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I am submitting herewith a thesis written by William K. desBordes entitled "Estimates of Variation, Heritabilities and Gains Obtained from Two Open-Pollinated Progeny Test Plantations of Eastern White Pine (*Pinus strobus* L.)." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

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ESTIMATES OF VARIATION, HERITABILITIES AND GAINS OBTAINED FROM TWO OPEN-POLLINATED PROGENY TEST PLANTATIONS OF EASTERN WHITE PINE (*Pinus strobus L.*)

A Thesis

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ABSTRACT

The objective of this study was to evaluate genetic and environmental sources of variation in height, diameter, volume, crown width, length of flush (terminal leaders), needle length, number of branches, and current and previous year needle colors in eastern white pine (*Pinus strobus* L.). Data from 2 8-year old plantations in Tennessee containing approximately 20,000 open-pollinated progenies from 128 half-sib families originating in 13 stands from Tennessee, North Carolina and Georgia were analyzed.

Progenies of 4 stands from Tennessee and Georgia grew fastest in both locations. These progenies had darker green and longer needles than progenies from other stands, indicating resistance to air pollution damage.

Variance components of the 2 locations revealed that the sources of variations were very similar. Variance components also indicate that height, diameter, volume, needle color and needle length were strongly inherited traits.

In addition to the individual location analyses, a combined location analysis was completed to obtain the interaction of location with stand and interation of location and family within-stand. Variance components in the combined location analysis were very similar in magnitude to those of the individual location analyses. The genotype and environmental interaction variance component evaluated (interaction of location with stand and interaction of location with family within-stand) for all variables were small and did not exceed 2% of the total variation.

Narrow-sense heritability estimates based on variance components for the individual locations and the combined locations for all variables measured were very similar.

Expected gains using the 2-stage selection scheme were computed for height, diameter and volume at the 2 locations. Selection of the best 40 families regardless of stands will result in average gains of 13, 17 and 29% for height, diameter and volume, respectively. Selection of the best tree within each family row-plot increased the total average genetic gain to 22% for height, 28% for diameter and 45% for stem volume.

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CHAPTER I

INTRODUCTION

Eastern white pine (*Pinus strobus* L.) is one of the most widely ranged conifers in the eastern United States and eastern Canada because it grows naturally on a much wider range of site conditions than any other eastern American conifer (Wright, 1970). It ranges from Newfoundland and Nova Scotia west to Southeast Manitoba, south through the Great Lakes and Southern Appalachian Mountain regions to Iowa, western Kentucky and northern Georgia. Also, it has been grown as an exotic in several parts of the world including Europe, Japan, South Africa and New Zealand.

The Southern Appalachian eastern white pine is native to Tennessee, but ranks behind three southern pines and several hardwood species with respect to growing stock volume (Thor, 1976).

A clinal variation pattern in height growth of eastern white pine from the Southern Appalachians is present; progenies from southern latitudes grow faster than those northern sources. In addition, there is evidence that ecotypic variation in height growth is present within this clinal pattern. Trees of Southern Appalachian seed sources have advantages over those from other sources due to their rapid growth rate and easy adaptability to different areas outside the natural range.

A progeny test established with 2-year old white pine seedlings from Southern Appalachia in 4 different physiographic regions in Tennessee proved that the East Tennessee sources were superior in height growth (Thor, 1974). Five-year data of growth rate from this progeny

test indicated the superiority of the east Tennessee sources (Thor and Gall, 1978). Results of height growth from Nebraska also revealed the superiority of the east Tennessee sources (Sprackling and Read, 1976).

There are a few difficulties in growing eastern white pine. These include the susceptibility of eastern white pine to air pollution damage, blister rust, white pine weevil and fire. In Tennessee, little or no damage has been caused by blister rust or white pine weevil; however, air pollution and fire have been main causes of white pine damage. Thor (1976) reported that air pollution from areas near the Copperhill smelting plant resulted in the removal of the most air pollution susceptible genotypes from that population; trees from the Copperhill smelting plant area have apparently undergone natural selection.

Currently, the uses of eastern white pine have increased considerably. It is used for high quality mill-work, panelling and trim lumber (Carson, 1976). Other uses of eastern white pine include pulp for paper-making, cardboard, craft papers and lumber. In Nebraska it is used for landscaping, Christmas trees and windbreaks (Sprackling and Read, 1976).

In Tennessee, approximately one-half million eastern white pine seedlings are planted each year for Christmas trees because of its foliage color and ability to retain needles. However, about half a million seedlings are also used for landscaping purposes. It is estimated that approximately 2,000,000 eastern white pine seedlings are planted each year in Tennessee (Thor, 1976). Considering the high number of eastern white pine trees planted each year for use as landscape and Christmas trees, it would be profitable to select for characteristics desired by nursery men and Christmas tree producers.

The objectives of this study are:

1. To determine genetic and environmental variation and their interaction with respect to height, diameter at breast height (DBH), volume, crown width at one-third height, length of last terminal leader flush, number of branches at last whorl, needle length at breast height, previous and current year needle color and needle form in 8-year old eastern white progeny test plantations.

2. To obtain estimates of variance components for characteristics mentioned.

3. To obtain estimates of heritability for all these characteristics.

4. To give an example of genetic gain which could be expected using different selection schemes in establishment of a seedling seed orchard.

CHAPTER II

LITERATURE REVIEW

Geographic Variation

Natural variation. Natural variation patterns are determined from observations of the phenotypes growing in natural stands. Very little information appears to be available on natural variation patterns in eastern white pine.

The only literature found on natural variation was by Thor (1965) in which he investigated variation in some wood properties of eastern white pine in Morgan County, Tennessee. He observed large phenotypic variation for most characteristics investigated but did not find any definite variation pattern.

Provenance tests. The definition of provenance by tree breeders means ultimate natural origin; provenance test is an experiment in which seeds are collected from widely scattered stands (usually natural) and the seedlings are grown under similar conditions (Wright, 1976a).

A rich source of information on eastern white pine provenance tests is the Forest Service Range-Wide Tests established in 1955. Its objectives were to determine the geographic variation in selected traits and make necessary recommendations for the movement of seeds over the species range (Demeritt and Kettlewood, 1975).

Two-range-wide provenance test results indicated that trees from the Southern Appalachian sources grew fastest even as far north as Pennsylvania and southern Michigan (Funk, 1965; Genys, 1968; Wright

et al., 1963). Similarly, seed sources from Georgia, Tennessee and North Carolina grew faster than those from Virginia, West Virginia and Maryland (Fowler and Heimburger, 1969; Wright, 1970). Also, provenance studies of Christmas trees in Ohio and Eastern Kentucky indicated that eastern white pine from Southern Appalachian sources (Tennessee, Georgia and North Carolina) and lower Michigan had the greatest Christmas tree potential for Eastern Kentucky. However, sources from Ohio, North Carolina and Michigan ranked highest in Ohio plantations (Walters, 1971). The Duncan's New Multiple Range Test indicated that three Southern Appalachian sources (Georgia, Tennessee and North Carolina) were the fastest growing sources in Southern Michigan, Virginia, Georgia and North Carolina (Sluder and Dorman, 1971; Wright et al., 1963). In Southern Appalachian plantations, the Southern Appalachian sources continued to be the fastest growing sources (Sluder, 1963; Thor, 1974). In Nebraska, provenance tests revealed that the Southern Appalachian sources were superior for landscape, windbreaks and Christmas trees (Sprackling and Read, 1976). Studies in Illinois, West Virginia, Indiana, Southern Michigan and Pennsylvania continued to reveal the superiority of the Southern Appalachian sources (Funk, 1965; Funk, 1971; Garrett et al., 1973; Maronek and Harrison, 1974; Wendel and Cech, 1976).

Only in the provenance trials conducted in Wisconsin and Minnesota did the Southern Appalachian sources grow slower than northern sources (King and Nienstaedt, 1969).

White pine foliage characteristics have been of great interest to Christmas tree breeders because of consumer preference for long,

straight, blue-green or dark green needles. Foliage characteristics also serve as an indicator of air pollution damage (Berry, 1973; Berry and Hepting, 1964; Costonis, 1973; Gall, 1978; Houston and Stairs, 1973). Results from provenance trials showed that the Southern Appalachian sources had longer needles and ranked higher in foliage color in Kentucky than in Ohio (Walters, 1971). Similarly, studies in Nebraska indicated that Southern Appalachian sources had greater average needle length but foliage color was not consistent within sources (Garrrett et al., 1973; Sprackling and Read, 1976). Other studies determined that Southern Appalachian sources had blue-green foliage and sources from Lake States had green foliage but no bluish cast (Wright et al., 1963). Thor (1976) evaluated Southern Appalachian eastern white pine origins and obtained significant differences in color between families from the same stands. Also, stands from Tennessee had longer and darker green needles when compared with stands from other areas of Southern Appalachia (Thor and Gall, 1978).

Provenance test results for branching habits of Southern Appalachian sources growing in Illinois and Southern Indiana indicated that Southern Appalachian sources had fewer branches than those from northern sources (Funk, 1971).

Progeny trials. Evidence of genetic diversity in growth rates among trees have led to various progeny trials in eastern white pine. Progeny tests could be based on either half-sib or full-sib families. In conifers half-sib progeny tests are preferable for first generation work and less expensive, whereas full-sib tests are used in more advanced breeding programs. Progeny tests are described as experiments designed

to compare the offspring of different parents or to compare performance of offspring and parents (Wright, 1976b).

Studies were conducted on progenies from 128 families in 13 Southern Appalachian *Pinus strobus* stands (Tennessee, Georgia and North Carolina); thus revealing differences in growth rate when planted in 3 locations in Tennessee (Thor, 1976). On the contrary, studies in various parts of Michigan revealed no differences in growth rates among progenies (Kuo et al., 1971). A report by Wendel and Cech (1976) indicated that 6 out of 13 stands had differences in 6-year seedling height among families within stands. Progeny tests in Ohio revealed height differences among 75 progenies which accounted for 19% of the total variance (Kriebel, 1972). In the Michigan half-sib progeny tests, differences in height growth among families from the same stand were reported (Wright, 1970). Provenance tests in Nebraska indicated that progenies from 1 parent tree from Polk County, Tennessee, showed superior performance in height growth compared with all other progenies in the study (Sprackling and Read, 1976).

Thor (1974) reported that within most stands some mother trees produced progenies with longer and darker needles than progenies from other mother trees in the same stand. Progenies from Buncombe County, North Carolina, had the longest needles when compared with those from other sources in provenance trials in Nebraska but foliage color was not consistent within progenies (Sprackling and Read, 1976). Analysis of variance on foliage color revealed highly significant differences among stands and among families within stands at the 1% level (Carson, 1976).

Most of the literature on progeny tests is recent and on juvenile growth. More meaningful results will be achieved when the trees reach rotation ages for specific uses.

Heritability and Gain Estimates

Narrow-sense heritability. The estimate of heritability is generally used as a guide to the amount of improvement possible in a measured trait. It is defined as an estimate of the proportion of phenotypic variance attributed to additive genetic effects; or it is a ratio of the genetic variance to the phenotypic variance which can be used for breeding purposes (Falconer, 1960).

The Variance Component Method has been the general method of estimating narrow-sense heritability. Recently, least square estimates of variance components compensate for missing observations which biased earlier heritability estimates. Errors encountered in the estimation of heritabilities are discussed by several authors (Evans, 1971; Namkoong et al., 1966; Rink, 1974; Rink and Thor, 1976; Stonecypher, 1966; Stonecypher et al., 1973).

Various studies on eastern white pine have been carried out in which narrow-sense heritabilities have been calculated. In a modified diallel, using progenies of eastern white pine from Central Ohio, heritability for height growth increased with increasing age of progeny. Heritability based on individual trees was 0.11 after 4 growing seasons and 0.28 after 6 growing seasons. Also, heritability estimates based on family means were 0.23 for 4 growing seasons and 0.48 for 6 growing seasons (Kriebel et al., 1974). On the contrary,

heritability estimates for height growth based on individual trees and plot total means for progenies from Ohio revealed a decline in heritability estimates with an increase in age (Kriebel et al., 1972). An individual tree narrow-sense heritability estimate for height growth at 5 years based on progenies from 30 open-pollinated families selected from 6 stands in the Southern Appalachians was 0.11 (Thor, 1974). In 3 test plantations, Thor and Gall (1978) obtained narrow-sense heritabilities for height growth which varied between 0.20 to 0.33 using 128 open-pollinated progenies from Tennessee, Georgia and North Carolina.

Narrow-sense heritability was also calculated for other characteristics such as needle length and needle color. An estimate of 0.32 was obtained for needle length and 0.64 for needle color in the same studies in Tennessee using progenies from North Carolina, Georgia and Tennessee (Thor and Gall, 1978).

Plot size affects heritability estimates as observed in a 5-year old white pine open-pollinated heritability test established in 2 locations in Tennessee (Gall and Thor, 1977).

Gains. Falconer (1960) defined gain as the product of selection intensity, appropriate phenotypic standard deviation and heritability. The calculation of this product stresses the response expected by using different selection schemes when breeding for a specific character.

Namkoong et al. (1966) formulated the additive methods of computing expected gains using multi-stage selection schemes. This method is used in phenotypic selection of the wild parent trees, followed by selection of the best individuals within the best families in an

open-pollinated progeny test. The formula used to obtain the expected gain from the above mentioned selection scheme is:

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

Where: $\sigma_1 = \sigma^2_w + \sigma^2_p + \sigma^2_{GE} + \sigma^2_G$

$$\sigma_2 = \frac{\sigma^2_T + \sigma^2_p}{NRE} + \frac{\sigma^2_{GE}}{E} + \frac{1}{4}\sigma^2_{A_1}$$

$$\sigma_3 = \sigma^2_w + \sigma^2_p + \sigma^2_{GE} + \frac{3}{4}\sigma^2_{A_1} + \sigma^2_D$$

σ^2_A = Total additive genetic variance for large random mating population.

