine to a large degree the precision attained.

When the number of entries is large, which is frequently the case in genetic variation studies, reduction in block size to obtain within block homogeneity should be considered. Reducing plot size or using an incomplete block design may both be used to reduce block size.

To obtain estimates of genetic and environmental variances of loblolly pine, Stonecypher (1967) found that a plot size of 10 to 15 trees was most efficient. However, Conkle (1963) showed that for four and five-year-old loblolly and slash pines, single tree plots were most efficient but multiple-tree plots were equally as efficient as one-tree plots for trees 8, 9, and 12 years old. In uniformity trials of red pine (Pinus resinosa Ait.) and

yellow-poplar (Liriodendron tulipifera L.), Wright and Freeland (1960) determined that one to three tree plots were statistically the most efficient. Twenty-five tree plots were suggested by Evans, et al. (1961).

Stonecypher (1967) suggested that if a plot size of ten trees is chosen the number of entries should be limited to about 31, if the block size is to be held below one-half acre. The size of the block depends on the homogeneity of the test site, but it has been Stonecypher's experience that block sizes much greater than one-half acre are too large on most test areas used for studies of forest trees. He suggested that a minimum of four replications per test site should be used in most forest genetic studies. Federer (1955) pointed out that the number of replications should depend on the degree of precision required, available resources, size of the experimental unit, and variability to be expected.

Snyder (1965) discussed the use of lattice and compact family design for three genetic studies with a large number of entries. Stonecypher (1966) employed a method of completely confounding entries in sets, as proposed by Comstock and Robinson (1952), to obtain estimations of components of variance.

Morgenstern (1969) used an analysis of variance model which assumed a completely randomized structure, but plot layout as a randomized block and modified lattice square

design. He stated that this simplified the presentation of results and the calculations of mean square coefficients, without resulting in large disadvantages.

Woessner (1965) analyzed an open and controlled pollinated progeny test of loblolly pine, but statistically significant differences were not found in cases where differences appeared to be quite large. He contributed the lack of significance to the use of large blocks, few replications, and single locations. He concluded that high coefficients of variation and large error variance lead to nonsignificant "F" ratios and was the result of inefficient plantation layout rather than lack of inherent differences.

# CHAPTER III

# MATERIALS AND METHODS

## Parent Populations

Selection of stands. Thirteen natural Virginia pine stands were selected in Kentucky and Tennessee. The locations of stands, shown in Figure 1, were determined by considering the distribution of the species, the physiographic regions to be represented, and the availability of co-operators. Since Virginia pine is more common in Tennessee than in Kentucky, nine stands were located in Tennessee and four in Kentucky. Stands were located in three major physiographic regions in Tennessee and Kentucky: the Mississippian embayment of western Tennessee and Kentucky, the Cumberland Plateau and Mountains, and the Great Valley.

Only essentially even aged stands of average or better than average quality were selected. Because parent trees were also used in a wood properties study and wood produced at diameter breast height (D.B.H.) between the tenth and twentieth year were to be analyzed, the stands could not be younger than 25 years old. Old stands were not accepted due to the difficulty in comparing pruning and other characteristics of such stands with younger stands.

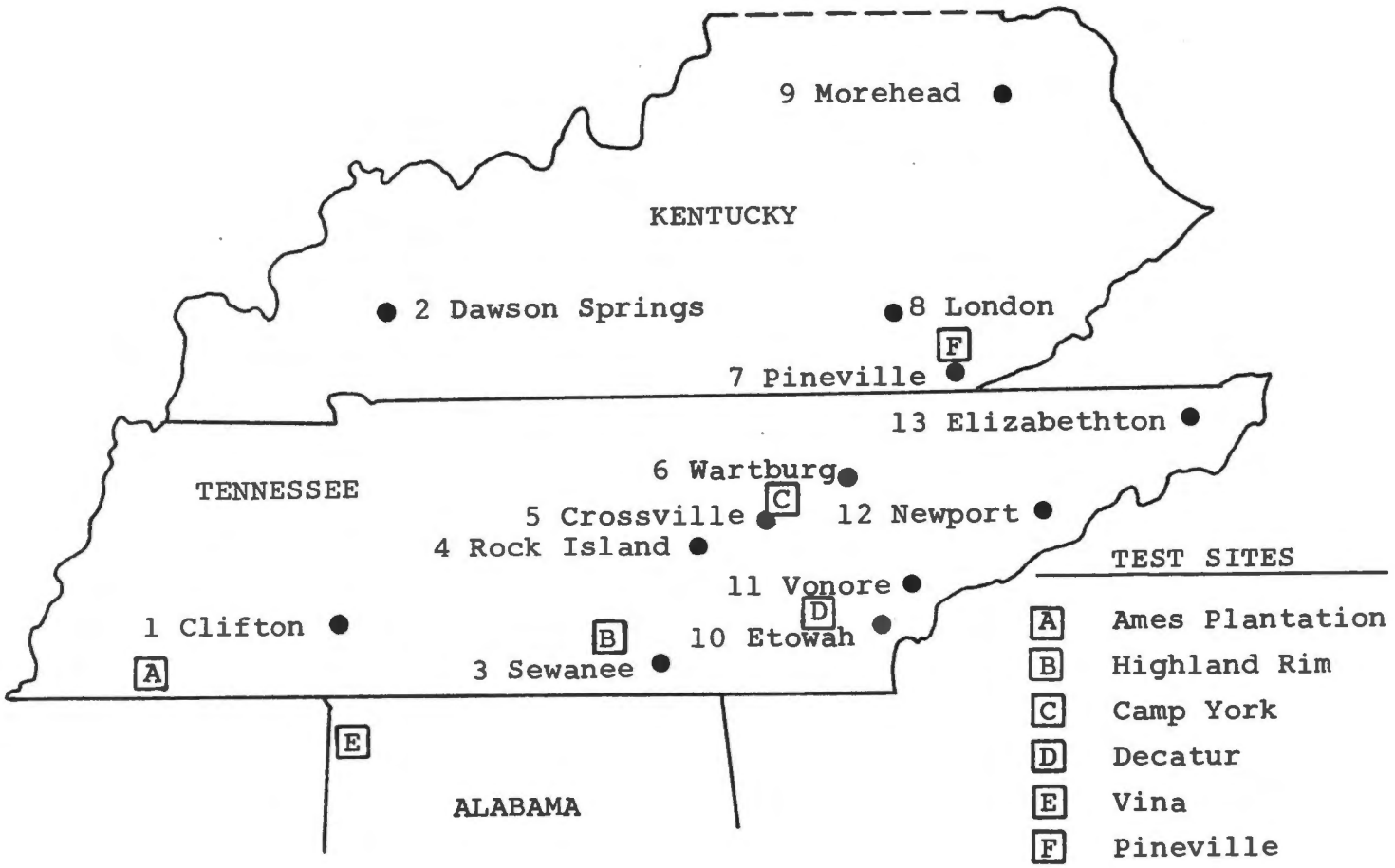



Figure 1. Locations of stands and test sites.

History and description of stands. All 13 Virginia pine stands, selected for this study were natural stands which had been established on abandoned fields. Only one stand, stand number 10, had undergone any significant management or silviculture practice practice; this stand was a seed production area and had been thinned by the U. S. Forest Service until only the desired seed trees remained.

Stands ranged in age from 28 to 53 years of age, and the site index ranged from 60 to 87 feet (Table 1). Average D.B.H. in the 13 stands ranged from 8.9 inches to 11.6 inches.

Parent trees. Fifteen Virginia pine parent trees were used in each of the 13 stands. Only dominants or co-dominants and trees judged safe to climb were used. Thus, a slightly biased sample in favor of taller and sturdier trees resulted. However, poor, average, and excellent phenotypes were selected in each stand. Cone production was not a selection criterion.

## Planting Material

Seed collection. It was thought that a minimum of 200 cones would be needed from each tree to produce enough seedlings to plant all test locations. Cones were collected in September and October of 1963, 1964, and 1965 in an effort to obtain sufficient number of cones. However, cone

TABLE 1. Location of sample plots, site indexes, and average values for D.B.H. and age. Averages are based on 15 trees per stand

| Stand No. | Physiographic Region | Location | Co-operator | Site Index (ft. at 50 yrs) | D.B.H. (inches) | Total Age (years) |
|---|---|---|---|---|---|---|
| 1 | West Tennesse | Clifton, Tenn. | Univ. of Tenn. | 75 | 9.0 | 28 |
| 2 | West Kentucky | Dawson Springs, Ky. | Ky. State Div. Forestry | 69 | 11.6 | 52 |
| 3 | Cumberland Plateau | Sewanee, Tenn. | USFS, Sewanee | 73 | 9.7 | 34 |
| 4 | Eastern Rim | Rock Island, Tenn. | Univ. of Tenn. | 74 | 10.2 | 42 |
| 5 | Cumberland Plateau | Crossville, Tenn. | Hiwassee Land Company | 68 | 9.0 | 37 |
| 6 | Cumberland Mountains | Wartburg, Tenn. | Univ. of Tenn. | 87 | 8.9 | 35 |
| 7 | Eastern Ridge | Pineville, Ky. | Ky. State Div. Forestry | 82 | 9.5 | 42 |
| 8 | Cumberland Plateau | London, Ky. | USFS, Berea | 83 | 10.9 | 47 |
| 9 | Cumberland Plateau | Morehead, Ky. | Cumberland National Forest | 69 | 8.8 | 32 |

TABLE 1. (continued)

| Stand No. | Physiographic Region | Location | Co-operator | Site Index (ft. at 50 yrs) | D.B.H. (inches) | Total Age (years) |
|---|---|---|---|---|---|---|
| 10 | Great Valley | Etowah, Tenn. | Cherokee National Forest | 81 | 9.0 | 34 |
| 11 | Great Valley | Vonore, Tenn. | Hiwassee Land Company | 60 | 9.8 | 53 |
| 12 | Great Valley | Newport, Tenn. | Univ. of Tenn. | 75 | 9.7 | 42 |
| 13 | Great Valley | Elizabethton, Tenn. | Cherokee National Forest | 64 | 11.1 | 43 |

production in many stands did not meet expectations. In the case of some parent trees as few as 50 cones were available.

Trees were climbed or cut down in order to collect the cones. Seeds were extracted from the cones and stored at 40°F in plastic bags until sowing.

Seedling production. Seedlings were grown at the Tennessee Valley Authority's nursery at Norris, Tennessee. Seeds were sown in unreplicated plots during the spring of 1966. After one growing season, seedlings were lifted, sorted into bundles of 10 seedlings per family and tagged. The biggest and healthiest looking seedlings were selected while small or deformed seedlings were culled. By selecting these better seedlings a bias was introduced which would tend to reduce the natural variation found within families. The required number of seedlings were packed in damp sphagumn moss and wrapped in seedling wrapping paper before being shipped to co-operators for planting.