$\sigma^2_{A_1}$ = Among family variance component or additive genetic variance component.

It is usually assumed that genetic variance is a result of recombination between parental and progeny generations and so $\sigma^2_{A_1} = \sigma^2_A$:

σ^2_T = Error variance of small plot.

σ^2_w = Within plot or individual tree variance component.

σ^2_p = Among replication variance component.

σ^2_{GE} = Genotype x environmental interaction variance component.

σ^2_G = Total genetic variance component.

σ^2_D = Total dominance variance component.

i_1 = First stage selection intensity (mass selection).

i_2 = Second stage selection intensity (among family selection)

i_3 = Third stage selection intensity (within family selection).

E = Environment.

R = Number of replications.

N = Number of trees in a plot.

G = Overall expected gain.

The formula for the overall gain can now be divided into 3 sections according to the different selection schemes.

Gain due to mass selection is:

$$i_1 \frac{\sigma^2_A}{\sigma_1}$$

Gain due to among family selection is:

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

Gain due to within family selection is:

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

Another method of estimating genetic gain can be found in Wright (1976a). In his formula, specifically designed for half-sib progeny tests, genetic gain was divided into two selection schemes: (1) gain due to family selection and (2) gain due to mass selection within families.

In order to calculate genetic gain from family selection, selection differential of family and family heritability are used as follows:

$$G_f = sd_f \times h_f^2$$

Where: G_f = Gain due to family selection.

sd_f = Selection differential for family.

= (Selected families - average families.)

h_f^2 = Family heritability.

Expected mass selection gain is derived from selection differential of single tree and single tree heritability. The formula is as follows:

$$G_w = sd_w \times h_w^2$$

Where: G_w = Gain due to mass selection.

sd_w = Selection differential for individual tree.

= (Selected trees - average trees.)

h_w^2 = Single tree heritability.

The selection differential and heritability in this method always applies to the same character. The total gain is obtained by adding up the 2 gains computed:

$$G_T = G_f + G_w$$

Where: G_T = Total gain.

Thor (1976) stated that by selecting the best individual progenies from the best families, it would be possible to obtain gains of about 20% in juvenile height growth of eastern white pine. This gain was the minimum gain from 1 generation of selection. The maximum gain expected was between 45 to 73%.

Kriebel et al. (1974) computed gains based on different selection schemes and obtained an increase in gain with increase in selection differential.

Genetic Assumptions Concerning Populations of Parents and Progenies

Interpretations of additive variance components in a progeny test can be more meaningful using a series of assumptions listed by Stonecypher (1966) and by Stonecypher et al. (1973). These assumptions were derived from components of parent and progeny populations, and most of them were formulated using the Hardy Weinberg Law of Equilibrium. These assumptions were:

1. Regular diploid, Mendelian inheritance.
2. Parent populations are in linkage equilibrium.
3. Parent and progenies are not inbred and are random members of non-inbred populations.
4. Open-pollinated progenies are half-sibs.
5. There is no epistatis.
6. There are no maternal effects.

The assumption that parent and progenies are not inbred has been generally used in most genetic studies in forestry. Even selfing is ignored for all practical purposes, for example, estimates of average coefficient of inbreeding for loblolly pine is very low (0.0003) (Franklin, 1971).

It is usually interpreted that the family component in an open-pollinated progeny study is one-quarter of the additive genetic variance because of the assumption that all progenies are half-sibs. This is possibly only when the percentage of inbred families is very low and therefore ignored (Franklin, 1971).

Genotype-Environment Interactions

There is a general agreement among plant breeders that interactions between genotype and environments have an important bearing on

the breeding of better varieties (Allard and Bradshaw, 1964). On less productive sites, where environmental factors are less than optimum, species tend to develop at the expense of adaption, thus losing much vigor (Namkoong, 1969).

Reports of genotype x environment interaction and genotypic stability in loblolly pine (*Pinus taeda* L.) progenies revealed that magnitude of additional genetic x environment interaction variance was large enough to cause upward biases on heritability estimates and genetic gain predictions of up to 60% for mass selection and up to 100% for mass selection plus half-sib family selection, mass selection plus full-sib family selection and mass selection followed by a seedling seed orchard breeding strategy (Owino et al., 1977). Kriebel et al. (1972 and 1974) suggested that there was no genotype x environment interaction in the incomplete diallel cross experiment with eastern white pine because the families selected were not sensitive to genotype and environment interactions.

Stonecypher (1966) reported that the genotype and environment interaction was low for the first and second year heights and high for survival in loblolly pine. In Douglas fir (*Pseudotsuga menziesii* Mirb.), family x location interaction was found to be a significant part of the test total variation for height growth (Campbell, 1972). In Virginia pine, genotype x environmental interaction for height growth accounted for less than 2% of the total variation and was disregarded for practical purposes (Rink, 1974).

Investigations based on a heritability study of loblolly pine suggested that there could be substantial biases in genetic gain predictions due to genotype x location interaction for some traits

such as volume, diameter, dry weight and trachied length (Barker, 1973). Owino (1977) indicates that few sets of families were below average stability in a loblolly pine progeny test and therefore the family sets were well-adapted to all environments. In most breeding programs, very small values of the genotype-environment interaction are of great advantage indicating adaptability of genotypes to various environments. To determine this, a range of progeny tests will be required.

CHAPTER III

MATERIAL AND METHODS

Parent Population Selection

This experiment was established in 1970 from open-pollinated seeds collected from 13 Southern Appalachian *Pinus strobus* L. stands in Georgia, North Carolina and Tennessee. Selection of these parent stands (seed sources) was limited to the extreme southern end of the species range because of the wide variation observed in height growth of southern trees in a pilot study (Thor, 1974). Nine of the stands were in Tennessee, 3 in North Carolina and 1 in Georgia as shown in Figure 1. These stands represent 3 major physiographic regions: Blue Ridge of North Carolina, Tennessee and Georgia, Cumberland Plateau and Great Valley of Tennessee (Figure 1). The parent stands ranged in age from 35 to 64 years. Stands selected were essentially even-aged and of average or better than average quality.

The only selection criteria used were that trees had to be dominants or co-dominants, safe to climb, and had an adequate cone crop. For each stand, 10 trees were selected as potential parent trees. Site index ranged from 75 to 105 feet and average diameter breast height in the 13 stands ranged from 15.9 inches to 23.8 inches (Table 1). The site index was calculated using site index curves for white pine at 50 years by Beck (1971).

Planting Materials

It was calculated that a minimum of 200 cones would be required from each parent tree in order to produce enough seedlings for planting

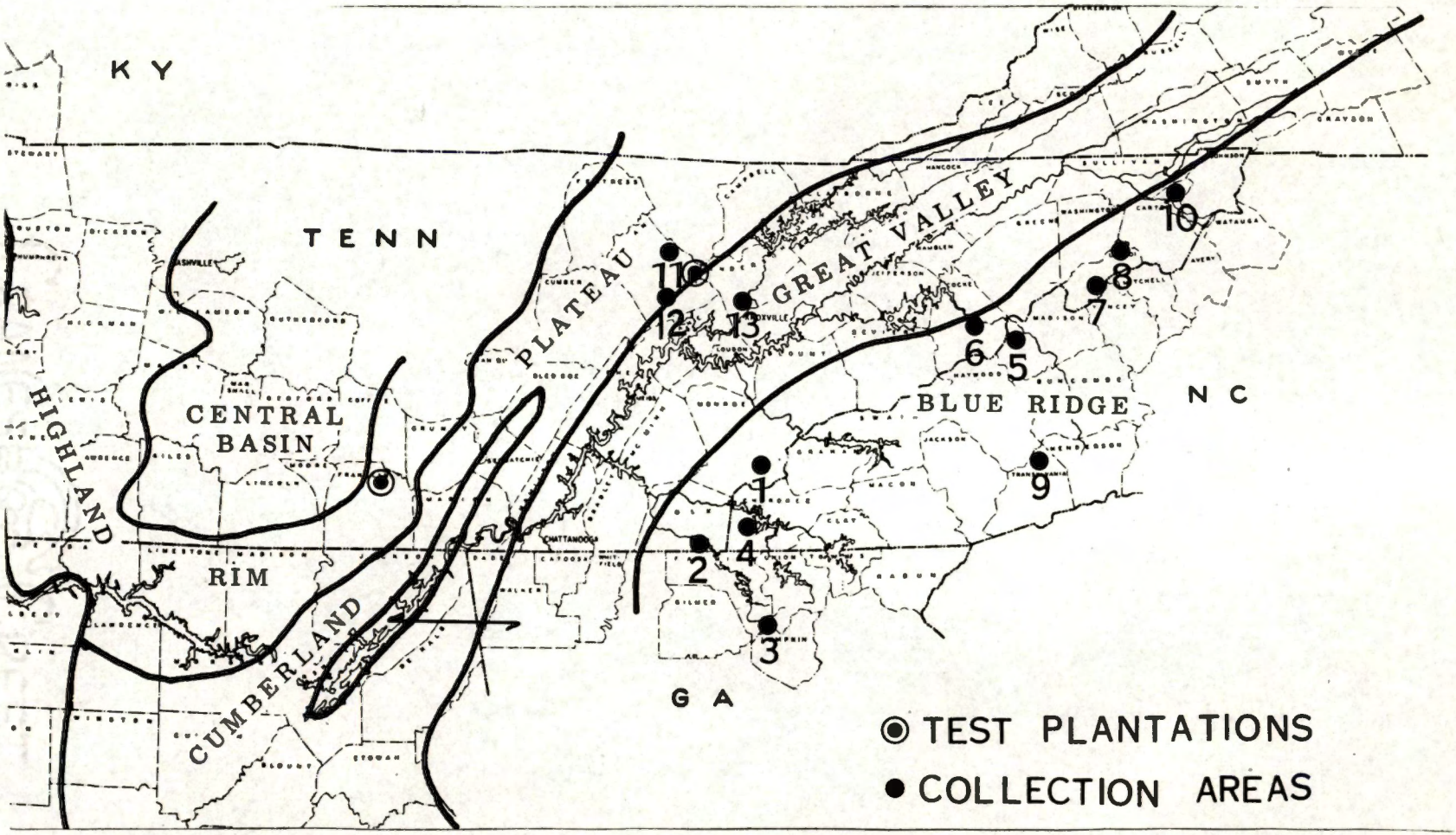


Figure 1. Collection areas and test plantations of eastern white pine (*Pinus strobus* L.) in Georgia, Tennessee and North Carolina.

Table 1. Physiographic region, location, site index, diameter breast height and age of parent stand. (Averages are based on 10 trees per stand)

Stand Number	Physiographic Region	Location	Site Index (feet at 50 years)	Diameter Breast Height	Age (Years)
1	Blue Ridge	East of Tellico Plains, Monroe County, Tennessee	96	18.2	44
2	Blue Ridge	West of Copperhill, Polk County, Tennessee	105	22.0	50
3	Blue Ridge	West of Suches, Fannin County, Georgia	93	17.4	37
4	Blue Ridge	West of Suit, Cherokee County, North Carolina	85	18.1	39
5	Blue Ridge	West of Hot Springs, Madison County, North Carolina	93	21.6	58
6	Blue Ridge	Northeast of Hartford, Cocke County, Tennessee	75	15.9	64
7	Blue Ridge	Highway 19-West near Summit, Unicoi County, Tennessee	No Data	No Data	No Data
8	Blue Ridge	Near Unicoi Unicoi County, Tennessee	90	22.5	46
9	Blue Ridge	North of Brevard, Transylvania County, North Carolina	96	23.8	53

Table 1 (continued)

Stand Number	Physiographic Region	Location	Site Index (feet at 50 years)	Diameter Breast Height	Age (Years)
10	Blue Ridge	Butler, Carter County, Tennessee	80	18.2	55
11	Cumberland Plateau	U.T., Morgan County Forest, Morgan County, Tennessee	84	18.2	95
12	Cumberland Plateau	U.T., Morgan County Forest, Morgan County, Tennessee	83	16.8	42
13	Great Valley	U.T., Oak Ridge Forest, Anderson County, Tennessee	102	18.4	59

in all test locations. Although eastern white pine has been known as a good producer of cones, some of the parent trees did not meet this minimum requirement. Cones were collected from 1962 to 1967; it took 5 years to collect all the cones required from all 13 stands because several promising cone crops were destroyed by the white pine cone beetle (*Conophthorus coniperda*).

Cones were harvested by climbing the parent tree or by cutting down branches with a high-powered rifle. Following cone collection and extraction, the seeds were stored at approximately 40°F in plastic bags until sowing.

Seedlings were grown at the Tennessee State Division of Forestry Nursery at Pinson, Tennessee. The seeds were planted with no replications in the nursery beds during the spring of 1968. Seedlings were grown for 2 years, then lifted, sorted into bundles of 10 seedlings per family and tagged. Only healthy-looking seedlings were selected while small and deformed seedlings were culled. Selected seedlings were packed in damp peat moss and wrapped in seedling wrapping paper prior to shipment to test locations for out-planting.

The maximum number of half-sib families out-planted was 128. All 128 sets of half-sib families was out-planted at the Highland Rim location, but only 96 half-sib families were out-planted at the Cumberland Mountain location because the number of progenies produced varied among parent trees. The number of families from each stand planted at each location can be found in Table 2.

Description of Plantation Sites

The two locations used in this study were on the Highland Rim

Table 2. Number of families per stand planted at each test location

Stand Number	Test Locations	
	Highland Rim	Cumberland Mountain
	Number of Families	
1	10	10
2	10	10
3	10	10
4	10	10
5	8	8
6	10	6
7	10	6
8	10	8
9	10	5
10	10	4
11	10	8
12	10	7
13	10	10
Total	128	96

and the Cumberland Mountain (Figure 1). The Geological Map of Tennessee (1965) and the Soil Association Map (1959) were referenced for information on the geology and environment of these sites. Most of the site conditions described are from observations of the sites by the author and personal communications with his major advisor. A complete summary of the site descriptions are presented in Table 3.