Of the original 195 parent trees chosen only 127 trees (67 percent) produced enough seedlings to warrant planting. Table 2 presents the number of families in each stand planted at each location. Henceforth, location can be referred to by the appropriate key letters presented in Table 2. The entire 127 families were planted at location B, while there were only enough seedlings to plant 57 families in location F. No parent tree in stand 5 produced

TABLE 2. Number of families per stand planted at each test site.

| Stand Number | Test Sites[a] A | B | C | D | E | F | Total |
|---|---|---|---|---|---|---|---|
| | Number of Families | | | | | | |
| 1 | 4 | 9 | 0 | 0 | 1 | 0 | 14 |
| 2 | 8 | 10 | 9 | 9 | 9 | 3 | 48 |
| 3 | 8 | 11 | 10 | 9 | 10 | 3 | 51 |
| 4 | 10 | 12 | 10 | 10 | 10 | 9 | 61 |
| 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | 9 | 12 | 10 | 8 | 10 | 4 | 53 |
| 7 | 10 | 10 | 10 | 10 | 10 | 10 | 60 |
| 8 | 9 | 12 | 9 | 8 | 7 | 4 | 49 |
| 9 | 8 | 11 | 8 | 7 | 7 | 6 | 47 |
| 10 | 9 | 10 | 9 | 10 | 10 | 10 | 58 |
| 11 | 9 | 13 | 8 | 10 | 9 | 3 | 52 |
| 12 | 0 | 7 | 0 | 0 | 0 | 0 | 7 |
| 13 | 6 | 10 | 7 | 9 | 7 | 5 | 44 |
| Total | 90 | 127 | 90 | 90 | 90 | 57 | 544 |

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

enough seedlings to warrent any planting. Only seven parent trees in stand 12 produced enough seedlings to plant one location. However, stands 4, 7, and 10 had at least nine families represented at every location. Stands 1 and 12 were not represented in all six locations. Of all the 127 families planted only 41 percent could be represented at all locations. Excluding the Pineville test site, the smallest planting, 62 percent of the families were represented in all the other five test locations.

## Descriptions of Test Sites

Six test sites were used in this study (Figure 1). Three test sites, Ames Plantation, Highland Rim, and Camp York, are managed by the University of Tennessee Forestry Department. Hiwassee Land Company, the Department of Forestry at Auburn University, and the United States Forest Service manage the three other test sites at Decatur, Tennessee; Vina, Alabama; and Pineville, Kentucky; respectively.

The sites are described below with respect to their environmental, geological, and site conditions. Reference was made to the Geologic Map of Tennessee (1965) for a geological description of the test sites. Most of the information on environmental conditions and soil descriptions were taken from the United States Department of Agricultural Soil Survey of the respective county in which

the site was located. Site conditions are described from on-site observation by the author and from personal communications with the co-operators who manage the test site.

Ames Plantation. The Ames Plantation test site is located in Fayette County near Grand Junction, Tennessee. Geologically, the site is located on what is known as the plateau slope of West Tennessee. This geological feature is typified as being a loess deposit overlaying a series of sands, clays, and gravels of the Mississippian embayment of West Tennessee.

The climate is characterized by mild winters and warm summers. Frost free days range from 200 to 210 days per year. The monthly maximum temperature exceeds 70°F from April to October. Normal highs and lows range from 95°F in the summer to 10°F in the winter (Flowers, 1964).

The planting site is of gentle rolling topography about 450 feet above mean sea level. The soil is sandy loam and is classified in the Ruston series. Prior to planting, the site was occupied by an oak-hickory forest; the trees were removed and the area mist-blown with 2, 4, 5, -T before the test was established.[2]

Highland Rim. This test site is located on the University of Tennessee's Highland Rim Forestry Field Station

---

[2]Personal communication with J. G. Warmbrod. University of Tennessee Forestry Extension. Jackson, Tennessee. 1970.

in Franklin County, four miles southeast of Tullahoma in Middle Tennessee. Geologically, the site is located on the Highland Rim of Middle Tennessee and is underlain by loess on Mississippian cherty limestone. The elevation is about 1000 feet.

The soil is of silty loam texture. A compact and relatively impervious fragipan occurs about 18 inches deep. This pan retards both root development and water movement resulting in wet winters and dry summer soils. The soil is classified in the Dickson series.

Monthly mean temperatures range from 41°F in January to 77°F in July. There are 190 frost free days. The greatest monthly precipitation (an average of six inches) occurs in March and the least amount of precipitation (an average of three inches) occurs in October (Love, et al., 1959).

Previously used for pasture, the site needed only light disking before planting. The site appeared to be relatively homogeneous in soil and site conditions among replications (Figure 2).

Camp York. The site is in Cumberland County, 12 miles west of Crossville, Tennessee on land owned by the University of Tennessee. The site is located on the Cumberland Plateau at an elevation of about 1,900 feet above sea level. The soil, classified as Hartsell, is sandy loam in texture. Sandstone bedrock occurs at about 18 inches below the surface.



Figure 2. Excellent survival and growth was obtained following two growing seasons at the Highland Rim test site. This is the most homogeneous site in the study, with the tallest mean first- and second-year height.

The climate is characterized by cool winters and mild summers. The average monthly temperature ranges from 38°F in January to 74°F in July. There is an average of 179 frost free days, extending from April 18 to October 14. Precipitation is relatively evenly distributed during the year, ranging from 3.17 inches in October to 5.92 inches in March (Hubbard, et al., 1950).

Camp York was once a World War II Prisoner of War Camp. Building foundations and remnants of barracks and old road beds are scattered throughout the area resulting in a very disrupted planting site. Replication and planting rows were especially arranged to circumvent most of these planting obstacles. However, in many cases seedlings were planted over hidden obstacles. Parts of the site had recently been used for pasture, but most of it had grown up with brush. This site was prepared with a rotary brush cutter, treated with mist-blown 2, 4, 5, -T, and disked before planting.

Decatur Test. This test site, owned by Hiwassee Land Company, is located about five miles northeast of Decatur, Tennessee in Meigs County in the Ridge and Valley region of East Tennessee. The site, previously a three years old cultivated field, is on the south aspect of a low ridge at an elevation of about 1,000 feet. The soil was a silt loam texture classified in the DeKalb series.

This site extends from just below the crest of the ridge to about midslope. One area is rather flat and has relatively deep soil. Another small area in the planting site was eroded to the point that the $B_1$ horizon was exposed. The replications were arranged so that the eroded area was confined to one replication. Old windrows of previously cleared trees were present in some replications; in many cases whole plots were planted amid the debris of the windrows.

The climate of the Decatur site is rather mild with a mean seasonal temperature varying from 39.9°F in the winter to 76.5°F in the summer. There are an average of 192 frost free days a year. Precipitation is evenly distributed with a mean seasonal high of 15.73 inches in the winter to 10.14 inches in the fall. The driest month is October with 3.27 inches of precipitation and the wettest is March with 6.39 inches (Sweet, et al., 1919).

Vina. The Vina test site is located near Vina, in Franklin County in northern Alabama. It is the southern most test site of this study, and is situated on the top of a long, high ridge at about 650 feet elevation. Soils are derived from Coastal Plain sedimants and are sandy loam in texture. Most of the replications are on level ground but they could not be arranged in any systematic fashion because several gullies dissect the site. The area was a 15 years old field (Andropagon-brush stage) when disked

and burned prior to planting.[3]

The average monthly precipitation ranges from 2.6 inches in October to 6.3 inches in February. Temperature ranges from an average daily minimum of 33°F in January to an average daily maximum of 90°F in June and July. Summers are generally long, with the growing season extending from May to September, approximately 150 days. There are 205 frost free days (Sherad, and Young, 1965).

Pineville Test Site. The Pineville test site is located on the United States Forest Service land about five miles east of Pineville, Kentucky in the extreme northeastern corner of Bell County.

This site at an elevation of 2,200 feet, probably offers the most extreme environmental conditions. It is situated on spoils resulting from mining the Hindman coal seam one year prior to planting. Six months prior to planting the site was graded to form a level bench. The overburden rock was predominantly sandstone, so the spoils were coarse texture with many large rock fragments. The site was extremely acid with average pH near 3.0 to 4.0.[4] Site conditions were extremely heterogeneous among and within replications (Figure 3).

---

[3]Personal communication with J. F. Goggans. Auburn University, Auburn, Alabama. 1970.

[4]Letter of communication between Dr. E. Thor, University of Tennessee and Dr. W. T. Plass, U. S. Forest Service. Berea, Kentucky. 1967.



Figure 3. Poor growth was obtained following two growing seasons at the Pineville test site. This planting was established on spoils of a strip mine.

This is the northern-most test site. There are only 175 to 180 frost free days a year and monthly mean temperature ranges from 38°F in January to 76°F in July. Precipitation is greatest in the month of April with an average of 4.91 inches and least in October with an average of 2.22 inches (McDonald and Blevins, 1965).

Experimental Design

A randomized complete block design was used. Half-sib families were planted in row-plots of 10 trees each at a spacing of four feet between trees within rows and eight feet between rows. There were 10 replications at locations A, B, C and E and nine replications at locations D and F.

As indicated in Table 2, there are different numbers of families planted in each location, therefore, block sizes vary. Block size ranged from 0.7 acres at location F to 0.42 acres at location B.

Extreme care was taken in laying out blocks to assure that the site within each block was relatively homogeneous in respect to soil and site conditions. Many times blocks could not be laid out in any systematic fashion because of site difference within planting locations. Therefore, some blocks were staggered, skewed, or in some other way oriented to assure homogeneity of site conditions within blocks. A two-tree border row consisting of a mixture of the progenies used in the test was planted around all replications.

## Measurements

Field measurements were made at the end of the 1967 and 1968 growing seasons. The seedlings at that time were two- and three-years old respectively. In 1967, one growing season after outplanting, seedling height was measured to the nearest tenth of a foot. In 1968, after the second growing season, four measurements were made on each seedling:

1. Height was measured to the nearest tenth of a foot.
2. Stem diameter was measured with calipers to the nearest tenth of an inch at a point one-half way up the stem. Measurement near any place with great swelling due to branches was avoided.
3. The length of the strongest branch of the first most perfect whorl of branches was measured to the nearest tenth of a foot.
4. The diameter of the above chosen branch was measured one inch from the base to the nearest tenth of an inch.

## Statistical Analysis

An analysis of variance was performed on an individual tree basis for each characteristic measured assuming a random effect model for each location. The total variation present in each experiment is represented by the following linear mathematical model:

$$Y_{rsfw} = u + S_s + R_r + RS_{(rs)} + F/S_{f(s)} + (F/S) \times R_{f(s)r} + T/(F/S) \times R_{w[f(s)r]}$$

where,

$Y_{rsfw}$ = Total variation

$u$ = Mean effect

$S_s$ = Stand effect

$R_r$ = Replication effect

$RS_{(rs)}$ = Replication and stand interaction effect

$F/S_{f(s)}$ = Family within stands effect

$(F/S) \times R_{f(s)r}$ = Family within stands and replication interaction effects

$T/(F/S) \times R_{wf(s)r}$ = Within plot effect.

Table 3 presents the analysis of variance model. Degrees of freedom and mean squares[5] of unequal-sized samples were calculated according to the methods as described by Snedecor (1965). In deriving the expected mean squares, the random effects model or model II of Steel and Torrie (1960) was used. Effects due to locations, stands, replications, families within stands, and trees within plots were assumed to be random.

All analyses were performed on an IBM 360 Model 35 computer. Programs were written specifically for this study by the University of Tennessee Program Services.

---

[5]Hereafter noted as D.F. and M.S., respectively.

TABLE 3. Form of analysis of variance used at each test site

| Source of Variation | D.F. | M.S. | Expected mean squares* |
|---|---|---|---|
| Replications | r-1 | 1 | |
| Stands | s-1 | 2 | $\sigma^2_w + w\sigma^2_{f(s)r} + wr\sigma^2_{f(s)} + wf\sigma^2_{rs} + wrf\sigma^2_s$ |
| Replications x stands | (r-1)(s-1) | 3 | $\sigma^2_w + w\sigma^2_{f(s)r} + wf\sigma^2_{rs}$ |
| Families in stands | (f-1)s | 4 | $\sigma^2_w + w\sigma^2_{f(s)r} + wr\sigma^2_{f(s)}$ |
| Families in stands x replications | (r-1)(f-1)s | 5 | $\sigma^2_w + w\sigma^2_{f(s)r}$ |
| Within plot | (w-1)rfs | 6 | $\sigma^2_w$ |

TABLE 3. (continued)

| | |
|---|---|
| $*\sigma^2_w$ | = within plot variance |
| $\sigma^2_{f(s)r}$ | = variance due to family within stand and replication |
| $\sigma^2_{f(s)}$ | = variance due to difference among families within stands |
| $\sigma^2_{rs}$ | = variance due replication and stand interaction |
| $\sigma^2_s$ | = variance due to differences among stands |
| w | = number of plants per plot |
| r | = number of replications |
| f | = number of families |
| s | = number of stands |
| $n_i$ | = number of plants in the ith random plot. |

Estimates of Components of Variance and Heritability

Estimates of components of variance were obtained by subtracting the appropriate mean squares and dividing with the coefficient of the components being estimated. To obtain an estimate of the stand component of variance ($\sigma_s^2$) an appropriate pseudo mean square was calculated as described by Steel and Torrie (1960).

In accordance with Namkoong, et al. (1965) the family within stand component of variance ($\sigma_{f(s)}^2$) as calculated in Table 3 was interpreted as estimating one-quarter of the additive genetic variance, ($\sigma_A^2$) and one-quarter of the additive environment interaction variance ($\sigma_{AE}^2$). The family within stand variance component was, therefore, written mathematically as estimating 1/4 ($\sigma_A^2 + \sigma_{AE}^2$).

Using components of variance as derived from Table 3 estimates of narrow sense heritability were made for all measured characteristics. Heritability estimates were obtained by using the following equation:

$$H^2 = \frac{4\sigma_{f(s)}^2}{\sigma_w^2 + \sigma_{f(s)r}^2 + \sigma_{f(s)}^2} \quad .$$

# CHAPTER IV

## RESULTS AND DISCUSSION

### Mean Values

Mean values of characteristics measured at all test sites are presented in Table 4. The largest first-and second-year mean height were at the Highland Rim test site and the smallest values were at the Pineville planting. However, direct comparisons of mean values at each test site are not a valid indication of environmental differences. As was indicated in Chapter III, all families were not planted at every test site. Therefore, differences in mean values among test sites must partially be contributed to families not common among compared test sites.

Valid comparisons among test sites mean values can only be made among common families. To facilitate this comparison, the mean value of second-year height among common families within ten stands common to all test sites is summarized in Table 5. Mean values of second-year height for all families at each test site are presented in Appendix, Table 26.

In examining Table 5 it is noted that the Highland Rim (B) site has the overall largest second-year mean height (3.42 feet) and that each stand mean value are larger than that observed for any other test site. Likewise, the smallest test site mean height (1.35 feet) was found at

TABLE 4. Mean values for first-year height and second-year heights, branch length, branch diameter, and stem diameter by individual test sites

| Test Sites | First-Year Height (feet) | Second-Year Height (feet) | Second-Year Branch Length (feet) | Second-Year Branch Diameter (inches) | Second-Year Stem Dia. (inches) |
|---|---|---|---|---|---|
| Ames | 1.10 | 2.42 | 1.03 | 0.14 | 0.28 |
| Highland Rim | 1.56 | 3.53 | 1.76 | 0.26 | 0.38 |
| Camp York | 1.04 | 2.08 | 0.75 | 0.15 | 0.29 |
| Decatur | 1.18 | 2.75 | 1.00 | 0.15 | 0.31 |
| Vina | 1.34 | 3.28 | 1.51 | 0.27 | 0.47 |
| Pineville | 0.73 | 1.36 | 0.68 | 0.19 | 0.42 |
| Average | 1.16 | 2.57 | 1.12 | 0.19 | 0.36 |

TABLE 5. Mean second-year height among common families within ten common stands at all test sites

| Stand | Test Sites | | | | | |
|---|---|---|---|---|---|---|
| | A | B | C | D | E | F |
| 2 | 2.36 | 3.19 | 1.82 | 2.47 | 3.18 | 1.24 |
| 3 | 2.32 | 3.33 | 1.95 | 2.34 | 3.13 | 1.37 |
| 4 | 2.40 | 3.48 | 2.21 | 2.78 | 3.31 | 1.28 |
| 6 | 2.36 | 3.36 | 1.94 | 2.74 | 3.13 | 1.29 |
| 7 | 2.38 | 3.41 | 2.04 | 2.72 | 3.22 | 1.47 |
| 8 | 2.41 | 3.26 | 1.93 | 2.56 | 3.16 | 1.25 |
| 9 | 2.39 | 3.47 | 2.20 | 3.18 | 3.22 | 1.34 |
| 10 | 2.61 | 3.64 | 2.23 | 2.86 | 3.51 | 1.40 |
| 11 | 2.51 | 3.47 | 2.04 | 2.80 | 3.42 | 1.56 |
| 13 | 2.54 | 3.56 | 2.00 | 2.85 | 3.45 | 1.34 |
| Average | 2.42 | 3.42 | 2.04 | 2.73 | 3.27 | 1.35 |

Pineville (F); consistently this strip mine site had the smallest stand mean height.

Table 6 presents the ranking at each test site of the mean second-year stand heights and reveals that some stands tend to consistently be ranked relatively high or low. For example, Stand 10 is ranked among the best three at all test sites, whereas, Stand 2 is consistently ranked lower than seventh. Furthermore, common among the stands ranked relatively high or low is a tendency for them to be from the same physiographic region. Stand 10, 11, and 13 of the Great Valley physiographic source (Table 1) rank in the upper 30 percent 13 times out of the possible 18 (72 percent). If the stands of this physiographic source were ranked randomly one would expect only 5 out of the possible 18 in the upper 30 percent of all stands.

The frequency with which any stand of each physiographic source ranked in second-year mean stand height across all test sites are presented in Table 7. The ten stands are grouped in four physiographic sources: Great Valley, Eastern Rim and Eastern Ridge, Cumberland Plateau, and east Kentucky. Table 7 indicates that there is a grouping of the frequencies of ranking within each physiographic source. The Great Valley source (Group I) tends to more frequently be ranked higher in second-year mean stand height at all test sites than do the other sources. Groups 2 and 3, from the Eastern Rim and Eastern Ridge

TABLE 6. Ranking of second-year mean height within each test site[a]

| Ranking | Test Sites | | | | | |
|---|---|---|---|---|---|---|
| | A | B | C | D | E | F |
| 1 | 10 | 10 | 10 | 9 | 10 | 11 |
| 2 | 11 | 13 | 4 | 10 | 13 | 7 |
| 3 | 13 | 4 | 9 | 13 | 11 | 10 |
| 4 | 8 | 9 | 7 | 11 | 4 | 3 |
| 5 | 4 | 11 | 11 | 4 | 7 | 9 |
| 6 | 9 | 7 | 13 | 6 | 8 | 13 |
| 7 | 7 | 6 | 3 | 7 | 2 | 6 |
| 8 | 2 | 3 | 6 | 8 | 8 | 4 |
| 9 | 6 | 8 | 8 | 2 | 3 | 8 |
| 10 | 3 | 2 | 2 | 3 | 6 | 2 |

[a]Stands ranked in decending order by mean height values presented in Table 5.

TABLE 7. Frequency that any stand of each physiographic source ranked in second-year mean stand height across all test sites

| Ranking | Groups[a] | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| 1 | 5 | 0 | 1 | 0 |
| 2 | 4 | 2 | 0 | 0 |
| 3 | 4 | 1 | 1 | 0 |
| 4 | 1 | 2 | 3 | 0 |
| 5 | 2 | 3 | 1 | 0 |
| 6 | 2 | 1 | 3 | 0 |
| 7 | 0 | 2 | 3 | 1 |
| 8 | 0 | 1 | 4 | 1 |
| 9 | 0 | 0 | 5 | 1 |
| 10 | 0 | 0 | 3 | 3 |

[a]Group 1 = Great Valley: Stands 10, 11, and 13
Group 2 = Eastern Rim and Eastern Ridge: Stands 4 and 7
Group 3 = Cumberland Plateau: Stands 3, 6, 8, and 9
Group 4 = West Kentucky: Stand 2

source, respectively, are mostly ranked in the middle, whereas, Eastern Kentucky frequently ranks the lowest. A chi-square test (Snedecor, 1956) indicates that the frequency with which each group was ranked was more than the result of random distribution. The chi-square test indicated significance at the .05 level of probability.

Analysis of Variance Mean Squares

Degrees of freedom and mean squares of the analysis of variance for first-year height and second-year height, branch length, branch diameter, and stem diameter of each test location are presented in Tables 8 through 15. All mean squares values are shown in the tables as MS x $10^{+2}$.

As was discussed under description of Test Sites, one replication of the Decatur test site was in a severely eroded area. Survival in that replication was less than 60 per cent and was, therefore, eliminated from the analysis.