Highland Rim. This site is located at the University of Tennessee Highland Rim Forestry Field Station in Tullahoma, Franklin County, Tennessee, at an elevation of about 1000 feet (Figure 1).

The texture of the soil is mainly silt loam with an impervious 18-inch deep fragipan. The classification of the soil series is Dickson (Table 3).

The mean annual precipitation is about 53 inches and the mean daily temperature ranges from 41.5°F in January to 77.6°F in July. There are 196 frost free days (Nelson and Zillgitt, 1969). Approximately 10 acres of land was available for this study. This land was previously used as pasture land; therefore only bush hogging was necessary for site preparation. The site was almost completely level.

Cumberland Mountain. This site was located at the University of Tennessee Cumberland Forestry Field Station near Wartburg, Morgan County, Tennessee. Physiographically, the site is located on the Cumberland Plateau at an elevation of about 1250 feet (Figure 1). The soil is a Muskingum silt loam with many large and small stones. The topography of the site is a steep north slope. Mean daily temperatures range from 40°F in January to 75°F in July, and the mean annual precipitation is about 54 inches. There are 180 frost free days (Nelson and Zillgitt,

Table 3. Climatic description (based on period 1931-1960),[1] elevation, location, physiography, previous land use, site preparation, soil properties and topography of test sites

Item	Test Sites	
	Highland Rim	Cumberland Mountain
Location	Franklin County, Tennessee	Morgan County, Tennessee
Elevation (feet)	1000	1250
Physiography	Highland Rim	Cumberland Plateau
Topography	Flat	Steep North Slope
Soil Series	Dickson	Muskingum
Soil Texture	Silt Loam	Silt Loam & Sandstone
Soil Depth	18 inches to Fragipan	Deep
Mean Annual Precipitation (inches)	53	54
Mean Daily Temperature for January (°F)	41.5	40
Mean Daily Temperature for July (°F)	77.6	75
Average Length of Freeze-Free Period (number of days)	196	180
Previous Land Use	Pasture	Forest
Site Preparation	Bush Hog	Clear cut, piked and burned, 2,4,5-T spray of hardwood sprouts

[1] T. C. Nelson and W. M. Zillgitt, 1969.

1969). This site was previously in forest and about 10 acres were cleared for this study; the slash burned and hardwood sprouts sprayed with 2,4,5-T. Three of the replications were on fairly level land at the bottom of the steep north slope where the other seven replications were located.

Measurements

Measurements were taken between July and December 1977, following 8 growing seasons in the field; 9 characteristics were measured in both plantations:

1. Stem diameter at breast height to the nearest 0.1 inch.
2. Total height to the nearest foot.
3. Width of crown at one-third of total height to the nearest foot.
4. Length of current year terminal leader flush to the nearest foot.
5. Number of branches at last whorl.
6. Current year needle length at breast height to the nearest millimeter.
7. Current year needle color based on numerical ranking from 1 to 8 (Table 4).
8. Previous year needle color based on numerical ranking from 1 to 8 was taken for 10 replications at the Highland Rim plantation and 3 replications at the Cumberland Mountain plantation (Table 4). The data from Cumberland Mountain plantation was discarded since it was obtained in the late growing season and all the previous year needles had turned yellow.

Table 4. Ranking, Munsell Color Code, and visual color of needles

Ranking	Munsell Color Code	Visual Color
1	7/6 Hue 2.5 G.Y.	Yellow
2	6/4 Hue 2.5 G.Y.	Light Green Yellow
3	6/4 Hue 5.0 G.Y.	Green Yellow
4	6/8 Hue 7.5 G.Y.	Light Yellow Green
5	6/6 Hue 7.5 G.Y.	Yellow Green
6	6/4 Hue 7.5 G.Y.	Green
7	4/4 Hue 5.0 G.Y.	Dark Green
8	4/4 Hue 7.5 G.Y.	Blue Green

9. Needle characteristics based on two rankings (rank 1 = straight needles, rank 2 = droop or bent needles).

Individual tree volume was computed using total height and diameter breast height measurements. The volume equation for young loblolly pine was used for the computation of the individual tree volume (Perry and Roberts, 1964). The equation includes:

$$V = (63.49 + 4.769D^2H)/1728$$

Where: V = Volume in cubic feet.

D = Stem diameter at breast height in inches.

H = Total height in feet.

Design and Analysis

Field design. A randomized complete block design was used in each test site with families randomized within each replication. Half-sib families were planted in 10-tree row plots with a spacing of 4 feet between trees in each family row plot and 8 feet between rows. Border rows were of a mixture of half-sib families planted in 2-tree rows around each test block. The size of each test site was about 10 acres consisting of 10 replications. The Highland Rim plantation contained 128 half-sib families and the Cumberland Mountain plantation contained 96 half-sib families.

Statistical analysis. Least square analyses were performed on both separate and combined locations using the General Linear Model (G.L.M.) procedure in the Statistical Analysis System (S.A.S.) (Barr et al., 1976). Analyses of variance were performed on 8 of the variables at the Highland Rim plantation and 7 at the Cumberland Mountain

plantation, based on individual trees. Needle characteristics were the only non-parametric data used; they were analyzed by stand frequencies. The individual location analysis was performed in accordance with "Model 3" by Henderson (1953). The assumption used was that all effects were random. The mathematical linear model for the individual location analysis is as follows:

$$Y_{rsfw} = \mu + R_r + S_s + RS_{rs} + F/S_{f(s)} + R \times (F/S)_{rf(s)} + E_{wrf(s)}$$

Where: Y_{rsfw} = Total variation.

μ = Mean effect.

R_r = Replication effect.

S_s = Stand effect.

RS_{rs} = Replication and stand interaction effect.

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

$R \times (F/S)_{rf(s)}$ = Replication and family within stand interaction effect.

$E_{wrf(s)}$ = Within plot effect.

The analysis of variance model, degrees of freedom and expected mean squares were estimated using the methods of Snedecor (1956). Expected mean squares of random effects were derived using "Model II" of Steel and Torrie (1960). Also, reference was made to the rule of thumb for determining expectations to mean squares in analysis of variance by Schultz (1955). Sources of variation, degrees of freedom and expected mean squares for each location are presented in Table 5.

Combined location analysis was performed on 8 variables in

Table 5. Sources of variation, degrees of freedom and expected mean square table for each test plantation analysis

Source of Variation	Degrees of Freedom	Expected Mean Squares[1]
Replications	r-1	$\sigma^2_w + w\sigma^2_{R(F/S)} + wf\sigma^2_{RS} + wsf\sigma^2_R$
Stands	s-1	$\sigma^2_w + w\sigma^2_{R(F/S)} + wr\sigma^2_{F/S} + wf\sigma^2_{RS} + wrf\sigma^2_S$
Replications x stands	(r-1)(s-1)	$\sigma^2_w + w\sigma^2_{R(F/S)} + wf\sigma^2_{RS}$
Families in stands	(f-1)s	$\sigma^2_w + w\sigma^2_{R(F/S)} + wr\sigma^2_{F/S}$
Replications x Families in stands	(f-1)(r-1)s	$\sigma^2_w + w\sigma^2_{R(F/S)}$
Within plot	(w-1)rfs	σ^2_w

[1]Meaning of symbols used:

σ^2_w = Within plot variance component.

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

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

σ^2_{RS} = Variance component of interaction of replication with stand.

σ^2_S = Variance component of among-stands.

σ^2_R = Variance component of among-replications.

Table 5 (continued)

w = Average number of plants per plot =

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

Where: t = Number of trees in each plot.

F = Average number of families within stand =

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

Where: fm = Number of families within each stand.

r = Number of replications.

s = Number of stands.

accordance with the Model "3" by Henderson (1953). This model was used because it is an overall least square analysis designed for unbalanced data and compatible with the Statistical Analysis System (Barr et al., 1976). The combined location analysis was partitioned into two models (Model I and Model II) as presented in Table 6. The analysis of variance table for the combined locations was obtained by adding the sum of squares obtained from individual location and Models I and II since the sum of squares are additive as presented in Table 7. Expected mean squares for the new model with all effects assumed at random are contained in Table 7. The mathematical model for the combined locations is:

$$Y_{lr(f/s)w} = \mu + L_l + R/L_{r/l} + S_s + LS_{ls} + S(R/L)_{s(r/l)} + F/S_{f/s} +$$

$$L(F/S)_{l(f/s)} + (R/L)(F/S)_{(r/l)(f/s)} + W_{lrw(f/s)}$$

Where: $Y_{lr(f/s)w}$ = Total variation.

μ = Mean effect.

L_l = Location effect.

$R/L_{r/l}$ = Replication within location effect.

S_s = Stand effect.

LS_{ls} = Location and stand interaction effects.

$S(R/L)_{s(r/l)}$ = Stand and replication within location interaction effects.

$F/S_{f/s}$ = Family within stand effect.

$L(F/S)_{l(f/s)}$ = Location and family within stand interaction effects.

Table 6. Analysis of variance table showing expected mean squares of 2 models from which combined location analysis was partitioned. Each stand was computed separately in Model 2

Source of Variation	Degrees of Freedom	Expected Mean Squares[1]
Model 1		
Locations	$(\ell-1)$	$\sigma^2_w + w\sigma^2_{L \times F} + wf\sigma^2_L$
Families	$(f-1)$	$\sigma^2_w + w\sigma^2_{L \times F} + wl\sigma^2_F$
Locations x Families	$(f-1)(\ell-1)$	$\sigma^2_w + w\sigma^2_{L \times F}$
Residual	$(w-1)$	σ^2_w
Model 2		
Locations	$(\ell-1)$	$\sigma^2_w + w\sigma^2_{L \times S} + ws\sigma^2_L$
Stands	$(s-1)$	$\sigma^2_w + w\sigma^2_{L \times S} + wl\sigma^2_S$
Locations x Stands	$(\ell-1)(s-1)$	$\sigma^2_w + w\sigma^2_{L \times S}$
Residual	$(w-1)$	σ^2_w

[1]Meaning of symbols:

σ^2_w = Within plot variance component.

$\sigma^2_{L \times S}$ = Location with stand interaction variance component.

σ^2_S = Among-stand variance component.

$\sigma^2_{L \times F}$ = Variance component for interaction of location with family.

σ^2_F = Among-family variance component.

σ^2_L = Among-location variance component.

w = Number of trees per plot.
r = Number of replications.
f = Number of families.
s = Number of stands.
l = Number of locations.

Table 7. Degrees of freedom, mean squares and expected mean squares for combined location analysis

Source Variation	d.f.	Mean Squares	Expected Mean Squares[1]
Locations[2]	$\ell-1$	M.S. 1	$\sigma^2_w + w\sigma^2_{R/L \times F/S} + wf\sigma^2_{S \times R/L} + wr\sigma^2_{L \times F/S} + swf\sigma^2_{R/L} + wrf\sigma^2_{L \times S} + wrfs\sigma^2_L$
Replications in locations	$(r-1)\ell$	M.S. 2	$\sigma^2_w + w\sigma^2_{R/L \times F/S} + wf\sigma^2_{S \times R/L} + swf\sigma^2_{R/L}$
Stands[2]	$s-1$	M.S. 3	$\sigma^2_w + w\sigma^2_{R/L \times F/S} + wf\sigma^2_{S \times R/L} + wr\sigma^2_{L \times F/S} + wrl\sigma^2_{F/S} + wrf\sigma^2_{L \times S} + wrfl\sigma^2_S$
Locations x stands[2]	$(\ell-1)(s-1)$	M.S. 4	$\sigma^2_w + w\sigma^2_{R/L \times F/S} + wf\sigma^2_{S \times R/L} + wr\sigma^2_{L \times F/S} + wrf\sigma^2_{L \times S}$
Stand x Replications/ Location	$(s-1)(r-1)\ell$	M.S. 5	$\sigma^2_w + w\sigma^2_{R/L \times F/S} + wf\sigma^2_{S \times R/L}$
Families in Stands	$(r-1)s$	M.S. 6	$\sigma^2_w + w\sigma^2_{R/L \times F/S} + wr\sigma^2_{L \times F/S} + wrl\sigma^2_{F/S}$
Locations x Families/ Stands	$(\ell-1)(f-1)s$	M.S. 7	$\sigma^2_w + w\sigma^2_{R/L \times F/S} + wr\sigma^2_{L \times F/S}$
Replications/Location x Families/Stands	$(f-1)(r-1)\ell s$	M.S. 8	$\sigma^2_w + w\sigma^2_{R/L \times F/S}$
Within Plot	$(w-1)rfs\ell$	M.S. 9	σ^2_w

Table 7 (continued)

[1]Expected mean squares were determined in accordance with the method of Schultz (1955).

[2]Effects will be tested by synthetic error terms.

Note: Assumptions of all effects were random.

σ^2_w = Within plot variance component.

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

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

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

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

$\sigma^2_{L \times S}$ = Variance component for interaction of location with stand.

σ^2_S = Among-stand variance component.

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

σ^2_L = Among-location variance component.

$(R/L)(F/S)_{(r/l)(f/s)}$ = Replications within location and family within stand interaction effects.

$W_{lrw(f/s)}$ = Within plot effect, w = number of individual trees per family plot

The sum of squares for the overall analysis in Table 7 was obtained in the following manner:

1. Sum of squares for locations, stands and the interactions of stands with locations were calculated using Model 2 (Table 6).
2. Sum of squares for family within stands and locations with families within stand interactions were obtained by adding all sum of squares of families and interactions of families with location over all stands from Model 1 (Table 6).
3. The remaining sources of variation (replications within locations, interactions of replications within locations with stands, interactions of replications within locations with families within stands and the within plot) were obtained by adding the sum of squares of the respective effects from each location analysis of variance (Table 5).