F-tests of statistical significance were performed on the stand, families within stand, and the families within stands replication interaction sources of variation. The families within stands and its interaction with replications were all highly significant (.01 probability level) for all characteristics measured.

Stand variances were significant (.05 or .01 probability level) for first-year height in all but two test locations (Ames and Pineville). At the end of the second

TABLE 8. Mean squares and degrees of freedom for analysis of variance of first-year heights for the Ames, Highland Rim, and Camp York test sites[a]

| Source | Test Sites | | | | | |
|---|---|---|---|---|---|---|
| | Ames | | Highland Rim | | Camp York | |
| | D.F. | M.S. | D.F. | M.S. | D.F. | M.S. |
| Replications | 9 | 377.22 | 9 | 211.33 | 9 | 192.99 |
| Stands | 10 | 67.53$^{NS}$ | 11 | 1417.90$^{**}$ | 9 | 175.41$^{*}$ |
| Replications x stands | 90 | 27.93 | 99 | 37.60 | 81 | 22.76 |
| Families/stands | 79 | 59.36$^{**}$ | 115 | 260.19$^{**}$ | 80 | 72.45$^{**}$ |
| Replications x families/stands | 689 | 19.79$^{**}$ | 1003 | 34.84$^{**}$ | 683 | 16.27$^{**}$ |
| Within plot | 6195 | 9.49 | 10442 | 17.62 | 5476 | 9.42 |

[a]Mean squares are presented as MS x $10^{+2}$.

$^{*}$Statistically significant at the .05 level.

$^{**}$Statistically significant at the .01 level.

$^{NS}$Not statistically significant.

TABLE 9. Mean squares and degrees of freedom for analysis of variance of first-year heights for the Decatur, Vina, and Pineville test sites[a]

| Source | Test Sites | | | | | |
|---|---|---|---|---|---|---|
| | Decatur | | Vina | | Pineville | |
| | D.F. | M.S. | D.F. | M.S. | D.F. | M.S. |
| Replications | 8 | 1529.96 | 8 | 1312.75 | 8 | 75.72 |
| Stands | 9 | 346.79** | 10 | 361.10** | 9 | 40.90NS |
| Replications x stands | 72 | 16.14 | 80 | 26.65 | 72 | 8.72 |
| Families/stand | 78 | 72.23** | 79 | 132.81** | 47 | 28.98** |
| Replications x families/stands | 533 | 25.71** | 626 | 29.48** | 368 | 6.30** |
| Within plot | 3764 | 13.84 | 6633 | 13.36 | 3298 | 3.31 |

[a]Mean squares are presented as MS x $10^{+2}$.

**Statistically significant at the .01 level.

NSNot statistically significant.

TABLE 10. Mean squares and degrees of freedom for analysis of variance of second-year height, branch length, branch diameter, and stem diameter at the Ames Plantation test site

| Source | D.F. | Mean Squares[a] | | | |
|---|---|---|---|---|---|
| | | Height | Branch Length | Branch Diameter | Stem Diameter |
| Replications | 9 | 3461.66 | 447.22 | 13.29 | 110.00 |
| Stands | 10 | 559.80* | 80.75NS | 1.64NS | 7.26* |
| Replications x stands | 90 | 105.83 | 28.92 | 0.62 | 1.93 |
| Families/stands | 79 | 212.61** | 42.33** | 0.76** | 3.30** |
| Replications x families/stands | 685 | 81.07** | 23.11** | 0.50** | 1.85** |
| Within plot | 6029 | 33.52 | 10.41 | 0.24 | 0.77 |

[a]Mean squares are presented as MS x $10^{+2}$.

*Statistically significant at the .05 level.

**Statistically significant at the .01 level.

NSNot statistically significant.

TABLE 11. Mean squares and degrees of freedom for analysis of variance of second-year height, branch length, branch diameter, and stem diameter at the Highland Rim test site

| Source | D.F. | Mean Squares[a] | | | |
|---|---|---|---|---|---|
| | | Height | Branch Length | Branch Diameter | Stem Diameter |
| Replications | 9 | 1363.55 | 340.55 | 15.24 | 38.55 |
| Stands | 11 | 3692.90** | 1035.00** | 41.27 | 76.24** |
| Replications x stands | 99 | 124.05 | 30.68 | 1.12 | 2.04 |
| Families/stands | 115 | 692.90** | 239.26** | 7.96** | 12.75** |
| Replications x families/stands | 1002 | 86.00** | 30.74** | 1.22** | 1.77** |
| Within plots | 10164 | 43.00 | 15.19 | 0.59 | 0.96 |

[a]Mean square are presented as MS x $10^{+2}$.

**Statistically significant at the .01 level.

TABLE 12. Mean squares and degrees of freedom for analysis of variance of second-year height, branch length, branch diameter, and stem diameter at the Camp York test site

| Source | D.F. | Mean Squares[a] | | | |
|---|---|---|---|---|---|
| | | Height | Branch Length | Branch Diameter | Stem Diameter |
| Replications | 9 | 1217.88 | 203.38 | 10.17 | 17.86 |
| Stands | 9 | 1245.33** | 136.18* | 4.12* | 32.85** |
| Replications x stands | 81 | 108.30 | 22.61 | 0.69 | 2.57 |
| Families/stands | 80 | 358.90** | 48.99** | 1.36** | 6.72** |
| Replications x families/stands | 674 | 88.37** | 16.27** | 0.46** | 2.02** |
| Within plot | 5253 | 43.62 | 9.83 | 0.32 | 1.01 |

[a]Mean squares are presented as MS x $10^{+2}$.

*Statistically significant at the .05 level.

**Statistically significant at the .01 level.

TABLE 13. Mean squares and degrees of freedom for analysis of variance of second-year height, branch length, branch diameter, and stem diameter at the Decatur test site

| Source | D.F. | Mean Squares[a] | | | |
|---|---|---|---|---|---|
| | | Height | Branch Length | Branch Diameter | Stem Diameter |
| Replications | 8 | 6973.12 | 1498.10 | 19.92 | 79.58 |
| Stands | 9 | 1017.22** | 92.84* | 2.89** | 21.67** |
| Replications x stands | 72 | 78.04 | 14.57 | 0.48 | 1.68 |
| Families/stands | 80 | 290.05** | 48.05** | 0.89** | 4.55** |
| Replications x families/stands | 525 | 103.32** | 17.16** | 0.48** | 2.04** |
| Within plots | 3690 | 47.72 | 8.66 | 0.25 | 0.87 |

[a]Mean square are presented as MS x $10^{+2}$.

*Statistically significant at the .05 level.

**Statistically significant at the .01 level.

TABLE 14. Mean squares and degrees of freedom for analysis of variance of second-year height, branch length, branch diameter, and stem diameter at the Vina test site

| Source | D.F. | Mean Squares[a] | | | |
|---|---|---|---|---|---|
| | | Height | Branch Length | Branch Diameter | Stem Diameter |
| Replications | 8 | 8265.87 | 729.75 | 58.14 | 67.94 |
| Stands | 10 | 1527.10** | 222.10* | 16.12** | 39.72** |
| Replications x stands | 80 | 114.91 | 26.53 | 1.63 | 3.43 |
| Families/stands | 79 | 502.41** | 90.98** | 3.85** | 9.07** |
| Replications x families/stands | 626 | 112.36** | 25.91** | 1.43** | 2.75** |
| Within plots | 6603 | 43.64 | 13.66 | 0.69 | 1.31 |

[a]Mean squares are presented as MS x $10^{+2}$.

*Statistically significant at the .05 level.

**Statistically significant at the .01 level.

TABLE 15. Mean squares and degrees of freedoms for analysis of variance of second-year height, branch length, branch diameter, and stem diameter at the Pineville test site

| Source | D.F. | Mean Squares[a] | | | |
|---|---|---|---|---|---|
| | | Height | Branch Length | Branch Diameter | Stem Diameter |
| Replications | 8 | 1391.18 | 644.56 | 35.68 | 186.27 |
| Stands | 9 | 282.09* | 93.93NS | 7.80** | 38.38** |
| Replications x stands | 72 | 40.35 | 20.74 | 0.97 | 4.64 |
| Families/stands | 47 | 127.62** | 48.10** | 2.78** | 13.21** |
| Replications x families/stands | 363 | 43.76** | 20.85** | 1.28** | 6.17** |
| Within plot | 3128 | 17.16 | 8.37 | 0.54 | 2.11 |

[a]Mean squares are presented as MS x $10^{+2}$.

*Statistically significant at the .05 level.

**Statistically significant at the .01 level.

NSNot statistically significant.

growing season, stand variances for seedling height were significant at all test sites. Second-year branch length showed no significance for stand variance only at the Ames and Pineville test sites while branch diameter was not significant for stands only at the Ames site. Second-year stem diameters were significant at least at the .05 probability level for stands at all locations.

Components of Variance

Components of variances were obtained from the analysis of variance by the method described in Chapter III. In accordance with Namkoong (1965) and Stonecypher (1966) the within plot variance ($\sigma^2_w$), the family within stand replication interaction variance ($\sigma^2_{f(s)r}$), and the family within stand variance ($\sigma^2_{f(s)}$) were interpreted to estimate the total phenotypic variance. The family within stand variances ($\sigma^2_{f(s)}$) were further assumed to estimate one-quarter of the additive genetic variance. However, it is recognized that a family variance estimated for single site also contains one-quarter of the additive genetic environment interaction, i.e., $\sigma^2_{f(s)} = 1/4\ \sigma^2_a + 1/4\ \sigma^2_{ae}$. These variance components and the standard error of the family variance of ($s[\sigma^2_{f(s)}]$) are presented for each test site in Tables 16 through 20.

Direct comparisons of variances components among test sites are not valid. Estimates of the components of variance at each test site was based on the total number of

TABLE 16. Estimates of components of variances and standard error of family within stand variance for first-year seedlings heights by individual test sites

| Test Sites | $\sigma^2_w$ | $\sigma^2_{f(s)r}$ | $\sigma^2_{f(s)}$ | $s[\sigma^2_{f(s)}]^a$ |
|---|---|---|---|---|
| Ames | 9.50[b] | 1.28 | 0.54 | 0.114 |
| Highland Rim | 17.63 | 1.82 | 2.39 | 0.340 |
| Camp York | 9.43 | 0.93 | 0.76 | 0.160 |
| Decatur | 13.84 | 1.86 | 0.81 | 0.200 |
| Vina | 13.37 | 1.74 | 1.24 | 0.256 |
| Pineville | 3.31 | 0.40 | 0.33 | 0.08 |

[a] $s[\sigma^2_{f(s)}]$ = Standard error of family within stand variance.

[b] Components of variances are presented as $\sigma^2 \times 10^{+2}$.

TABLE 17. Estimates of components of variances and standard error of family within stand variance for second-year seedlings heights by individual test sites

| Test Sites | $\sigma^2_w$ | $\sigma^2_{f(s)r}$ | $\sigma^2_{f(s)}$ | $s[\sigma^2_{f(s)}]^a$ |
|---|---|---|---|---|
| Ames | 33.52[b] | 6.01 | 1.66 | 0.41 |
| Highland Rim | 43.02 | 4.66 | 6.58 | 0.99 |
| Camp York | 43.63 | 6.26 | 3.78 | 0.89 |
| Decatur | 47.72 | 8.82 | 3.29 | 0.79 |
| Vina | 43.64 | 7.46 | 4.70 | 0.97 |
| Pineville | 17.16 | 3.67 | 1.28 | 0.41 |

[a] $s[\sigma^2_{f(s)}]$ = Standard error of family within stand variance.

[b] Components of variances are presented as $\sigma^2 \times 10^{+2}$.

TABLE 18. Estimates of variances and standard error of family within stand variance for second-year branch length by individual test sites

| Test Sites | $\sigma^2_w$ | $\sigma^2_{f(s)r}$ | $\sigma^2_{f(s)}$ | $s[\sigma^2_{f(s)}]^a$ |
|---|---|---|---|---|
| Ames | 10.42[b] | 1.61 | 0.24 | 0.08 |
| Highland Rim | 15.19 | 1.69 | 2.26 | 0.12 |
| Camp York | 9.84 | 0.97 | 0.49 | 0.11 |
| Decatur | 8.67 | 1.35 | 0.55 | 0.13 |
| Vina | 13.66 | 1.33 | 0.78 | 0.18 |
| Pineville | 8.38 | 1.72 | 0.42 | 0.16 |

[a] $s[\sigma^2_{f(s)}]$ = Standard error of family within stand variance.

[b] Components of variances are presented as $\sigma^2 \times 10^{+2}$.

TABLE 19. Estimates of components of variances and standard error of family within stand variance for second-year branch diameter by individual test sites

| Test Sites | $\sigma^2_w$ | $\sigma^2_{f(s)r}$ | $\sigma^2_{f(s)}$ | $s[\sigma^2_{f(s)}]^a$ |
|---|---|---|---|---|
| Ames | 0.245[b] | 0.034 | 0.003 | 0.001 |
| Highland Rim | 0.592 | 0.068 | 0.073 | 0.010 |
| Camp York | 0.321 | 0.021 | 0.013 | 0.003 |
| Decatur | 0.257 | 0.036 | 0.007 | 0.002 |
| Vina | 0.691 | 0.081 | 0.029 | 0.007 |
| Pineville | 0.543 | 0.103 | 0.023 | 0.009 |

[a] $s[\sigma^2_{f(s)}]$ = Standard error of family within stand variance.

[b] Components of variances are presented as $\sigma^2 \times 10^{+2}$.

TABLE 20. Estimates of variances and standard error of family within stand variance for second-year stem diameter by individual test sites

| Test Sites | $\sigma^2_w$ | $\sigma^2_{f(s)r}$ | $\sigma^2_{f(s)}$ | $s[\sigma^2_{f(s)}]^a$ |
|---|---|---|---|---|
| Ames | 0.777[b] | 0.136 | 0.018 | 0.006 |
| Highland Rim | 0.961 | 0.088 | 0.119 | 0.017 |
| Camp York | 1.016 | 0.142 | 0.066 | 0.015 |
| Decatur | 0.874 | 0.186 | 0.044 | 0.013 |
| Vina | 1.310 | 0.157 | 0.076 | 0.018 |
| Pineville | 2.111 | 0.561 | 0.108 | 0.042 |

[a] $s[\sigma^2_{f(s)}]$ = Standard error of family within stand variance.

[b] Components of variances are presented as $\sigma^2 \times 10^{+2}$.

families at that site, however, as emphasized in Chapter III, all families are not represented in every site. Therefore, differences in variances and means among test sites are not totally environmental. Variances and means among families not common in the compared sites, contributed to these differences.

To make a valid comparison among test sites only families common to all sites should be included in an analysis. However, comparisons of the preceeding tables will be made on the assumption that variance and means among the uncommon families are the same as the variances and means of the common families. To make more reliable comparisons, the Pineville test site, the smallest planting, had to be eliminated, therefore, increasing the number of common families among test sites from 54 to 79 families.

In examining the estimates of Tables 16 and 17, it is apparent that estimates for both variances and mean values (Table 4) for first and second-year height were greater at the Highland Rim test site than at other test sites. It is also apparent that variances among test sites tend to reflect the fluctuation of mean heights. The condition of having variances dependent on means, as in this case, is a phenomenon known as the scale effect (Falconer, 1967). Stonecypher (1966) noted similar relationships in a loblolly pine heritability study.

Coefficients of variations calculated for first- and second-year mean heights at each test site also indicate the effects of scale (Table 21). Coefficients of variation, calculated as

$$C.V. = \frac{\sigma_w}{\text{Mean Height}} \times 100,$$

express the within plot or error standard deviation as a percent of the test site mean height. Coefficient of variance at test sites with the smallest first-year mean heights (Ames, Camp York, and Pineville) were also notably small. However, after the second growing season there were little differences among these values.

TABLE 21. Coefficients of variation for first- and second-year height at each test site

| Characteristic | Test Sites | | | | | |
|---|---|---|---|---|---|---|
| | A | B | C | D | E | F |
| First-year height | 8.6 | 11.3 | 9.1 | 11.7 | 10.0 | 4.2 |
| Second-year height | 13.2 | 12.2 | 21.0 | 17.4 | 13.3 | 12.6 |

The family replication interaction variance components ($\sigma^2_{f(s)r}$) reflect the amount of genotype environment interaction at each test site and indirectly reflects the amount of variability among replications. An illustration of this relationship is observed in the first and second-year heights in Tables 16 and 17. The Highland Rim test site, described in Chapter III as being a very homogeneous site, has a very small family replication interaction variance in comparison to the site mean second-year height, whereas, the Decatur site with more diverse site conditions among replications has a large interaction variance.

The standard errors of the family within stand variance were in general very small. Average standard errors were 20 to 25 percent of the family variance. In comparison, Stonecypher (1966) experienced standard error from about 32 to 110 percent of the family variance for second-year height growth.

The family variances and standard errors for branch length, branch diameter and stem diameter (Tables 18, 19, and 20) follow closely the same pattern as did heights. The similarities in these patterns are not surprising for an obvious positive correlation exists among height and branch length, branch diameter and stem diameter.

## Estimates of Heritability

Using the components of variance in Tables 16 through 20, estimates of narrow sense heritabilities on an

individual tree basis were made by test sites for all characteristics measured (Table 22). Heritability values were calculated using the following equation:

$$h^2 = \frac{4\sigma^2_{f(s)}}{\sigma^2_w + \sigma^2_{f(s)r} + \sigma^2_{f(s)}} \quad .$$

Examination of Table 17 shows heritabilities of all characteristics to be highly variable among test sites. Heritability values of first-year heights range from 0.17 at Ames to 0.44 at Highland Rim. Among the Camp York, Vina, and Pineville test sites heritability values range around 0.30 for first-year heights. Decatur had a heritability of 0.20.

Heritability estimates for second-year heights ranged between the Highland Rim (0.48) and Ames (0.16) test sites. Four test sites (Highland Rim, Camp York, Decatur, and Vina) showed an increase of one to four points in heritability of second-year height, whereas, the two other test sites (Ames and Pineville) dropped one and ten points in heritability, respectively. Sites which increased in heritability of height were generally accompanied by increases in the family within stand variance ($\sigma^2_{f(s)}$) with a proportional decrease in the within plot variance ($\sigma^2_w$). This indicates an increase of among family differences and a decrease of within family differences in heights from the first to the second year.

TABLE 22. Heritability estimates of first-year and second-year height, second-year branch length and diameter, and second-year stem diameter for each test site

| Test Sites | First-Year Height | Second-Year Height | Branch Length | Branch Diameter | Stem Diameter |
|---|---|---|---|---|---|
| Ames | 0.17 | 0.16 | 0.08 | 0.05 | 0.08 |
| Highland Rim | 0.44 | 0.48 | 0.47 | 0.40 | 0.41 |
| Camp York | 0.27 | 0.28 | 0.17 | 0.15 | 0.21 |
| Decatur | 0.20 | 0.22 | 0.21 | 0.10 | 0.16 |
| Vina | 0.30 | 0.34 | 0.20 | 0.14 | 0.20 |
| Pineville | 0.33 | 0.23 | 0.16 | 0.14 | 0.16 |
| Average | 0.28 | 0.28 | 0.21 | 0.16 | 0.20 |

The two test sites which increased the most in heritability (Highland Rim and Vina) and showed proportionally large relative increase in family variance ($\sigma^2_{f(s)}$) were, also, sites which had the greatest increase in mean heights. It is suspected that first year seedlings, still influenced by nursery effects and planting shock, mask family and site effects. However, during the second growing season seedlings expressed more family and site differences. Sites which had a larger mean heights expressed more family variance. This is an example of the previously mentioned scale effect.

The Pineville test site dropped from a first year heritability of 0.33 to 0.23 the second year. This relatively large change was indirectly the result of a relative increase in the family replication interaction variance ($\sigma^2_{f(s)r}$). Again, it is suspected that the first-year the seedlings had not completely responded to the site effects, whereas, the second-year they had adjusted to these effects and showed more family replication interaction variance.

Trends in heritabilities of second-year branch length, branch diameter, and stem diameter among the test sites follow the same pattern among test sites as did second-year heights. As was mentioned in the proceeding section, this trend was expected because of the high correlation among measured characteristics.

The Highland Rim test site ranked highest in heritability of all measured characteristics and the Ames test site

ranked lowest. Heritability averaged for all test sites: 0.21 for branch length, 0.16 for branch diameter, and 0.20 for stem diameter. The maximum and minimum heritabilities were 0.47 and 0.05, 0.40 and 0.05, and 0.41 and 0.08 for branch length, branch diameter, and stem diameter, respectively.

## Estimates of Genetic Gains

Estimates of phenotypic and genetic variance are of little practical value by themselves. The ultimate use of the estimates is to predict the amount of improvement, i.e., genetic gain, possible for a particular breeding program.

Namkoong (1965) demonstrated a method for calculating genetic gains based upon the initial mass selection of the phenotypes and the selection of families and individuals within families for half-sib progenies. His methods are readily adaptable to this study for estimating gain of any measured characteristic at each test site. To demonstrate the methods for calculating gain an example will be provided.