All analyses were performed on IBM 360 Model 65 and IBM 370 Model 148 computers at the University of Tennessee Computing Center. The programs used were written for this study by the University of Tennessee Program Services, and provisions were made for all missing cells.

Variance Components

Variance components for the individual and combined locations were estimated by subtracting the appropriate mean squares and dividing

the results by the harmonic means calculated for the specific components being estimated. This method is using the mean squares for different effects in the combined location analysis and equating them to their expected mean squares (Table 7). The resulting equations can then be solved for variance components by a modification of the method described by Stonecypher et al. (1973) and presented in Table 8.

Components of variance can be interpreted as shown in Table 9 based on the parent and progeny population assumptions. The interpretation of the variance components as shown in Table 9 is in accordance with Namkoong et al. (1966) where variance component for family within stand was calculated to be one-quarter of the additive genetic variance.

Heritabilities

Narrow-sense heritability was estimated for all parametric characteristics using the variance component method. The heritabilities for the characteristics measured in the individual locations were obtained by using the following equation:

$$h^2 = \frac{4\sigma^2_{F/S}}{\sigma^2_w + \sigma^2_{R(F/S)} + \sigma^2_{F/S}}$$

Where: h^2 = Narrow-sense heritability.

The equation for the heritabilities of the characteristics measured in the combined locations is as follows:

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

Where: h^2 = Narrow-sense heritability.

Table 8. Equations used for estimating variance components based on calculated mean squares from Table 7

σ^2_w	= M.S. 9
$\sigma^2_{R/L \times F/S}$	= (M.S. 8 - M.S. 9)/w
$\sigma^2_{L \times F/S}$	= (M.S. 7 - M.S. 8)/wr
$\sigma^2_{F/S}$	= (M.S. 6 - M.S. 7)/wrl
$\sigma^2_{S \times R/L}$	= (M.S. 5 - M.S. 8)/wf
$\sigma^2_{R/L}$	= (M.S. 2 - M.S. 5)/swf
$\sigma^2_{L \times S}$	= (M.S. 4 - M.S. 5 - M.S. 7 + M.S. 8)/wrf
σ^2_S	= (M.S. 3 - M.S. 4 - M.S. 6 + M.S. 7)/wrfl
σ^2_L	= (M.S. 1 - M.S. 2 - M.S. 4 + M.S. 5)/wrfs

Table 9. Variance components interaction for an open-pollinated progeny test from Table 8

σ^2_w	= EP + AH
$\sigma^2_{R/L \times F/S}$	= ER
$\sigma^2_{L \times F/S}$	= HCL
$\sigma^2_{F/S}$	= HF
σ^2_S	= HS

EP = Environmental variance among plants in plots.

ER = Variance component of the interaction of half-sib families among replications within locations.

AH = Genetic variance among half-sibs (= $3/4\ \sigma^2_A + \sigma^2_D$).

HCL = Variance component of the interaction of half-sib families by location.

HF = Additional genetic variance among progeny due to maternal parent differences (=$1/4\ \sigma^2_A$).

HS = Genetic variance among stands.

σ^2_A = Additive genetic variance.

σ^2_D = Dominant genetic variance.

The heritability formulae used are in accordance with Namkoong et al. (1966). These are based on the genetic assumptions of parent and progeny populations described in Chapter II. Estimates from these formulae are guides to the improvements possible in measured traits, since this is a proportion of the phenotypic variance attributed to the additive genetic effect.

CHAPTER IV

RESULTS AND DISCUSSION

Individual Location Analyses

Mean value for 8 characteristics at the Cumberland Mountain and 9 characteristics at the Highland Rim plantations are presented in Table 10. Comparison of the 8 mean values showed great similarities at the two locations (Table 10). Means of stands and families within stands for 6 characteristics measured at the two locations (height, diameter at breast height, crown width, length of flush, previous year needle color and needle length) are presented in the Appendix (Tables 22 and 23). These averages may be useful for future selections.

Degrees of freedom, mean squares and levels of significance of 8 characteristics evaluated at the Cumberland Mountain plantation are presented in Table 11; 9 characteristics at the Highland Rim plantation are presented in Table 12. F-tests for statistical significance were performed for replications, stands, interaction of replications and stands, families within stands, and interactions of replications and families within stands for all characteristics at 1 or 5% probability levels.

Estimates of variance components for all characteristics are presented in Tables 13 and 14. These estimates are also presented as percentages of the total variation for each characteristic to make comparisons between locations more meaningful (Tables 13 and 14).

Table 10. Mean value for 8-year heights, diameter breast height, volume, crown width, flush length (terminal leader), number of branches at last whorl, needle length, previous year needle color and current year needle color by individual locations

Variables	Highland Rim	Cumberland Mountain	Average
Height (ft)	14.82	14.41	14.62
Diameter Breast Height (inches)	2.26	2.14	2.20
Volume (cubic ft)	0.30	0.34	0.32
Crown Width (ft)	7.69	7.35	7.52
Flush Length (ft) (terminal leader)	3.69	3.24	3.46
Number of Branches at Last Whorl	8.06	8.01	8.04
Needle Length (mm)	82.71	78.31	80.51
Previous Year Needle Color[1]	5.63		5.63
Current Year Needle Color[1]	6.32	5.41	5.86

[1]See ranking of visual color of needles as in Table 4, page 25.

Table 11. Degrees of freedom, mean squares and levels of significance for 8 characteristics evaluated at the Cumberland Mountain Plantation

	Replications	Stands	Replications x Stands	Families/ Stands	Replications x Families/Stands	Within Plot
Degrees of Freedom	9	12	108	83	739	6201
Height	1166.86**	3359.35**	35.23^{NS}	157.99**	35.03**	17.21
Diameter Breast Height	48.39**	117.47**	1.50^{NS}	6.06*	1.48*	0.96
Volume	2.99**	6.36**	0.13^{NS}	0.38**	0.11**	0.07
Length of Flush	78.65**	214.74*	2.40^{NS}	9.77*	2.11*	1.25
Last Whorl Number of Branches	115.20**	493.93**	9.76^{NS}	34.01*	10.21*	6.35
Crown Width	294.93**	458.96**	8.40^{NS}	30.92**	7.84*	4.37
Needle Length	4226.58**	5730.26**	369.84^{NS}	994.52*	355.11**	160.88
Current Year Needle Color	93.57**	57.89**	4.16^{NS}	5.01*	2.20**	0.97

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

*$P < 0.05$.

**$P < 0.01$.

Table 12. Degrees of freedom, mean squares and levels of significance for 9 characteristics evaluated at the Highland Rim Plantation

	Replications	Stands	Replications x Stands	Families/ Stands	Replications x Families/Stands	Within Plot
Degrees of Freedom	9	12	108	116	1002	7332
Height	119.93**	1724.97**	15.54^{NS}	75.73**	15.12*	7.94
Diameter Breast Height	6.54*	64.03**	0.84^{NS}	3.55**	0.75*	0.48
Volume	0.45**	3.48**	0.05^{NS}	0.20*	0.05*	0.03
Length of Flush	7.52**	86.04**	1.34^{NS}	5.08**	1.22*	0.78
Last Whorl Number of Branches	538.09**	138.83**	11.18^{NS}	20.27*	7.23*	5.30
Crown Width	121.62**	174.11**	4.58^{NS}	15.91**	3.96**	1.86
Needle Length	2874.42**	2958.78**	271.30^{NS}	874.94**	221.70*	128.76
Previous Year Needle Color	118.46**	556.45**	5.10^{NS}	26.20**	5.08**	2.43
Current Year Needle Color	30.43**	6.19^{NS}	1.16^{NS}	1.68*	0.86**	0.29

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

*$P < 0.05$.

**$P < 0.01$.

Table 13. Variance component and heritability estimates based on 8 characteristics of the eastern white pine open-pollinated heritability test for the Cumberland Mountain Plantation. Numbers in parentheses indicate the percent combination of the respective component to total variation

	σ^2_w	$\sigma^2_{R \times F/S}$	$\sigma^2_{F/S}$	S.E.($\sigma^2_{F/S}$)[1]	$\sigma^2_{R \times S}$	σ^2_S	σ^2_R	Total Variation	Mean	h^2[2]	S.E.(h^2)[3]
Volume	(74.5) 0.0697	(5.3) 0.0050	(3.8) 0.0036	±0.0008	(0.4) 0.0004	(11.6) 0.0109	(4.3) 0.0040	0.0936	0.3356	0.1839	±0.0409
Height	(60.0) 17.212	(8.2) 2.361	(5.8) 1.651	±0.344	(0.0) 0.004	(20.5) 5.872	(5.5) 1.574	28.674	14.407	0.311	±0.065
Diameter Breast Height	(70.6) 0.9615	(5.1) 0.0694	(4.5) 0.0615	±0.0132	(0.0) 0.0004	(15.0) 0.2043	(4.8) 0.0653	1.3624	2.1372	0.2252	±0.0483
Crown Width	(69.0) 4.370	(7.3) 0.460	(4.9) 0.310	±0.067	(0.1) 0.010	(12.4) 0.784	(6.3) 0.399	6.333	7.347	0.241	±0.052
Length of Flush	(64.0) 1.251	(5.8) 0.114	(5.3) 0.103	±0.021	(0.3) 0.005	(19.2) 0.375	(5.4) 0.106	1.954	3.237	0.280	±0.058
Number of Branches	(77.7) 6.355	(6.3) 0.511	(3.9) 0.320	±0.074	N.C.[4]	(10.3) 0.844	(1.8) 0.147	8.177	8.048	0.178	±0.041
Needle Length	(76.8) 160.88	(12.3) 25.73	(4.1) 8.58	±2.17	(0.1) 0.27	(4.1) 8.66	(2.6) 5.37	209.49	78.31	0.180	±0.04
Current Year Needle Color	(68.2) 0.972	(11.4) 0.162	(2.6) 0.037	±0.011	(2.5) 0.035	(6.5) 0.093	(8.8) 0.124	1.426	5.414	0.117	±0.034

[1] S.E.($\sigma^2_{F/S}$) = Standard error of family within stand variance component (Anderson and Bancroft, 1952).

$$\sqrt{\frac{2}{K^2_{F/S}}\left(\frac{MS^2_{F/S}}{df + 2}\right) + \left(\frac{MS^2_{R \times F/S}}{df + 2}\right)}$$

Table 13 (continued)

[2] h^2 = Narrow-sense heritability.

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

[3] $S.E.(h^2)$ = Standard error of heritability (Rink, 1974).

$$\frac{4\ S.E.(\sigma^2_{F/S})}{\sigma^2_w + \sigma^2_{R \times F/S} + \sigma^2_{F/S}}$$

[4] N.C. = Estimate of variance component was negative.

Table 14. Variance component and heritability estimates based on 9 characteristics of the eastern white pine open-pollinated heritability test for the Highland Rim Plantation. Numbers in parentheses indicate the percent contribution of the respective component to total variation.[1]

	σ^2_w	$\sigma^2_{R \times F/S}$	$\sigma^2_{F/S}$	S.E.$(\sigma^2_{F/S})$[1]	$\sigma^2_{R \times S}$	σ^2_S	σ^2_R	Total Variation	Mean	h^2	S.E.(h^2)[3]
Volume	(72.6) 0.0281	(6.7) 0.0026	(5.9) 0.0023	±0.0003	(0.5) 0.0002	(13.3) 0.0051	(1.0) 0.0004	0.0387	0.3023	0.2788	±0.0364
Height	(63.2) 7.937	(8.1) 1.013	(7.2) 0.911	±0.140	(0.0) 0.006	(20.6) 2.583	(0.9) 0.118	12.568	14.817	0.370	±0.057
Diameter Breast Height	(72.9) 0.4896	(5.5) 0.0367	(6.3) 0.0421	±0.0065	(0.2) 0.0014	(14.2) 0.954	(0.9) 0.0064	0.6716	2.2591	0.2963	±0.0457
Crown Width	(68.2) 1.862	(10.8) 0.296	(6.6) 0.180	±0.029	(0.3) 0.009	(9.1) 0.249	(4.8) 0.132	2.728	7.693	0.307	±0.038
Length of Flush	(75.4) 0.784	(6.0) 0.062	(5.6) 0.058	±0.009	(0.2) 0.002	(12.2) 0.127	(0.6) 0.007	1.040	3.689	0.256	±0.042
Number of Branches	(80.3) 5.302	(4.1) 0.272	(3.0) 0.196	±0.038	(0.9) 0.058	(2.7) 0.180	(9.0) 0.596	6.604	8.057	0.136	±0.026
Needle Length	(81.2) 128.76	(8.3) 13.11	(6.2) 9.82	±1.62	(0.5) 0.73	(2.0) 3.19	(1.8) 2.94	158.55	82.71	0.260	±0.04
Previous Year Needle Color	(59.5) 2.427	(9.2) 0.374	(7.8) 0.318	±0.048	(0.0) 0.001	(20.4) 0.831	(3.1) 0.128	4.079	5.628	0.407	±0.062
Current Year Needle Color	(67.7) 0.2862	(19.0) 0.0803	(2.9) 0.0122	±0.0032	(1.1) 0.0045	(1.6) 0.0066	(7.8) 0.0331	0.4229	6.3249	0.1289	±0.0338

[1] See explanation of symbols in Table 13.

Sources of variation.