Genetic gains for selection of the best stands and the best families and individuals within families was calculated for second-year heights at the Highland Rim test site. It is assumed that there was no genetic gain made in the initial selection of parent trees. Therefore, initial mass selection was assumed to be zero. The formula for

predicting the genetic gain (G), for family and within family selection is represented mathematically as:

$$G = i_1 \frac{\sigma^2_{f(s)}}{\sigma_1} + i_2 \frac{3\sigma^2_{f(s)}}{\sigma_2}$$

where:

$i_1$ = family selection intensity

$i_2$ = within family selection intensity

$$\sigma_1^2 = \frac{\sigma^2_w}{nr} + \frac{\sigma^2_{f(s)r}}{r} + \sigma^2_{f(s)}$$

$$\sigma_2^2 = \sigma^2_w + \sigma^2_{f(s)r} \quad .$$

The gain formula is made up of two parts; the estimated gain from the family selection, assuming no inbreeding within families

$$(i_1 \frac{\sigma^2_{f(s)}}{\sigma_1}),$$

and the gain from within family selection

$$(i_2 \frac{3\sigma^2_{f(s)}}{\sigma_2}) \quad .$$

As Namkoong states the first gain is in the family-testing stage; it is made on the basis of a numerator of the covariance of half-sibs ($1/4\ \sigma^2_A$) since the open-pollinated families are being mated among one another. The second gain is based on individual variation with half-sib

families, therefore, is made on the basis of the total within-family genetic variance, or 3/4 $\sigma_A^2$ (Falconer, 1967). This is the total genetic variance after the variance among the half-sib families is removed.

Genetic gains were calculated for two selection schemes at the Highland Rim Plantation. The two schemes differ only in that in Scheme I the tallest families would be chosen from families of all stands, and in Scheme II the tallest families would be chosen from families of the seven stands with greatest mean height.

Table 23 presents the selection intensities of both schemes. It was determined that there was an average of 9.2 trees per family plot. Since only one tree per family plot was selected the selection intensity within families would be 11.0 percent or a selection intensity of 1.70 unit of standard deviations.[6] However, the family selection intensity was 1.04 for Scheme I and 0.60 for Scheme II by selection of the tallest 45 families.

Components of variances used for the gain estimations of Scheme I and II (Table 24) were derived from an analysis of variance using all the families for Scheme I, and using only families of the selected seven stands for Scheme II. The most striking difference between the variance components from these analysis is the larger (27 percent) among family

---

[6]Selection intensities were interpolated from graphs by Namkoong and Snyder, 1969.

TABLE 23. Number of stands, families, and individuals selected and percent and selection intensity for families and within families selections of Scheme I and II at the Highland Rim test site

| Selection Scheme[a] | Number of Stands | Number of Families | Number Families and Individuals Selected | Percent Selection | | Selection Intensity | |
|---|---|---|---|---|---|---|---|
| | | | | Family | Within Family | Family | Within Family |
| I | 12 | 127 | 45 | 35.4 | 11.0 | 1.04 | 1.70 |
| II | 7 | 72 | 45 | 62.5 | 11.0 | 0.60 | 1.70 |

[a]Scheme I - selection of tallest individuals of the tallest 45 families of all stands.

Scheme II - selection of tallest individuals of the tallest 45 families of the best seven stands.

variance for the selected seven tallest stands ($\sigma^2_{f(s)}$). The within family variance ($\sigma^2_w$) and the family-replication interaction variance ($\sigma^2_{f(s)}$) also were slightly greater in the select stand analysis.

TABLE 24. Estimates of components of variances and mean of second-year heights for all stands and the selected seven best stands at the Highland Rim test site

| Selection Scheme | $\sigma^2_w$ | $\sigma^2_{f(s)r}$ | $\sigma^2_{f(s)}$ | $S(\sigma^2_{f(s)})$ | Mean Height |
|---|---|---|---|---|---|
| I | 0.4302 | 0.0466 | 0.0658 | 0.01 | 3.53 |
| II | 0.4409 | 0.0485 | 0.0838 | 0.16 | 3.66 |

Estimated genetic gains from the two proposed selection schemes are presented in Table 25. It is surprising that both selection schemes give essentially the same total gains. Gains from selection Scheme I and II were 0.74 and 0.77 feet, respectively. It could have been anticipated that Scheme II, with a much lower family selection intensity would have produced a smaller genetic gain. But, offsetting the lower selection intensity was the larger family within stand variance and therefore, higher additive genetic variance.

TABLE 25. Gains from family and within family selection and estimated mean heights of two-year-old seedlings at the Highland Rim test site

| Selection Schemes | Gains (feet) | | | Estimated Population Mean Height (feet)[a] |
|---|---|---|---|---|
| | Family | Within Family | Total | |
| I | 0.25 | 0.49 | 0.74 | 4.27 |
| II | 0.16 | 0.61 | 0.77 | 4.43 |

[a]Estimated second-year mean height of a population derived from random mating of selected trees.

An initial gain of 0.13 feet was made from the selection of the best seven stands. The base population mean height from which the estimates of variances for Scheme I was 3.53 feet, whereas, it was 3.66 feet for Scheme II (Table 25). Any gain estimate for a population is in effect added to the mean of that population to estimate the mean of the new population produced from the selected parents (Falconer, 1967). Therefore, the mean height of two-year-old seedlings planted on sites similar to those at Highland Rim is estimated to be 4.27 feet if bred from trees selected by Scheme I or 4.43 feet by Scheme II. This is an expected gain of 21 or 25 percent from Scheme I or II, respectively.

In comparison to selection Schemes I and II a less desirable selection method would be mass selection. Mass selection would entail the selection of the best 45 individuals irregardless of family or stand consideration.

Expected gain, calculated as:

$$G = i \cdot \frac{h^2}{4} \cdot \sigma_3$$

where;

$$i = 2.15$$

$$h^2 = 0.48$$

$$\sigma_3^2 = \sigma_w^2 + \sigma_{f(s)r}^2 + \sigma_{f(s)}^2 \quad ,$$

would be only 0.19 feet (5 percent). The possible effects of selecting parent trees from the same family and, therefore, inbreeding is ignored. Hence, selection Schemes I and II are four and five times effective, respectively.

# CHAPTER V

## SUMMARY AND CONCLUSIONS

The study was undertaken to determine the genetic and environmental variance and narrow sense heritability for the natural population of Virginia Pine (Pinus virginiana Mill.) in Kentucky and Tennessee. The major objectives of this study were to develop the techniques and analytical procedures for estimating components of variance, calculating heritabilities and gains.

Open-pollinated progeny from 7 to 13 families each of the 13 natural stands were planted in 10-tree row plots in 9 or 10 replications at 6 test sites. Altogether about 52,000 trees were measured and analyzed for first- and second-year height growth, second-year branch length and diameter, and second-year stem diameter.

The average second-year mean height ranged from 3.42 feet at the Highland Rim test site to 1.34 feet at the Pineville planting. In second-year stand mean heights at all test sites, stands from the Great Valley physiographic source tended to rank higher than the Western Ridge and Western Rim, Cumberland Plateau, and West Kentucky physiographic sources.

An IBM program was developed to perform an analysis of variance and to estimate the components of variance. The analyses were performed on each test site separately. All

sites did not have the same complement of families represented, therefore, any direct comparison among variances and heritabilities of each test site is not completely valid. Sixty-two percent of all the families were common to five test sites and some general conclusions were drawn from their comparisons.

Variance components values were highly variable among test sites. It was apparent that these variances tend to fluctuate with the mean values at each site. Sites with the largest mean values generally had the largest variances. Standard errors for family within stand variances were 20 to 25 percent of the family variance.

For all the characteristics measured, the relative size of the variance components compared among locations were about the same. This pattern was evidently the result of the close correlation among all characteristics, i.e., it would be expected that the tallest plants also had longest branches and the largest diameter branches and stems. It could be suggested, for practical application to tree breeding, that future analyses be made on the ratio of height or volume to branch length and diameter.

Narrow sense heritabilities were highly variable among test sites for all characteristics. Heritability for second-year height ranged from 0.16 to 0.48. Heritability of first- and second-year height and second-year branch length, branch diameter, and stem diameter averaged 0.28,

0.28, 0.21, 0.16, and 0.20, respectively, among all test sites. Heritabilities of each characteristic ranked essentially in the same order among test sites.

Estimates of genetic gain based on second-year height was calculated for the Highland Rim test site using two selection schemes. The criteria of Scheme I was to select the tallest individuals of the tallest 45 families. Since variation among stands was determined to be statistically significant, therefore, in Scheme II the tallest individuals were selected from the tallest 45 families of the tallest seven stands.

Gain of 0.13 feet in Scheme II was made from the initial stand selection. Gains from the family and within family selection were estimated to be 0.74 and 0.77 feet for Scheme I and II, respectively. Therefore, Scheme I and II were estimated to produce a 21 and 25 percent total gain, respectively, for second-year seedling height. Surprisingly, one advantage Scheme II had over Scheme I was the increase in the family within stand variance and, therefore, a larger additive genetic variance.

Further study should be made of these data to determine the most efficient experimental design which could obtain reliable estimates of genetic variance in a study of this type. There is also a need for a combined analysis across all or any combination of test sites to estimate the genetic environment (test site) interaction.

# LITERATURE CITED

## LITERATURE CITED


Allard, R. W. 1966. Principles of Plant Breeding. John Wiley and Sons, Inc. New York. 185 pp.

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

Barber, J. C. 1964. Inherent variation among slash pine progenies at the Ida Cason Callaway Foundation. U. S. Forest Service. Res. Paper SE-10. 90 pp.

_____. K. W. Dorman, and R. A. Jordan. 1955. Slash pine crown width differences appear at early age in one parent progeny test. U. S. Forest Service Southeastern Forest Expt. Sta. Res. Notes 86. 2 pp.

Ceck, F. C. 1963. Breeding methods in tree improvement. Proceeding 7th South. Conf. Forest Tree Imp. Gulfport, Mississippi. pp. 27-30.

Comstock, R. E. and H. F. Robinson. 1952. Estimation of average dominance of genes. Heterosis. Iowa State College Press. pp. 494-516.

Conkle, M. T. 1963. The determination of experimental plot size and shape in loblolly and slash pines. School of Forestry, North Carolina State College. Raleigh, N. C. Tech. Rep. No. 17. 32 pp.

Dietrichson, Joh. 1969. Genetic variation of cold damage growth rhythm and height growth in 4 years old black spruce (Picea mariana (Mill.) B.S.P.. Rep. of Norwegian Forest Res. Inst.: 27, No. 97. Vollebekk, Norway. pp. 113-127.