Replication effect. At the two locations the replication effect for all characteristics was highly significant; this is an indication of successful experimental layout and some variation in site quality. The importance of the replication effect is shown in the height variance component which was different at the two locations. Height accounts for 5.5% of the total variation at the Cumberland Mountain plantation but only 0.9% at the Highland Rim plantation (Tables 13 and 14). The high variance component at the Cumberland Mountain plantation is indicative of the heterogeneity of the site while the low variance component at the Highland Rim plantation is indicative of the homogeneity of that site. Replication variance components for current year needle colors followed a similar pattern to that of height. This may be due to the varying degrees of air pollution at the two plantation sites prior to the time of measurement. Trees at the Highland Rim plantation were evaluated in the summer (July and August) while those on the Cumberland Mountain plantation were evaluated in the fall and early winter (September and December), 1977. Air pollution levels may have been low during the summer of 1977 at the Highland Rim plantation as compared to air pollution levels during the summer, fall and winter at the Cumberland Mountain plantation.

On the contrary, the variance component for the number of branches was low at the Cumberland Mountain plantation and high at the Highland Rim plantation. Lack of uniformity for this variance component may be due to differences in the counting of branches by different observers.

Stand effect. The stand effect for all characteristics was significant except for current year needle color at the Highland Rim plantation (Tables 11 and 12). Low levels of air pollution at the Highland Rim plantation during the spring and summer of 1977 may account for the lack of differences among seed sources in susceptibility to air pollution damage.

Variance components for stands were generally high at the 2 locations. The stand component for total height accounts for 20.6% of total variation at the Highland Rim and 20.5% at the Cumberland Mountain plantation (Tables 13 and 14), indicating that seed source is of great importance in eastern white pine. Comparison of the stand components with that of the families within stand reveals that the stand component is about 3 times the size of the family variance.

The variance component for the previous year needle color at the Highland Rim plantation accounts for 20.4% of the total variation (Table 14). This difference in variance components between previous and current year needle colors at the Highland Rim may be due to the longer duration of exposure of the older needles to air pollution.

Stand mean separation. Stand mean separation tables for the different characteristics at both locations are presented in Tables 15 and 16. The Duncan's New Multiple Range test indicates that at the 1% level of probability trees from stands 2, 11, 12, and 13 show superiority in height growth at the 2 locations. These stands represent progenies from Anderson, Morgan and Polk counties in Tennessee. Stand 9 (Transylvania County in North Carolina) ranked poorest in height growth (Tables 15 and 16).

Table 15. Ranking of 13 eastern white pine stands according to 9 characteristics and Duncan's New Multiple Range Test for mean separation of 8-year old progenies growing at the Highland Rim Plantation. Stand Numbers are in parentheses

Characteristics	Stand Mean and Stand Number[1]												
Height (ft)	17.14 (13)	16.61 (12)	16.17 (11)	15.86 (2)	15.26 (3)	14.99 (8)	14.90 (1)	14.53 (7)	14.45 (5)	13.98 (6)	12.74 (4)	11.87 (10)	11.76 (9)
Diameter (in)	2.66 (12)	2.61 (11)	2.56 (13)	2.43 (2)	2.31 (8)	2.30 (3)	2.27 (1)	2.25 (7)	2.25 (5)	2.16 (6)	1.80 (4)	1.73 (10)	1.61 (9)
Volume (cu ft)	0.40 (12)	0.39 (13)	0.39 (11)	0.34 (2)	0.30 (1)	0.30 (8)	0.30 (7)	0.30 (3)	0.28 (5)	0.28 (6)	0.21 (4)	0.18 (10)	0.16 (9)
Number of Branches	8.67 (12)	8.62 (5)	8.46 (2)	8.38 (11)	8.34 (1)	8.32 (8)	8.18 (6)	8.00 (7)	7.66 (3)	7.65 (9)	7.61 (13)	7.38 (10)	7.30 (4)
Crown Width (ft)	8.38 (12)	8.14 (11)	8.05 (13)	8.05 (3)	8.04 (2)	7.82 (8)	7.74 (1)	7.66 (5)	7.59 (7)	7.51 (6)	7.01 (4)	6.84 (9)	6.56 (10)
Length of Flush (ft)	4.18 (13)	4.06 (2)	4.01 (12)	4.01 (11)	3.79 (3)	3.71 (1)	3.70 (8)	3.61 (5)	3.56 (7)	3.50 (6)	3.27 (4)	3.02 (9)	2.98 (10)

Table 15 (continued)

Characteristics	Stand Mean and Stand Number[1]												
Needle Length (mm)	85.66 (12)	85.49 (8)	85.08 (3)	84.34 (7)	84.25 (11)	82.68 (9)	82.43 (5)	82.34 (1)	82.20 (2)	82.16 (6)	80.56 (13)	79.65 (4)	78.89 (10)
Previous Year Needle Color[2]	6.71 (11)	6.63 (12)	6.52 (2)	6.39 (13)	5.98 (3)	5.72 (1)	5.66 (8)	5.49 (5)	5.25 (7)	4.98 (6)	4.42 (10)	4.24 (4)	3.74 (9)
Current Year Needle Color[2]	6.47 (11)	6.43 (9)	6.43 (2)	6.42 (12)	6.36 (5)	6.34 (3)	6.32 (1)	6.27 (13)	6.27 (6)	6.27 (8)	6.23 (4)	6.22 (7)	6.12 (10)

[1]Horizontal lines connect stands not significantly different at 1% level according to Duncan's New Multiple Range Test.

[2]See ranking of visual color of needles as in Table 4.

Table 16. Ranking of 13 eastern white pine stands according to 8 characteristics and Duncan's New Multiple Range Test for mean separation of 8-year old progenies growing at the Cumberland Mountain Plantation. Stand numbers are in parentheses

Characteristics	Stand Mean and Stand Number[1]												
Height (ft)	17.29 (12)	17.15 (13)	16.76 (11)	16.31 (2)	14.88 (8)	14.77 (7)	13.84 (3)	13.78 (1)	13.03 (10)	12.83 (6)	11.61 (5)	10.66 (4)	8.98 (9)
Diameter (in)	2.74 (12)	2.64 (11)	2.52 (13)	2.50 (2)	2.22 (8)	2.20 (7)	2.07 (1)	1.99 (3)	1.90 (10)	1.88 (6)	1.59 (5)	1.43 (4)	1.10 (9)
Volume (cu ft)	0.50 (12)	0.45 (11)	0.44 (13)	0.41 (2)	0.36 (7)	0.33 (8)	0.32 (1)	0.29 (6)	0.28 (3)	0.24 (10)	0.19 (5)	0.19 (4)	0.14 (9)
Number of Branches	9.36 (12)	9.22 (11)	8.80 (2)	8.40 (13)	8.36 (8)	8.16 (10)	8.11 (1)	7.89 (7)	7.57 (3)	7.27 (6)	7.24 (5)	6.57 (4)	5.74 (9)
Crown Width (ft)	8.51 (12)	8.18 (11)	8.15 (13)	8.10 (2)	7.62 (8)	7.47 (7)	7.31 (3)	7.09 (1)	6.90 (10)	6.81 (6)	6.32 (5)	5.94 (4)	5.18 (9)
Length of Flush (ft)	3.88 (12)	3.85 (13)	3.83 (11)	3.79 (2)	3.38 (8)	3.33 (7)	3.23 (3)	3.09 (1)	3.05 (10)	2.71 (6)	2.51 (5)	2.32 (4)	1.75 (9)

Table 16 (continued)

Characteristics	Stand Mean and Stand Number[1]												
Needle Length (mm)	84.58 (12)	82.36 (3)	80.46 (11)	79.31 (7)	78.88 (2)	78.81 (8)	78.54 (13)	77.81 (1)	77.47 (10)	77.24 (9)	76.68 (6)	74.13 (4)	71.92 (5)
Current Year Needle Color[2]	5.87 (12)	5.80 (11)	5.72 (13)	5.62 (2)	5.60 (8)	5.46 (3)	5.41 (10)	5.36 (7)	5.18 (1)	5.07 (6)	5.04 (4)	4.97 (5)	4.74 (9)

[1]Horizontal lines connect stands not significantly different at 1% level according to Duncan's New Multiple Range Test.

[2]See ranking of visual color of needles as in Table 4.

At the two locations, the mean separation for diameter was similar to that of height with stands 2, 11, 12 and 13 from Anderson, Morgan and Polk counties in Tennessee having the greatest diameter. At the Cumberland Mountain plantation means from stands 2, 11, 12 and 13 were not significantly different from each other at the 1% level of probability, while stand 2 at the Highland Rim plantation had a significantly smaller diameter than stands 11, 12 and 13 (Tables 15 and 16).

Stands 2, 11, 12 and 13 from Tennessee were superior for volume growth at the two locations. Progeny of stand 2 had significantly less volume than those from stands 11, 12 and 13 at the Highland Rim plantation and stand 12 progeny had significantly more volume than all other progenies in the Cumberland Mountain plantation.

Progenies from these Tennessee stands also had the largest number of branches at the Cumberland Mountain plantation (Table 16). Duncan's New Multiple Range Test indicated no significant differences among the 4 stands at the Highland Rim plantation (Table 15); only 2 of the 4 stands (11 and 12) were not significantly different at the Cumberland Mountain plantation (Table 16). Stands 2, 11, 12 and 13 from Tennessee and stand 3 from Fannin County, Georgia, had wide-crowned progenies at the Highland Rim plantation and trees of stand 12 origin had the widest crowns (Table 15).

The same 4 stands (2, 11, 12 and 13) proved superior for length of flush at the 2 locations (Tables 15 and 16). At the Cumberland Mountain plantation there were no differences among these stands at the 1% level while stand 13 was significantly different from stands 11 and 12 at the 1% level at the Highland Rim plantation.

At the Highland Rim plantation, stands 3, 7, 8, 11 and 12 had progenies with longer needles while trees from stand 12 had the longest needles at the Cumberland Mountain plantation. Since short needles are associated with air pollution damage, it is assumed that these stands have undergone natural selection and are therefore resistant. Stands 2, 11, 12 and 13 were also superior for color of the previous year needles at the Highland Rim plantation. Stand 9 from Transylvania County, North Carolina, ranked second for current year needle color at the Highland Rim plantation. This high ranking of the Transylvania source may be due to the varying degree of air pollution at the 2 plantation sites, with a probability of low air pollution levels during the 1977 growing season at the Highland Rim plantation compared with the Cumberland Mountain plantation. However, the low tolerance level of the Transylvania progenies is noted by the yellow color of previous year needles at the Highland Rim plantation and the yellow color of current year needles at the Cumberland Mountain plantation (Tables 15 and 16). Progenies from stands 11 and 12 in Morgan County, Tennessee, continued to have the greatest dark-green current year needle color.

Replications and stands interaction effect. At the 2 locations the replications and stands interaction effects were non-significant for all characteristics. Apparently, variation in site within a location does not affect the relative performance or ranking of the seed sources (stands).

Families within stand effect. All characteristics for the families within stand effect were significant at the 2 locations (Tables 11 and 12, pages 41 and 42). This indicates that all characteristics are inherited traits in eastern white pine. However, variance components for this effect are relatively moderate at the 2 locations. The current year needle color variance component for the 2 locations was fairly equal and accounts for 2.9% of the total variation at the Highland Rim plantation as compared with 2.6% at the Cumberland Mountain plantation (Tables 13 and 14, pp. 43 and 45). This may be due to lack of long exposure of different families to air pollution damage.

The families within stand variance components for volume were lower than those for height and diameter (Tables 13 and 14); this does not conform with the results obtained for Virginia and loblolly pines (Rink, 1974; Stonecypher, 1966). The reason may be that eastern white pine is more shade tolerant permitting suppressed trees to stay alive for a longer period of time; as a result, the within plot variance component will be greater and reduce the relative size of the family within stand variance component.

Replications and families within stands interaction effects. At the 2 locations the replications and families within stands interaction effects were significant at either the 1 or 5% levels of probability for all characteristics (Tables 11 and 12). The variance components generally varied between 4 and 19%, thus indicating some inconsistency in the performance of families in stands in all replications.

In the two locations, most variance components were relatively

moderate (Tables 13 and 14, pages 43 and 45), but tended to be larger than those for families within stands. The crown width variance components were large (7.3% at the Cumberland Mountain Plantation and 10.8% at the Highland Rim Plantation) and may be due to different survival rates; also, crown width may be strongly influenced by neighboring family row plots.

The variance component for current year needle color was large at the Highland Rim plantation (19.0% of the total variation) (Table 14, page 45). This large component may be due to a 5-week time lapse between measurements of the first and last replications.

Within plot effect. This is an error term, therefore significance was not computed (Tables 11 and 12, pages 41 and 42). Variance components for the within plot effect were large for all characteristics. The within plot variance components for previous and current year needle colors and crown width were the smallest at the Highland Rim Plantation (Table 14). Number of branches and needle length variance components were the most variable within plot (Tables 13 and 14). Between 60 and 80% of all variation was accounted for by this component. High within plot variance components are expected since at least three-quarters of the genetic effect plus micro-environmental effects are contained within the family row plot.

Estimates of heritabilities for the individual location analyses. Narrow-sense heritability estimates are presented in Tables 13 and 14. These estimates are obtained by using the formula for heritability for individual locations. Heritabilities for height growth were relatively high at the 2 locations with

h^2 = 0.311 at the Cumberland Mountain plantation and h^2 = 0.370 at the Highland Rim plantation. This is in conformity with results by Kriebel et al. (1972), Thor (1974) and Thor and Gall (1978). Diameter breast height heritabilities for the 2 locations were 0.225 and 0.296 at the Cumberland Mountain and Highland Rim plantations, respectively.

Heritability estimates for volume were smaller than those for height and diameter (h^2 = 0.1839 and h^2 = 0.2788 for the Cumberland Mountain and Highland Rim plantations, respectively). This estimate was expected to be slightly larger than that for diameter since diameter is squared in the formula for volume while height is just included in the first power. However, this did not occur because the family within stand variance component was low, reflecting the large within plot variance for volume. It is believed that as the progenies grow older, most of the suppressed trees will die; this mortality should reduce the within plot variance and increase the heritability estimates for volume.

Estimates of heritabilities for crown width were moderate in the 2 locations (h^2 = 0.241 and h^2 = 0.307 for the Cumberland Mountain and Highland Rim plantations, respectively). Comparison of crown width heritability with those for height and diameter indicates that they are fairly similar. The reason for this can be seen in the phenotypic correlation coefficient for crown width and height which is 0.863 and the phenotypic correlation coefficient between diameter and crown width which is 0.855 (Table 17).

Heritability estimates of length of flush are almost equal in the 2 locations (h^2 = 0.280 and h^2 = 0.256 at Cumberland Mountain and Highland Rim plantations, respectively). This estimate is fairly

Table 17. Combined locations phenotypic coefficient of correlation between characteristics evaluated

Correlation Between:	Correlation Coefficient[1]
Height and Diameter Breast Height	0.917
Height and Volume	0.826
Height and Flush Length (Internode)	0.819
Height and Number of Branches Last Whorl	0.463
Height and Needle Length	0.254
Height and Crown Width	0.863
Height and Current Year Needle Color	0.356
Volume and Diameter Breast Height	0.923
Volume and Flush Length (Internode)	0.567
Volume and Number of Branches Last Whorl	0.334
Volume and Needle Length	0.162
Volume and Crown Width	0.744
Volume and Current Year Needle Color	0.188
Diameter Breast Height and Flush Length (Internode)	0.717
Diameter Breast Height and Number of Branches Last Whorl	0.441
Diameter Breast Height and Needle Length	0.249
Diameter Breast Height and Crown Width	0.855
Diameter Breast Height and Current Year Needle Color	0.338
Flush Length and Number of Branches Last Whorl	0.437
Flush Length and Needle Length	0.307
Flush Length and Crown Width	0.724
Flush Length and Current Year Needle Color	0.429
Number of Branches Last Whorl and Needle Length	0.148
Number of Branches Last Whorl and Crown Width	0.438
Number of Branches Last Whorl and Current Year Needle Color	0.207
Needle Length and Crown Width	0.302
Needle Length and Current Year Needle Color	0.372
Crown Width and Current Year Needle Color	0.384

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

similar to that of total height; the phenotypic correlation (r = 0.819) indicates a strong relationship between these two variables (Table 17). Number of branches had a heritability value of only 0.178 at the Cumberland Mountain plantation and 0.136 at the Highland Rim plantation. Needle length heritabilities were 0.180 and 0.260 for the Cumberland Mountain and Highland Rim plantations, respectively.

Previous year needle color had a heritability value of 0.407 at the Highland Rim plantation where measurements were obtained in the summer. Heritabilities for the current year needle color were low (h^2 = 0.117 at the Cumberland Mountain plantation and h^2 = 0.129 at the Highland Rim plantation). This might indicate that air pollution levels in 1977 were not sufficiently high to differentiate susceptible and resistant families.

Combined Location Analyses

Degrees of freedom, mean squares and levels of significance for the 8 characteristics are presented in Table 18. F-tests of statistical significance were performed on locations, replications within locations, stands, families within stands, interaction of locations and stands, interaction of stands and replications within locations, interaction of locations and families within stands and interactions of replications within locations and families within stands for the 8 characteristics at either 1 or 5% probability levels. The F-test was performed with the assumption that all effects were random.

Variance components were calculated from mean squares by the same method used in the individual location analyses (Table 8, p. 36). Estimates of variance components for the 8 characteristics measures are shown in Table 19.

Table 18. Analysis of variance of 8 characteristics for the combined locations

	Locations	Replications/ Locations	Stands	Locations x Stands	Stands x Replications Within Locations	Families/ Stands	Locations x Families/ Stands	Families/ Stands x Replications/ Locations	Within Plot
Degrees of Freedom	1	18	12	12	216	116	83	1739	13533
Height	1505.84^{NS}	643.40**	4838.43**	476.90**	25.38*	187.95**	36.30^{NS}	23.60*	12.19
Diameter Breast Height	93.74^{NS}	27.46**	174.35**	15.80*	1.18*	7.84**	1.66*	1.06*	0.70
Volume	2.11^{NS}	1.72**	9.46**	0.75**	0.09*	0.46**	0.11^{NS}	0.07*	0.05
Length of Flush	942.05^{NS}	43.08**	277.76*	41.44**	1.87*	11.84**	3.01*	1.60*	0.99
Last Whorl Number of Branches	74.90^{NS}	326.65**	505.50^{NS}	196.22**	10.47*	38.25*	13.05^{NS}	8.50*	5.78
Crown Width	708.04^{NS}	208.28**	568.34*	101.40**	6.49*	36.54**	7.73^{NS}	5.61*	3.01
Needle Length	70062.1**	3550.5**	6935.9^{NS}	1750.4**	135.6^{NS}	1566.2*	385.2^{NS}	287.4*	143.5
Current Year Needle Color	3005.36**	60.15**	40.36^{NS}	29.74**	2.57*	4.91*	2.35*	1.39**	0.58

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

*$P < 0.05$.

**$P < 0.01$.

Table 19. Variance component and heritability estimates based on 8 characteristics for the combined locations analyses of the eastern white pine open-pollinated heritability test. Numbers in parentheses indicate the percent contribution of the respective component to total variation

	σ^2_w	$\sigma^2_{R/L \times F/S}$	$\sigma^2_{L \times F/S}$	$\sigma^2_{F/S}$	$\sigma^2_{S.E.}(\sigma^2_{F/S})$[1]	$\sigma^2_{S \times R/L}$	$\sigma^2_{L \times S}$	σ^2_S	$\sigma^2_{R/L}$	σ^2_L	Total Variation	Mean	h^2[2]	S.E.(h^2)[3]
Volume	(73.8) 0.0472	(5.3) 0.0034	(0.9) 0.0006	(3.9) 0.0025	±0.0004	(0.3) 0.0002	(1.6) 0.0010	(11.1) 0.0071	(3.1) 0.002	N.C.[4]	0.064	0.3175	0.186	±0.030
Height	(60.4) 12.187	(7.8) 1.564	(0.9) 0.182	(5.4) 1.084	±0.177	(0.1) 0.029	(3.7) 0.742	(17.6) 3.559	(3.8) 0.770	(0.3) 0.053	20.170	14.630	0.289	±0.047
Diameter Breast Height	(70.3) 0.7021	(5.0) 0.0495	(0.8) 0.0085	(4.4) 0.0442	±0.0074	(0.2) 0.0018	(2.4) 0.0237	(12.9) 0.1288	(3.3) 0.0328	(0.7) 0.0067	0.9981	2.2036	0.220	±0.037
Crown Width	(67.7) 3.012	(8.0) 0.356	(0.7) 0.030	(4.6) 0.206	±0.035	(0.3) 0.014	(3.5) 0.157	(8.3) 0.370	(5.7) 0.252	(1.2) 0.053	4.450	7.535	0.229	±0.038
Length of Flush	(62.8) 0.9980	(5.2) 0.0827	(1.3) 0.0202	(4.0) 0.0631	±0.0114	(0.3) 0.0044	(4.1) 0.0645	(12.1) 0.1923	(3.2) 0.0514	(7.0) 0.1118	1.5884	3.484	0.217	±0.053
Number of Branches	(78.4) 5.784	(5.1) 0.373	(0.9) 0.065	(2.5) 0.180	±0.038	(0.4) 0.032	(4.1) 0.306	(3.3) 0.240	(5.3) 0.394	N.C.[4]	7.374	8.053	0.113	±0.024
Needle Length	(74.9) 143.47	(10.3) 19.72	(0.7) 1.400	(4.4) 8.44	±1.50	N.C.[4]	(1.3) 2.56	(1.8) 3.38	(2.2) 4.26	(4.4) 8.44	191.67	80.71	0.200	±0.030
Current Year Needle Color	(46.7) 0.5819	(8.9) 0.1106	(1.1) 0.0138	(1.5) 0.0183	±0.0052	(1.5) 0.0192	(3.6) 0.0443	(0.5) 0.0068	(5.8) 0.0718	(30.4) 0.3795	1.2462	5.9354	0.101	±0.029

[1] S.E.($\sigma^2_{F/S}$) = Standard error of family within stand variance component (Anderson and Bancroft, 1952).

$$\frac{2}{k^2_{F/S}}\left(\frac{MS^2_{F/S}}{df+2}\right) + \left(\frac{MS^2_{L \times F/S}}{df + 2}\right)$$

[2] h^2 = Narrow-sense heritability.

$$\frac{4\,\sigma^2_{F/S}}{\sigma^2_w + \sigma^2_{R/L \times F/S} + \sigma^2_{L \times F/S} + \sigma^2_{F/S}}$$

[3] S.E.(h^2) = Standard error of heritability (Rink, 1974).

$$\frac{4 \text{ S.E.}(\sigma^2_{F/S})}{\sigma^2_w + \sigma^2_{R/L \times F/S} + \sigma^2_{L \times F/S} + \sigma^2_{F/S}}$$

[4] Actual estimate of variance component was negative.

Interpretations of the variance components are given in Table 9, page 38, and are based on genetic assumptions discussed by Stonecypher (1966) and Stonecypher et al. (1973).

Sources of variation.

Replications within location effect. For the combined location analysis, the replication within locations effects were highly significant for all characteristics (Table 18). This result is similar to that obtained for the individual locations and it is an indication of successful block layout and variation in site quality within locations.

Variance components were similar to those of the individual location analyses. Needle length variance component was rather low (2.2% of the total variation)(Table 19) indicative of uniformity in air pollution levels within both locations. The current year needle color variance component accounts for 5.8% of the total variation; these relatively large components are probably due to the time elapsed between measurements of the first and last replications within each location.

Stand effect. Most of the characteristics were significant except needle length, current year needle color and number of branches. The non-significant results for the needle length and current year needle color may be due to differences in the seasons of the year that measurements were taken.

Variance components for stands were generally large and conform with the individual location analyses. The height variance component

was largest of all characteristics in the combined location analysis and similar in magnitude to those of the single location analyses.

Families within stand effect. The families within stand effects were highly significant for all characteristics (Table 18). This result is similar to that obtained from the individual locations (Tables 11 and 12, pages 41 and 42).

Variance components for combined locations were moderately large and similar to those obtained for the individual locations with the exception of current year needle color which had a component of only 1.5% (Table 18). Also, the component for the number of branches was small accounting for only 2.5% of the total variation (Table 19).

Stands and replications within location interaction effect. All characteristics measured were significant at the combined level except needle length (Table 18). Variance components for this effect were generally small for all characteristics and ranged from 0.1 to 1.5% (Table 19). This confirms the estimates of the interaction of replications and stand effect in the individual location analyses (Tables 13 and 14, pages 43 and 45). Such small variance components may be disregarded for practical purposes.

Interactions of replications within locations and families within stand effect. Although all characteristics were significant in the combined locations analysis, the variance components were relatively moderate with needle length, crown width and current year needle color being somewhat higher (Table 19). The variance component for crown width may be due to differences in survival rates among replications

at both locations; this is manifested in the negative correlation obtained between crown width and survival (r = -0.41). The large variance component for current year color may be due to differences in sampling time at both locations.

Location effect. For this effect all characteristics were non-significant except needle length and current year needle color (Table 18, page 59). The significance of these needle characteristics are indications of differences in the levels of air pollution damage between locations and differences in time of sampling.

All variance components were small except current year needle color which accounted for 30.4% of the total variation (Table 18). Needles at one location (Highland Rim) had not been exposed to air pollution for long periods of time before measurements and thus had not, on an average, been damaged as much as those on the Cumberland Mountain.

Interaction effect of locations and stands. This effect was highly significant for all characteristics (Table 18). Stands did not rank in the same order at both locations, as suggested by the stand mean separations presented in Tables 15 and 16, pages 48 and 50.

This effect had a relatively moderate variance component which ranged from 1.3 to 1.4% (Table 19). For height this component accounted for 3.7% of the total variation, but the same 4 stands ranked best in both locations. Thus, for practical purposes total height is a rather stable characteristic at the stand level.

Interaction effect of locations and families within stands. In spite of the large degrees of freedom; height, volume, crown width,

needle length and number of branches had non-significant effects at the interaction of locations and families within stands level. Also, diameter, length of flush and current year needle colors were only significant at the 5% level of probability.

All variance components account for less than 1.5% of the total variation (Table 19). These variance component estimates are in conformity with those calculated for Virginia pine (Rink, 1974). Apparently, there is good stability at the family level for all characteristics.

Within plot effect. This is an overall error term, therefore significance was not computed (Table 18, page 59). The within plot variance component accounts for the largest amount of variation for all variables and ranged from 46.7 to 78.4% (Table 19). However, this within plot variance component was not as large as those obtained for the individual location analyses which ranged from 60 to 80% of the total variation (Tables 13 and 14, pages 43 and 45). This is due to the introduction of 3 new effects (location, interaction of location and stand and interaction of location and families within stands) at the combined location level.

Estimates of heritabilities for the combined location analysis. Heritability estimates for all variables based on variance components from the combined location analysis are presented in Table 19. These estimates were obtained by the heritability estimate method for combined locations by Namkoong et al. (1966) described in Chapter III. These heritability values are very similar to those computed for individual locations (Table 13 and 14).

Heritability for height growth was 0.289 while that of diameter was 0.220. Heritability estimate for volume was lower than that of height and diameter breast height (h^2 = 0.186); this was similar to estimates obtained for the individual locations. Heritabilities for the remaining variables were in close agreement with those obtained for the individual locations with the heritability value for current year needle color and number of branches being the lowest values for the combined location analysis (h^2 = 0.101 and h^2 = 0.113, respectively).