Evans, T. C., J. C. Barber, and A. E. Squillace. 1961. Some statistical aspects of progeny testing. Proc. 6th Southern Conf. of Forest Tree Imp. School of Forestry, University of Florida. Gainesville, Florida. pp. 73-79.

Falconer, D. S. 1967. Introduction to Quantitative Genetics. The Ronald Press Company. New York. 365 pp.

Farmer, R. E. 1968. Variation and inheritance of eastern cottonwood growth and wood properties under two soil moisture regimes. Silvae Genetica 19:5-8.

_____. and J. R. Wilcox. 1966. Variation in juvenile growth and wood properties in half-sib cottonwood families. U. S. Forest Service Res. Pap. NC-6. 4 pp.

Federer, W. T. 1955. Experimental Design. The MacMillan Company. New York. 544 pp.

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

Fowells, H. A. 1965. Silvics of Forest Trees of the United States. U. S. Dept. of Agri. Agri. Handbook, No. 271. 762 pp.

Fox, C. T., T. E. Beesley, and R. G. Leighty. 1958. Soil Survey of Franklin County Tennessee. U.S.D.A. Series 1949. No. 8. 91 pp.

Geologic Map of Tennessee. 1965. Division of Geology, Dept. of Ed. State of Tennessee.

Goddard, R. E. and C. L. Brown. 1961. An explanation of seed orchard concepts. Jour. Forestry 59:252-256.

Goggans, J. F. 1962. The correlation, variation, and inheritance of wood properties in loblolly pine (Pinus taeda L.). School of Forestry, North Carolina State College. Tech. Rep. No. 14. 155 pp.

Hanover, J. W., and B. V. Barnes. 1962. Heritability of height growth in year-old western white pine. Proceeding of a Forest Genetics Workshop. Macon, Georgia. pp. 71-76.

Hanson, W. D., and J. Robinson. 1963. Heritability in Statistical Genetics and Plant Breeding. National Academy of Science. National Research Council Publication 982. Washington, D. C. pp. 135-140.

Harlow, W. M., and E. S. Harrar. 1958. Textbook of Dendrology. McGraw-Hill Book Company, Inc. 561 pp.

Hattemer, H. H. 1963. Estimates of heritability published in forest tree breeding research. World Consultation on Forest Genetics and Tree Improvement. Stockholm. pp. 23-30.

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

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

McDonald, H. P., and R. L. Blevins. 1965. Reconnaissance soil survey of Fourteen counties in eastern Kentucky. U.S.D.A. Series 1962, No. 1. 72 pp.

McIntyre, A. C. 1933. Virginia pine in Pennsylvania. Pa. Agri. Expt. Sta. Tech. Bul. 300. 31 pp.

Morgenstern, E. K. 1969. Genetic Variation in Seedlings of Picea mariana (Mill.) B.S.P. Silvae Genetica 18:161-167.

Namkoong, G. 1970. The timing of genetic control of height growth in two species of forest trees. Abstracts of the First North American Forest Biology Workshop. Michigan State University. 27 pp.

_____. A. C. Barefoot, and R. G. Hitchings. 1969. Evaluating control of wood quality through breeding. TAPPI 52:1935-1958.

_____. E. G. Snyder, and R. W. Stonecypher. 1965. Heritability and gain concept for evaluating breeding systems such as seedling orchards. Silvae Genetica 15:76-83.

Nichols, J. W. P., H. E. Dadswell, and J. M. Fielding. 1964. The heritability of wood characteristics of Pinus radiata. Silvae Genetica 13:68-71.

Nilsson, B. 1958. Om sambandet mellan modertrad och avkomma hos tall och gran. Svenska skogsvardsfor. Tidskr. Nafte 1, pp. 52-65.

Pederick, L. A. 1970. Variation and inheritance of stem form and bark thickness in young loblolly pine. School of Forestry, North Carolina State University. Tech. Rep. No. 41. 44 pp.

Potzger, J. E. 1931. Some observations on Pinus virginiana in Monroe County, Indiana. Ind. Acad. Sci. Proc. 41:153-174.

Ruden, T. 1963. Results from an 11 years old progeny test with Picea abies (L.) Karst in Southeastern Norway. Food and Agri. Org. of U.N. FAO/Forgen. 63:2a/9. 65 pp.

Sargent, C. S. 1965. Manuel of the Trees of North America. Dover Publications, Inc. New York. 934 pp.

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

Slocum, G. K. and Miller, W. D. 1953. Virginia pine. North Carolina Agri. Expt. Sta. Tech. Bul. 100. 52 pp.

Snedecor, G. W. 1956. Statistical Methods. The Iowa State College Press. Ames, Iowa. 534 pp.

Snyder, E. B. 1959. Glossary for forest tree improvement workers. U. S. Forest Service. South. Forest Expt. Sta. 22 pp.

_____. 1965. Lattice and compact family block designs in forest genetics. Proc. 2nd Genetics Workship of the Soc. of American Foresters and the 7th Lake States Forest Tree Impr. Conf. pp. 12-17.

_____. 1969. Parental selection versus half-sib family selection of longleaf pine. Proc. of the 10th South. Conf. Forest Tree Impr. Houston, Texas. pp. 84-88.

Steel, R. G., and R. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Company, Inc. New York. 481 pp.

Sterrett, W. D. 1911. Scrub pine. U. S. Forest Service. Tech. Bul. 94. 27 pp.

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. Bul. No. 5. 128 pp.

_____. 1967. Field Testing and data handling in forest genetic research. Proc. 9th South. Conf. Forest Tree Impr. Knoxville, Tenn. pp. 15-19.

_____. R. C. Cech, and B. J. Zobel. 1964. Inheritance of specific gravity in two and three years old seedlings of loblolly pine. TAPPI 47:405-407.

_____. B. J. Zobel. 1966. Inheritance of specific gravity in five years old seedlings of loblolly pine. TAPPI 49:303-305.

Squillace, A. E. 1967. Where we stand on techniques and seed orchard culture-selection of superior trees. Proc. 9th South. Conf. Forest Tree Impr. Knoxville, Tennessee. pp. 1-9.

_____. and G. W. Bengtson. 1961. Inheritance of gum yield and other characteristics of slash pine. Proc. 6th South. Forest Tree Impr. Conf. Gainesville, Fla. pp. 85-96.

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

Thor, E. 1964. Variation in Virginia pine. Part 1: Natural variation in wood properties. Jour. Forestry 62:258-262.

Toda, R. 1967. Variation in heritability of some quantitative characteristics in Cryptomeria. Silvae Genetica 7:87-93.

Trousdell, D. B., K. W. Dorman, and A. E. Squillace. 1963. Inheritance of branch length in young loblolly pine progeny. U. S. Forest Service Res. Paper SE-1. 2 pp.

van Buijtenen, J. P. 1962. Heritability estimates of wood density in loblolly pines. TAPPI 45:602-605.

Woessner, R. A. 1965. Growth, form and disease resistance in four year old control and five years old open-pollinated progeny of loblolly pine selected for use in seed orchards. School of Forest Res., North Carolina State University. Tech. Rep. No. 28. 67 pp.

Wright, J. W. 1962. Genetics of Forest tree improvement. Food and Agri. Org. of the U. N., Rome. FAO/Forestry and Forest Products Studies. No. 16. 399 pp.

Wright, J. W., and D. F. Freeland. 1960. Plot size and experimental efficiency in forest genetic research. Michigan State University, Agri. Exp. Sta. Tech. Bul. 280. 28 pp.

_____. 1963a. Genetic variation among 140 half-sibs Scotch pine families derived from 9 stands. Silvae Genetica 12:83-89.

_____. 1963b. Selective breeding and the production of new forest tree varieties. Agri. Science Review 1:27-37.

Zobel, B. 1961. Inheritance of wood properties in conifers. Silvae Genetica 10:65-70.

# APPENDIX

TABLE 26. Second-year family mean heights and stand mean heights at each test sites.

| Stand | Family | Test Sites A | B | C | D | E | F |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 1.96 | 3.16 | | | | |
| | 2 | | 3.76 | | | | |
| | 3 | | 3.93 | | | | |
| | 6 | | 3.90 | | | | |
| | 7 | 2.32 | 3.69 | | | | |
| | 9 | 2.68 | 4.12 | | | | |
| | 12 | 2.26 | 3.35 | | | 3.56 | |
| | 13 | | 3.82 | | | | |
| | 15 | | 4.08 | | | | |
| Mean Stand Height | | 2.35 | 3.74 | | | 3.56 | |
| 2 | 1 | 2.49 | 3.40 | 1.93 | 2.45 | 3.41 | 1.27 |
| | 3 | 2.27 | 3.25 | 1.87 | 2.40 | 3.18 | 1.34 |
| | 4 | | 3.32 | | | | |
| | 7 | 2.31 | 2.93 | 1.66 | 2.57 | 2.94 | 1.12 |
| | 8 | 2.25 | 2.88 | 1.69 | 2.49 | 2.82 | |
| | 9 | 2.09 | 2.81 | 1.59 | 2.36 | 2.87 | |
| | 10 | 2.12 | 2.97 | 1.81 | 1.59 | 2.36 | 2.87 |
| | 11 | 2.14 | 2.97 | 1.74 | 2.60 | 2.82 | |
| | 12 | | 2.97 | 1.80 | 2.30 | 3.08 | |
| | 14 | 2.18 | 3.09 | 1.84 | 2.67 | 2.99 | |
| Mean Stand Height | | 2.24 | 3.05 | 1.77 | 2.48 | 3.00 | 1.26 |
| 3 | 2 | | 3.63 | 2.29 | | | |
| | 3 | | | 1.97 | | | |
| | 4 | 2.45 | 3.25 | 1.99 | 2.63 | 3.04 | |
| | 5 | | 3.55 | 1.67 | | 3.36 | |
| | 6 | 2.08 | 2.94 | 1.97 | 2.38 | 2.74 | |
| | 7 | 2.43 | 3.24 | 1.69 | 2.41 | 3.29 | |
| | 8 | 2.27 | 3.24 | 1.93 | 2.57 | 2.94 | 1.48 |
| | 9 | 2.50 | 3.47 | 1.68 | 2.69 | 3.43 | |
| | 10 | 2.31 | 3.15 | | 2.91 | 3.23 | |
| | 12 | 2.42 | 3.63 | 2.13 | 2.06 | 3.62 | 1.46 |
| | 14 | | 3.49 | | 2.89 | 3.23 | |
| | 15 | 2.28 | 3.13 | 1.79 | 2.39 | 2.83 | 1.17 |
| Mean Stand Height | | 2.34 | 3.33 | 1.92 | 2.68 | 3.18 | 1.39 |

TABLE 26. (continued)

| Stand | Family | Test Sites A | B | C | D | E | F |
|---|---|---|---|---|---|---|---|
| 4 | 1 | 2.56 | 3.29 | 2.14 | 2.72 | 3.12 | 1.26 |
| | 2 | 2.25 | 3.51 | 2.08 | 2.82 | 3.26 | 1.45 |
| | 4 | 2.34 | 3.46 | 2.01 | 2.86 | 3.27 | 1.17 |
| | 5 | 2.37 | 3.36 | 2.94 | 2.50 | 3.18 | 1.19 |
| | 6 | 2.34 | 3.35 | 2.06 | 2.49 | 3.11 | 1.33 |
| | 7 | | 4.25 | | | | |
| | 8 | 2.47 | 4.05 | 2.59 | 3.43 | 4.00 | 1.45 |
| | 9 | | 3.84 | | 3.09 | 3.50 | |
| | 10 | 2.45 | 3.27 | 2.10 | 2.87 | 3.12 | |
| | 12 | 2.43 | 3.32 | 1.74 | 2.74 | 3.15 | 1.25 |
| | 13 | 2.47 | 3.50 | 2.14 | 2.70 | 3.36 | 1.19 |
| | 14 | 2.60 | 3.68 | 2.48 | | | 1.45 |
| Mean Stand Height | | 2.44 | 3.55 | 2.13 | 2.82 | 3.31 | 1.36 |
| 6 | 2 | | 3.70 | 2.20 | | | |
| | 3 | 2.56 | 3.25 | 1.92 | 2.71 | 3.17 | |
| | 4 | 2.22 | 3.38 | 1.92 | 2.51 | 3.05 | 1.48 |
| | 6 | 2.40 | 3.26 | 2.21 | 2.33 | 3.15 | |
| | 7 | 2.29 | 3.35 | 1.93 | 2.48 | 2.83 | |
| | 8 | 2.47 | 3.35 | 1.92 | 2.82 | 3.37 | 1.33 |
| | 9 | | 3.66 | 2.45 | | 3.18 | |
| | 10 | 2.37 | 3.40 | 1.99 | 2.82 | 3.01 | 1.12 |
| | 11 | 2.38 | 3.30 | 1.92 | 2.83 | 3.11 | 1.25 |
| | 12 | 2.53 | 3.62 | 2.20 | 2.78 | 3.55 | |
| | 14 | 2.75 | 3.65 | | | 3.64 | |
| | 15 | | 3.45 | | | | |
| Mean Stand Height | | 2.44 | 3.45 | 2.07 | 2.65 | 3.22 | 1.30 |
| 7 | 1 | 2.16 | 3.27 | 1.95 | 2.72 | 2.96 | 1.43 |
| | 4 | 2.54 | 3.41 | 1.30 | 2.68 | 3.20 | 1.48 |
| | 5 | 2.29 | 3.17 | 2.15 | 2.48 | 2.81 | 1.67 |
| | 6 | 2.29 | 3.33 | 2.43 | 2.76 | 3.25 | 1.29 |
| | 8 | 2.26 | 3.41 | 2.10 | 2.67 | 3.23 | 1.26 |
| | 10 | 2.26 | 3.16 | 1.86 | 2.21 | 2.66 | 1.48 |
| | 11 | 2.17 | 3.51 | 1.90 | 2.61 | 3.20 | 1.43 |
| | 13 | 2.32 | 3.40 | 2.10 | 3.46 | 3.44 | 1.48 |
| | 14 | 2.85 | 3.74 | 2.42 | 2.89 | 3.71 | 1.51 |
| | 15 | 2.64 | 3.68 | 2.23 | 2.72 | 3.72 | 1.69 |
| Mean Stand Height | | 2.40 | 3.40 | 2.16 | 2.66 | 3.21 | 1.49 |

TABLE 26. (continued)

| Stand | Family | Test Sites A | B | C | D | E | F |
|---|---|---|---|---|---|---|---|
| 8 | 3 | 2.40 | 3.26 | 2.05 | 2.51 | 3.08 | 1.26 |
| | 4 | | 3.86 | 2.41 | | | |
| | 5 | 2.57 | 3.68 | 2.21 | 3.16 | 3.50 | 1.29 |
| | 6 | 2.41 | 3.16 | 1.92 | 2.74 | 3.25 | |
| | 8 | | 3.71 | 2.21 | | | |
| | 9 | 2.39 | 3.33 | 1.97 | 2.53 | 3.00 | 1.39 |
| | 10 | 2.28 | 3.43 | 1.95 | 2.53 | 3.27 | |
| | 11 | | 3.75 | | | | |
| | 12 | 2.47 | 3.42 | | | | |
| | 13 | 2.51 | 3.65 | 2.57 | 3.51 | 3.52 | |
| | 14 | 2.28 | 2.77 | 1.48 | 2.40 | 3.04 | 1.04 |
| | 15 | 2.66 | 3.62 | 3.03 | | | |
| Mean Stand Height | | 2.44 | 3.47 | 2.09 | 2.77 | 3.24 | 1.24 |
| 9 | 1 | 2.51 | 3.78 | 2.18 | 2.98 | 3.55 | 1.24 |
| | 3 | | 3.64 | | | | |
| | 4 | 2.64 | 3.52 | 2.29 | 3.02 | 3.28 | 1.31 |
| | 5 | 2.34 | 3.55 | 2.37 | 3.87 | 3.15 | 1.47 |
| | 6 | 2.19 | 3.31 | 2.20 | 3.38 | 3.06 | 1.31 |
| | 7 | 2.45 | 3.39 | 2.10 | 2.71 | 3.08 | 1.27 |
| | 9 | 2.05 | 3.22 | 1.81 | 2.68 | 2.80 | |
| | 10 | 2.24 | 3.25 | 2.06 | 3.13 | 3.17 | 1.45 |
| | 11 | | 3.48 | | | | |
| | 12 | 2.70 | 4.13 | 2.61 | | | |
| | 13 | | 3.62 | | | | |
| Mean Stand Height | | 2.40 | 3.53 | 2.22 | 2.78 | 3.16 | 1.34 |
| 10 | 2 | 2.73 | 3.92 | 2.64 | 3.05 | 4.00 | 1.39 |
| | 3 | 2.52 | 3.72 | 2.24 | 3.15 | 3.35 | 1.38 |
| | 4 | 2.86 | 3.81 | 2.25 | 2.96 | 3.70 | 1.54 |
| | 5 | 2.66 | 3.40 | 2.18 | 2.60 | 3.77 | 1.16 |
| | 6 | 2.58 | 3.26 | 1.97 | 2.87 | 3.21 | 1.48 |
| | 9 | 2.36 | 3.70 | 2.24 | 3.05 | 3.58 | 1.38 |
| | 10 | 2.60 | 3.53 | 2.35 | 2.45 | 3.39 | 1.29 |
| | 11 | | 3.73 | | 3.07 | 3.42 | 1.29 |
| | 14 | 2.67 | 4.05 | 2.34 | 3.02 | 3.41 | 1.38 |
| | 15 | 2.49 | 3.37 | 1.76 | 2.59 | 3.22 | 1.42 |
| Mean Stand Height | | 2.60 | 3.66 | 2.23 | 2.90 | 3.51 | 1.38 |

TABLE 26. (continued)

| Stand | Family | Test Sites A | B | C | D | E | F |
|---|---|---|---|---|---|---|---|
| 11 | 1 | | 4.14 | | | | |
| | 2 | 2.65 | 3.48 | | 2.80 | 3.28 | |
| | 3 | 2.70 | 3.28 | 1.80 | 3.14 | 3.31 | 1.37 |
| | 4 | | 4.04 | | 2.80 | | |
| | 5 | 2.40 | 3.31 | 1.97 | 2.36 | 3.44 | 1.40 |
| | 6 | 2.42 | 3.83 | 2.35 | 2.91 | 3.51 | 1.91 |
| | 7 | | 4.44 | | | | |
| | 8 | | 4.08 | | | | |
| | 9 | 2.54 | 3.34 | 1.96 | 2.62 | 3.24 | |
| | 10 | 2.37 | 3.16 | 1.91 | 2.60 | 2.98 | |
| | 11 | 2.39 | 3.55 | 2.18 | 2.80 | 3.38 | |
| | 14 | 2.40 | 3.37 | 2.08 | 2.66 | 3.16 | |
| | 15 | 2.33 | 3.25 | 1.60 | 2.53 | 3.02 | |
| Mean Stand Height | | 2.46 | 3.63 | 1.99 | 2.69 | 3.25 | 1.55 |
| 12 | 5 | | 3.34 | | | | |
| | 6 | | 3.48 | | | | |
| | 7 | | 3.99 | | | | |
| | 10 | | 3.68 | | | | |
| | 12 | | 3.93 | | | | |
| | 14 | | 3.52 | | | | |
| | 15 | | 3.40 | | | | |
| Mean Stand Height | | | 3.75 | | | | |
| 13 | 1 | 2.51 | 3.52 | 1.83 | 2.85 | 3.55 | 1.42 |
| | 2 | 2.63 | 3.60 | 1.97 | 2.63 | 3.41 | 1.44 |
| | 3 | 2.72 | 3.83 | 2.41 | 3.22 | 3.32 | |
| | 4 | 2.54 | 3.87 | 2.57 | 3.02 | 3.25 | |
| | 6 | 2.26 | 3.49 | 2.17 | 2.99 | 3.25 | 1.09 |
| | 7 | | 3.67 | | 2.86 | | 1.46 |
| | 9 | | 3.86 | 2.29 | 3.27 | 3.49 | |
| | 11 | 2.41 | 3.65 | 2.01 | 2.94 | 3.58 | 1.39 |
| | 14 | | 4.13 | | | | |
| | 15 | | 4.04 | | 3.37 | | |
| Mean Stand Height | | 2.50 | 3.76 | 2.18 | 3.02 | 3.47 | 1.37 |

# VITA

Richard Martin Evans was born in Nashville, Tennessee on July 16, 1945. He attended elementary and high school in Nashville, and graduated from Madison High School in 1964. He entered the University of Tennessee in 1964 and received the degree of Bachelor of Science in Forestry in August, 1968.

In September, 1968 he entered the University of Tennessee Graduate School to begin working towards a Master's Degree in Forestry, specializing in tree improvement and with a minor in Botany.

During the summer of 1965 he was employed by the United States Forest Service. While in Graduate School, he was employed as a Graduate Research Assistant in Forestry. During the summer of 1969, he was employed by the Department of Forestry as an instructor in Forestry Summer Camp. Presently, he is Assistant Geneticist for the Western Gulf Forest Tree Improvement Program.

Richard Evans is married to the former Carole Clinton, and they have one son, Clayton Daniel, born in 1967.

He is a member of the Society of American Foresters.