CHAPTER V

APPLICATION OF RESULTS

Although estimates of genetic and phenotypic variances are important to tree breeding, the ultimate use of these estimates is to predict the amount of improvement or genetic gain possible in a particular breeding program. Stonecypher et al. (1966) disclosed that the phenotypic and genetic variances are necessary for prediction of genetic gains that would be expected from individual trait selection. Results by Thor (1976) indicated that it would be possible to obtain a minimum gain of about 20% and maximum gains of about 45 to 75% in juvenile height growth in eastern white pine.

Phenotypic coefficients of correlation among all characteristics based on individual trees for the combined locations are presented in Table 17, page 57. Height, diameter and volume had the highest phenotypic coefficients; they are also of the greatest economic importance and therefore were chosen to demonstrate a selection scheme and the gains expected from such selection.

A method for calculating genetic gains based upon the initial mass selection of phenotypes and the selections of families and individuals within families for half-sib progenies was demonstrated by Namkoong (1966).

Another method of estimating genetic gain for half-sib progeny test is by using the selection differential and heritability (Wright, 1976a). In this method, the selection differential and heritabilities must apply to the individual trees (mass selection) or families for

which gains are to be computed. A description of this method is also given by Falconer (1960).

Genetic gains were calculated based on selection of the best families and individuals within families for the two locations. This method of calculating genetic gains is known as two-stage selection. It is assumed that there was no initial mass selection in the actual stands, and that there was no inbreeding within families. For family selection, the best 35 and 40 families were selected from the Cumberland Mountain and Highland Rim plantations, respectively (Table 20).

The formulas used for predicting the genetic gain from family selection is as follows:

$$G_f = Sd_f \times h_f^2$$

Where: G_f = Gain from family selection.

SD_f = Selection differential for families.

h_f^2 = Family heritability.

Where: $h_f^2 = h^2 \times \frac{1 + (n-1)r}{1 + (n-1)t}$

n = Number of individuals in the family.

r = 1/4 (with half-sib families).

t = Correlation of phenotypic values of members of the family.

h^2 = Individual tree heritability.

The formula used for calculating gains expected from within family selection is as follows:

$$G_w = i\sigma_w h_w^2$$

Table 20. Mean for volume, height and diameter breast height of the selected and unselected population, number of families selected from the population, selection differential and the within-family selection intensities for the two-stage selection at individual locations

	Cumberland Mountain			Highland Rim		
	Height	Diameter	Volume	Height	Diameter	Volume
Mean of Families Selected	16.84 ft	2.64 in	0.46 ft^3	16.53 ft	2.65 in	0.40 ft^3
Mean Unselected Population	14.41 ft	2.14 in	0.34 ft^3	14.82 ft	2.26 in	0.30 ft^3
Selection Differential	2.43 ft	0.50 in	0.12 ft^3	1.71 ft	0.39 in	0.10 ft^3
Total Number of Families Selected	35	35	35	40	40	40
Total Number of Trees Selected	350	350	350	400	400	400
Within-Family Selection Intensity[1]	1.4	1.4	1.4	1.4	1.4	1.4
Average Number of Trees Per Plot	7.55	7.55	7.55	7.09	7.09	7.09

[1]G. Namkoong and E. B. Snyder, 1969. Accurate Values for Selection Intensities, Silvae Genetica, 18:172-173.

Where: G_w = Gain from within family selection.

i = Intensity of selection.

σ_w = Phenotypic standard deviation for within families.

h_w^2 = Within family heritability.

Where: $h_w^2 = h^2 \times \frac{1 - r}{1 - t}$

Selection intensities for the within family selection are presented in Table 21. This was determined on an average of 7 trees per family plot, and only 1 tree per family plot was selected. The selection intensity for the within families was 14.0% or 1.4 units of phenotypic standard deviations interpolated from selection intensity graphs by Namkoong and Snyder (1969).

Total genetic gains were obtained by totaling the gains from family selection with gains from within family selection:

$$G_T = G_f + G_w$$

Where: G_T = Total genetic gains.

Gains from family selection are larger than those obtained from within family selection for the 3 variables computed in the 2 locations. Total gains for height were 3.64 feet (25.2%) and 2.76 feet (18.6%) at the Cumberland Mountain and Highland Rim plantations, respectively (Table 21). This is in conformity with Thor (1976) in which gains of about 20% were obtained for juvenile height growth in eastern white pine. Substantial gain for height at the Cumberland Mountain plantation is largely due to the high selection differential for this trait in that location (Table 20).

Gains for diameter account for 25.6 and 30.8% while volume

Table 21. Heritabilities and expected gains from 2-stage selection for height, diameter and volume at individual locations

	Cumberland Mountain			Highland Rim		
	Height	Diameter	Volume	Height	Diameter	Volume
h_w^2	0.253	0.179	0.144	0.305	0.240	0.225
h_f^2	0.895	0.829	0.812	0.915	0.881	0.872
Gains from Family Selection	2.17 ft 15.0%	0.414 in 19.3%	0.098 ft^3 28.8%	1.56 ft 10.53%	0.344 in 15.2%	0.087 ft^3 29.1%
Gains from Within Family Selection	1.47 ft 10.2%	0.246 in 11.5%	0.053 ft^3 15.6%	1.20 ft 8.1%	0.235 in 10.4%	0.053 ft^3 17.7%
Total Gains	3.64 ft 25.2%	0.660 in 30.8%	0.151 ft^3 44.4%	2.76 ft 18.6%	0.579 in 25.6%	0.140 ft^3 46.8%
Estimated Mean of New Population	18.05 ft	2.80 in	0.50 ft^3	17.58 ft	2.84 in	0.44 ft^3

accounts for 46.8 and 44.4% respectively at the Highland Rim and Cumberland Mountain plantations (Table 21).

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, 1960). Therefore, gains obtained from the different variables were added to the mean of the unselected population to obtain the estimated mean of the new population as presented in Table 21. This table shows a new height mean of 18.05 feet and 17.58 feet compared with the mean of the unselected population of 14.41 feet and 14.82 feet for Cumberland Mountain and Highland Rim plantations, respectively (Table 21). Similarly, diameter and volume have new population means of 2.80 inches and 0.50 cubic feet for Cumberland Mountain and 2.84 inches and 0.44 cubic feet for the Highland Rim plantation (Table 21).

Results from the combined analysis of variance indicate that the genotype and environment interaction components accounted for less than 2% of the total variation (Table 19, page 60). Also, the mean separations reflect that sources from Anderson and Morgan counties in Tennessee have great stability for all characteristics (Tables 15 and 16, pages 48 and 50). These sources have also been stable and performed above average in Michigan, Ohio, Illinois, Indiana, Nebraska, West Virginia, Australia and New Zealand (Wright et al., 1978). Similarly, 5-year results indicate that the Anderson and Morgan county sources had superior progenies in a plantation near Oak Ridge, Tennessee (Thor, 1976).

Based on the consistency of these results, it can be assumed

that eastern white pine from Anderson and Morgan counties in Tennessee are very stable varieties. Thus, these varieties can be recommended for planting in many areas outside their natural habitat.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The objectives of this study were to determine the genetic and environmental variation and their interactions with respect to height, diameter, volume, crown width, length of flush, number of branches at last whorl, needle length, previous and current year needle color and needle form in eastern white pine (*Pinus strobus* L.) at two plantations in Tennessee. In addition, estimates of variance components, heritabilities and genetic gains were desired as a guide for future breeding programs.

Eight-year old open-pollinated progenies from 13 stands in Tennessee, North Carolina and Georgia had been planted in 10-tree row plots and replicated 10 times. About 20,000 trees representing 128 families were measured.

Results for the individual location analyses revealed similarities between locations in variance components for each source of variance. Height, diameter, crown width, previous year needle color, length of flush and stem volume had the largest stand and family within stand variance; variance components for the combined location analyses followed a similar pattern. The genotype and environmental interactions accounted for about 2% of the total variation in both the individual and combined location analysis.

Heritability estimates for height, diameter, crown width and previous year needle color were large while those for current year

needle color and needle length were small in both individual and combined location analyses. Genetic gains from a 2-stage selection scheme (family and within family selection) were computed for height, diameter and volume for individual locations. Total genetic gain for height was 18.6 and 25.2% while diameter was 25.6 and 30.8%, and volume was 46.8 and 44.4% for the Highland Rim and Cumberland Mountain plantations, respectively. This selection method could be used for the establishment of a seedling seed orchard for breeding of genetically improved seeds desired by nursery men and Christmas tree producers.

Stand mean separations revealed that progeny of 3 stands from Tennessee and 1 from Georgia were superior in growth rate when compared with progeny from 3 North Carolina stands.

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APPENDIX

Table 22. Mean values for height[1], diameter at breast height[2] (DBH), and current year length of flush[3] at the Highland Rim and Cumberland Mountain following 8 growing seasons

Stand	Family	Highland Rim			Cumberland Mountain		
		Height	DBH	Flush	Height	DBH	Flush
1	1	17.1	2.8	4.1	16.2	2.6	3.6
	2	14.8	2.4	3.6	14.9	2.5	3.2
	3	13.3	2.0	3.4	10.8	1.6	2.3
	4	14.0	2.1	3.6	10.2	1.3	2.3
	5	14.8	2.1	3.8	14.1	2.0	3.3
	6	16.0	2.5	3.6	16.6	2.6	3.8
	7	14.1	2.1	3.6	11.6	1.6	2.3
	8	12.6	1.8	3.4	10.4	1.3	2.5
	10	15.7	2.4	3.8	14.2	2.1	3.3
	Stand Mean	14.9	2.3	3.7	13.8	2.1	3.1
2	1	16.1	2.5	4.2	15.7	2.4	3.8
	2	15.8	2.4	4.1	17.6	2.7	4.1
	3	15.5	2.4	3.8	16.0	2.4	3.7
	4	15.8	2.5	3.8	15.2	2.3	3.5
	5	16.3	2.6	4.1	15.9	2.5	3.7
	6	16.1	2.5	4.2	16.7	2.6	3.9
	7	13.6	2.0	3.9	14.8	2.2	3.5
	8	15.8	2.4	4.0	16.0	2.5	3.7
	9	15.8	2.2	4.2	17.8	2.6	4.1
	10	17.2	2.7	4.3	17.0	2.6	3.8
	Stand Mean	15.9	2.4	4.1	16.3	2.5	3.8

Table 22 (continued)

Stand	Family	Highland Rim Height	DBH	Flush	Cumberland Mountain Height	DBH	Flush
3	1	16.1	2.4	4.0	14.5	2.1	3.4
	2	16.0	2.5	3.8			
	3	14.2	2.0	3.5			
	4	14.0	2.3	3.8	13.8	2.0	3.2
	5	14.5	2.2	3.4	12.9	1.8	3.0
	6	15.2	2.4	3.8	13.9	2.0	3.2
	7	15.7	2.4	3.9			
	8	14.6	2.2	3.9			
	9	15.3	2.3	3.9	14.1	2.0	3.4
	10	15.5	2.3	3.8	____	___	___
	Stand Mean	15.2	2.3	3.8	13.8	2.0	3.2
4	1	12.5	1.8	3.3	10.1	1.4	2.1
	2	12.8	1.7	3.4	11.3	1.4	2.6
	3	13.9	2.0	3.4	11.5	1.6	2.6
	4	11.8	1.6	3.0	11.2	1.6	2.5
	5	13.4	1.9	3.6	10.9	1.4	2.4
	6	14.3	2.2	3.7	11.7	1.6	2.5
	7	13.6	2.0	3.4	13.0	1.8	3.1
	8	11.3	1.5	3.0	8.0	0.9	1.7
	9	11.5	1.6	2.8	7.4	0.8	1.4
	10	12.4	1.7	3.0	10.9	1.6	2.1
	Stand Mean	12.7	1.8	3.3	10.6	1.4	2.3

Table 22 (continued)

Stand	Family	Highland Rim			Cumberland Mountain		
		Height	DBH	Flush	Height	DBH	Flush
5	1	18.2	3.3	4.2			
	2	15.3	2.4	3.7	12.6	1.8	2.8
	3	13.2	2.0	3.4	11.2	1.6	2.3
	4						
	5	14.2	2.0	3.7	12.0	1.6	2.6
	6	14.8	2.3	3.9	12.4	1.8	2.8
	7	12.0	1.8	2.8	10.1	1.3	2.0
	8	13.9	2.1	3.5	9.9	1.2	1.9
	9	15.6	2.5	4.0	12.3	1.6	2.9
	10	16.2	2.7	3.7	12.9	1.9	2.8
	Stand Mean	14.4	2.2	3.6	11.6	1.6	2.5
6	1	16.5	2.6	4.1			
	2	14.7	2.3	3.7			
	3	11.9	1.8	2.9			
	4	13.7	2.2	3.4	14.0	2.2	2.9
	5	12.4	1.9	3.0	10.5	1.4	2.0
	6	14.6	2.2	3.7	10.5	1.4	2.2
	7	12.7	1.8	3.3			
	8	12.4	1.8	2.9			
	9	15.4	2.5	3.8	14.4	2.2	3.2
	10	16.5	2.6	4.4	13.8	2.0	3.0
	Stand Mean	14.0	2.2	3.5	12.8	1.9	2.7

Table 22 (continued)

Stand	Family	Highland Rim Height	DBH	Flush	Cumberland Mountain Height	DBH	Flush
7	1	17.4	2.8	4.1	16.5	2.1	3.7
	2	13.7	2.2	3.2			
	3	11.5	1.6	2.9	11.0	1.5	2.3
	4	14.5	2.2	3.5			
	5	15.0	2.3	3.6			
	6	13.4	2.1	3.3	13.0	1.9	2.7
	7	14.4	2.3	3.6	15.8	2.5	3.7
	8	15.8	2.6	3.6			
	9	14.6	2.3	3.7	15.9	2.3	3.7
	10	14.5	2.2	3.9	15.1	2.3	3.5
	Stand Mean	14.5	2.2	3.6	14.8	2.2	3.3
8	1	14.4	2.2	3.6	14.4	2.2	3.2
	2	15.1	2.4	3.8	16.8	2.7	3.7
	3	14.6	2.2	3.6	14.7	2.1	3.1
	4	14.4	2.1	3.6	14.8	2.1	3.5
	5	15.8	2.5	3.9	14.0	2.0	3.4
	6	15.1	2.3	3.5	14.8	2.2	3.3
	7	16.4	2.7	3.9			
	8	13.8	1.9	3.6			
	9	14.8	2.2	3.7	13.5	1.9	3.3
	10	15.8	2.5	3.8	16.0	2.4	3.6
	Stand Mean	15.0	2.3	3.7	14.9	2.2	3.4

Table 22 (continued)

Stand	Family	Highland Rim Height	DBH	Flush	Cumberland Mountain Height	DBH	Flush
9	1	11.4	1.6	3.0			
	2	9.3	1.1	2.4			
	3	12.7	1.8	3.3	9.9	1.3	1.9
	4	13.4	2.1	3.4			
	5	13.0	1.9	3.4	9.7	1.2	1.9
	6	11.0	1.4	2.8	7.1	0.7	1.4
	7	9.9	1.2	2.5			
	8	10.6	1.4	2.6	6.5	0.7	1.0
	9	13.7	1.9	3.5			
	10	12.2	1.6	3.1	10.5	1.4	2.3
	Stand Mean	11.8	1.6	3.0	8.9	1.1	1.8
10	1	11.8	1.8	2.9			
	2	13.0	1.8	3.3	12.5	1.7	2.9
	3	11.2	1.6	2.7			
	4	11.9	1.7	3.2	12.7	1.7	3.1
	5	11.9	1.7	2.9			
	6	13.4	2.1	3.3	13.2	2.0	3.1
	7	14.0	2.1	3.6	13.6	2.1	3.1
	8	7.2	0.8	1.5			
	9	9.7	1.3	2.3			
	10	13.2	2.0	3.4	____	___	___
	Stand Mean	11.9	1.7	3.0	13.0	1.9	3.0

Table 22 (continued)

Stand	Family	Highland Rim Height	DBH	Flush	Cumberland Mountain Height	DBH	Flush
11	1	16.4	2.6	4.2	17.1	2.7	4.0
	2	16.3	2.6	3.9	16.8	2.6	4.0
	3	16.3	2.7	3.9	17.2	2.8	3.9
	4	15.0	2.4	3.8	16.3	2.6	3.8
	5	16.5	2.5	4.3			
	6	15.7	2.5	3.9	16.0	2.5	3.5
	7	17.6	3.1	4.0	17.7	2.8	4.1
	8	16.8	2.7	4.0			
	9	16.0	2.6	4.1	17.0	2.6	3.8
	10	15.0	2.4	3.9	16.8	2.6	3.6
	Stand Mean	16.2	2.6	4.0	16.8	2.6	3.8
12	1	14.6	2.4	3.2			
	2	16.7	2.8	4.0	17.4	2.8	3.9
	3	17.0	2.7	4.2	18.6	2.9	4.3
	4	15.6	2.6	3.8	16.8	2.8	3.8
	5	17.7	3.0	4.0			
	6	15.6	2.3	4.1			
	7	18.5	2.8	4.3	19.2	2.9	4.0
	8	16.8	2.6	4.2	16.9	2.7	4.0
	9	16.4	2.7	3.8	16.9	2.7	3.9
	10	16.4	2.8	3.9	14.8	2.3	3.2
	Stand Mean	16.6	2.7	4.0	17.3	2.7	3.9

Table 22 (continued)

Stand	Family	Highland Rim Height	DBH	Flush	Cumberland Mountain Height	DBH	Flush
13	1	17.4	2.6	4.3	15.9	2.2	3.6
	2	17.4	2.5	4.2	18.1	2.6	4.0
	3	17.1	2.6	4.2	18.9	2.9	4.1
	4	16.0	2.3	3.9	15.2	2.1	3.5
	5	16.7	2.6	4.1	16.8	2.6	3.9
	6	16.6	2.7	3.8	16.0	2.5	3.6
	7	17.3	2.7	4.3	16.7	2.5	3.6
	8	16.8	2.4	4.2	16.3	2.3	3.8
	9	18.5	2.7	4.5	19.2	2.8	4.2
	10	17.6	2.6	4.4	17.6	2.6	4.0
	Stand Mean	17.1	2.6	4.2	17.1	2.5	3.8

[1]All measurements in feet.

[2]All measurements in inches.

[3]All measurements in feet.

Table 23. Mean values for previous year needle color[1], needle length[2], crown width at the Highland Rim and Cumberland Mountain following 8 growing seasons.

		Highland Rim			Cumberland Mountain	
Stand	Family	Previous Year Needle Color	Needle Length	Crown Width	Needle Length	Crown Width
1	1	6.47	81.65	8.54	82.38	8.19
	2	5.60	81.78	8.26	75.19	7.88
	3	5.62	79.64	7.64	73.98	5.82
	4	4.66	77.37	7.08	70.30	5.44
	5	5.60	87.04	7.67	85.51	7.31
	6	6.69	90.60	8.41	81.94	8.16
	7	5.34	81.84	7.22	71.16	6.34
	8	4.11	79.93	6.92	78.84	5.67
	9	6.58	85.82	7.68	79.57	8.08
	10	6.39	77.99	7.89	76.17	6.95
	Stand Mean	5.72	82.34	7.74	77.81	7.09
2	1	6.94	80.36	8.17	77.99	8.11
	2	6.19	83.46	8.21	82.83	8.65
	3	6.15	83.65	8.19	76.32	8.02
	4	6.71	79.01	8.31	77.30	7.86
	5	6.49	82.32	8.00	78.99	7.77
	6	6.60	82.08	8.20	75.27	8.62
	7	6.39	84.78	7.28	79.22	7.42
	8	6.88	84.43	7.69	73.83	7.67
	9	6.60	83.68	7.98	85.24	8.35
	10	6.67	79.08	8.21	81.04	8.30
	Stand Mean	6.52	82.20	8.04	78.88	8.10

Table 23 (continued)

Stand	Family	Highland Rim			Cumberland Mountain	
		Previous Year Needle Color	Needle Length	Crown Width	Needle Length	Crown Width
3	1	6.88	84.97	8.21	82.06	7.50
	2	6.03	81.16	8.40		
	3	5.52	85.09	7.42		
	4	5.97	81.06	7.74	79.71	6.91
	5	4.92	84.43	7.83	84.42	7.09
	6	6.15	84.63	8.26	81.86	7.21
	7	5.71	93.42	8.41		
	8	6.10	88.14	7.41		
	9	6.48	85.26	8.26	83.97	7.92
	10	5.81	83.02	8.19	____	____
	Stand Mean	5.98	85.08	8.05	82.36	7.31
4	1	4.42	79.09	7.22	79.79	5.84
	2	4.48	82.69	6.91	79.63	6.06
	3	5.16	86.00	7.14	75.78	6.08
	4	3.79	80.60	6.59	74.88	6.27
	5	4.41	82.79	7.25	73.54	5.98
	6	5.00	81.18	7.73	76.97	6.68
	7	4.47	82.16	7.48	84.25	6.80
	8	2.88	74.62	6.61	66.52	4.87
	9	3.29	75.85	6.24	65.37	4.43
	10	4.70	71.59	6.96	64.33	6.04
	Stand Mean	4.24	79.65	7.01	74.13	5.94

Table 23 (continued)

Stand	Family	Highland Rim			Cumberland Mountain	
		Previous Year Needle Color	Needle Length	Crown Width	Needle Length	Crown Width
5	1	8.00	84.40	9.60		
	2	5.54	84.00	7.84	71.55	6.53
	3	5.54	81.82	7.31	70.78	6.22
	4					
	5	5.12	76.52	7.40	66.46	6.59
	6	5.93	88.59	7.89	78.26	6.54
	7	4.02	74.74	6.78	65.36	5.82
	8	4.86	82.90	7.61	71.49	5.44
	9	6.20	87.62	7.77	77.59	6.47
	10	6.41	83.33	8.58	75.10	7.14
	Stand Mean	5.49	82.43	7.66	71.92	6.32
6	1	6.32	85.90	8.65		
	2	5.80	79.17	7.42		
	3	4.07	71.98	6.31		
	4	4.91	86.04	7.70	76.69	7.50
	5	4.30	80.07	6.86	72.10	5.69
	6	5.02	83.70	7.49	80.03	5.75
	7	3.82	82.23	7.47		
	8	4.40	81.74	6.86		
	9	5.97	80.94	8.36	77.24	7.49
	10	5.70	88.27	8.33	76.49	7.19
	Stand Mean	4.98	82.16	7.51	76.68	6.81

Table 23 (continued)

Stand	Family	Highland Rim			Cumberland Mountain	
		Previous Year Needle Color	Needle Length	Crown Width	Needle Length	Crown Width
7	1	6.39	87.74	8.63	83.69	7.85
	2	4.47	83.79	7.31		
	3	3.67	90.44	6.28	77.06	5.92
	4	5.42	77.07	7.50		
	5	5.71	80.92	7.67		
	6	4.50	82.77	7.06	73.08	6.52
	7	4.63	89.49	7.70	83.49	8.21
	8	6.38	82.16	8.35		
	9	5.62	83.89	7.94	78.82	8.02
	10	5.03	87.40	7.42	77.38	7.68
	Stand Mean	5.25	84.34	7.58	79.31	7.47
8	1	5.34	87.76	7.36	77.01	7.31
	2	6.05	38.98	7.90	81.84	8.67
	3	5.04	84.23	7.37	75.32	7.19
	4	5.23	86.47	7.69	82.66	7.55
	5	5.21	85.03	8.29	79.34	7.62
	6	6.08	86.74	7.88	79.46	7.30
	7	6.28	80.89	8.18		
	8	5.26	86.16	7.67		
	9	5.54	87.78	7.37	76.95	7.04
	10	6.41	83.20	8.61	78.01	8.14
	Stand Mean	5.66	85.49	7.82	78.81	7.62

Table 23 (continued)

Stand	Family	Highland Rim			Cumberland Mountain	
		Previous Year Needle Color	Needle Length	Crown Width	Needle Length	Crown Width
9	1	3.70	76.09	6.50		
	2	2.23	83.79	5.50		
	3	4.35	85.52	7.16	79.14	5.73
	4	4.36	85.07	7.58		
	5	4.72	84.52	7.42	82.50	5.55
	6	2.05	83.12	7.19	75.46	4.46
	7	3.86	80.42	6.04		
	8	2.72	84.70	6.43	71.52	4.16
	9	4.74	81.79	7.59		
	10	4.41	80.19	6.88	76.79	5.69
	Stand Mean	3.74	82.68	6.84	77.24	5.18
10	1	3.59	77.50	6.53		
	2	4.93	80.82	6.82	74.50	6.52
	3	3.40	79.79	6.40		
	4	4.95	88.56	6.78	80.55	6.63
	5	3.82	77.02	6.38		
	6	5.38	79.80	7.29	78.12	7.18
	7	6.47	78.80	7.42	76.25	7.20
	8	1.61	63.10	4.00		
	9	3.29	70.32	5.61		
	10	5.64	90.16	7.64	____	____
	Stand Mean	4.41	78.89	6.56	77.47	6.89

Table 23 (continued)

Stand	Family	Highland Rim			Cumberland Mountain	
		Previous Year Needle Color	Needle Length	Crown Width	Needle Length	Crown Width
11	1	6.60	86.08	8.13	84.66	8.33
	2	6.82	82.23	8.41	82.90	8.80
	3	6.51	85.74	8.60	80.99	8.53
	4	6.61	86.06	7.62	79.26	7.78
	5	6.99	84.96	8.36		
	6	6.85	79.56	7.53	76.00	7.63
	7	7.06	85.21	8.72	81.58	8.33
	8	6.26	81.97	8.26		
	9	6.71	87.63	8.17	82.54	8.19
	10	6.71	83.54	7.52	75.09	7.79
	Stand Mean	6.71	84.25	8.14	80.46	8.18
12	1	6.17	83.91	7.77		
	2	7.10	87.90	8.47	88.11	8.44
	3	6.79	84.34	8.58	85.75	9.02
	4	6.29	89.13	7.82	88.33	8.25
	5	6.84	82.80	8.58		
	6	6.44	84.02	8.28		
	7	7.12	88.18	8.98	83.13	8.67
	8	6.35	86.94	8.45	81.98	8.59
	9	6.69	84.09	8.32	83.47	8.83
	10	6.25	83.94	8.31	82.06	7.57
	Stand Mean	6.63	85.66	8.38	84.58	8.51

Table 23 (continued)

Stand	Family	Highland Rim			Cumberland Mountain	
		Previous Year Needle Color	Needle Length	Crown Width	Needle Length	Crown Width
13	1	6.42	76.14	8.00	78.46	7.33
	2	6.57	80.72	8.16	82.95	8.77
	3	6.62	81.40	8.13	83.14	9.06
	4	6.38	76.80	7.36	72.34	7.15
	5	6.62	82.16	8.15	77.76	8.33
	6	6.38	85.78	8.02	77.51	7.59
	7	5.96	78.90	8.40	78.17	7.92
	8	5.96	75.04	8.04	73.51	7.99
	9	6.56	82.70	7.97	78.21	8.77
	10	6.40	85.16	8.29	82.38	8.36
	Stand Mean	6.39	80.56	8.05	78.54	8.15

[1]Each tree was rated 1 through 8 as in Table 4, page 25.

[2]All measurements in millimeters.

[3]All measurements in feet.

VITA

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