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LOBLOLLY PINE PROVENANCE TESTING IN TENNESSEE

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

John B. McRae

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ABSTRACT

Six loblolly pine (*Pinus taeda* L.) provenance test plantations distributed across Tennessee (ages 19 to 26 years from planting) were evaluated on an individual tree basis for total height, dbh, volume and basal area. In addition, wood specific gravity and percentage composition of cortical monoterpenes were evaluated at the Ames Plantation in west Tennessee and the Highland Rim Forestry Field Station near Tullahoma. Significant differences among provenances were found at Ames Plantation, the Highland Rim Forestry Field Station, the Counce plantation in west Tennessee and the Stephen's Switch plantation in the lower elevations of the Cumberland Mountains.

At the Stephen's Switch plantation, trees from southeast Tennessee, north Alabama and the North Carolina Piedmont and Coastal Plain produced significantly more volume and basal area on a per hectare basis than trees from the Georgia Piedmont or the South Carolina Coastal Plain. At Ames Plantation, trees from Tishomingo, MS (upper-Coastal Plain), Accomac, VA (eastern shore), Johnston, SC (Piedmont), Chilesburg, VA (Piedmont) and Crossett, AR (upper-Coastal Plain) consistently produced the most volume per hectare, basal area per hectare and tonnes of wood per hectare. Intermediate production was attained by trees from Griffin, GA and Cullman, AL, both of the upper-Coastal Plain region. Low production was associated with provenances that originated near Georgetown, SC (Coastal Plain) and in Gulf Coastal Plain localities.

Trees in the Counce plantation varied significantly only in diameter and volume per tree. Trees from the South Carolina Coastal Plain, south Alabama and the North Carolina Coastal Plain were largest in diameter and volume, while those from the Georgia Piedmont, Maryland Coastal Plain and northeast Mississippi were smallest.

No significant differences among provenances for unextracted and extracted specific gravity, or extractives were evident at either Ames Plantation or the Highland Rim. However, extractives were produced at the Highland Rim in significantly greater amounts than at Ames. With one exception, a general pattern of decreasing specific gravity from the Atlantic Coastal Plain (.475 to .471), inland into the Piedmont region (.466 to .463) was indicated.

Considerable variation was found in cortical monoterpene composition; beta-pinene, myrcene, limonene, and beta-phellandrene showed bimodality, while the alpha-pinene data had normal distribution. Combined data from the Ames and Highland Rim plantations revealed that 12 of 16 possible phenotypes occurred when each tree was classified as being "high" or "low" for each of the 4 monoterpenes showing bimodality. High amounts of limonene and beta-phellandrene occurred in greater percentages in trees of western origins, while high amounts of myrcene were frequently found in eastern trees. Distribution of beta-pinene was patchy and no trend was identified. A trend of increasing percent alpha-pinene content in a southwest to northeast pattern was indicated.

It was recommended that trees best suited to west Tennessee growing conditions included those from Virginia, the Carolina Piedmonts and north Mississippi. Loblolly pine plantations on the Highland Rim

should consist of trees from Virginia and the Carolina Piedmonts. Trees from southeast Tennessee, north Alabama and the North Carolina Piedmont were recommended for planting in the lower elevations of the Cumberland Mountains.

Trees planted at the Friendship Forest (ridge and valley) and Norris (ridge and valley) did not indicate statistically significant differences among provenances. Future measurements of these provenance tests were not recommended.

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CHAPTER I

INTRODUCTION

The South is a timber-growing region; many of its rural people own forest land, and many of its industries are based on wood and own large areas devoted to tree plantations. The state of Tennessee is no exception. Forests occupy 13.1 million acres or 50% of the land area in Tennessee, 12.8 million of which are classified as commercial (Murphy, 1972). The state's primary wood-using industries amount to more than a one billion dollar business to Tennessee's manufacturing economy, ranking third behind only chemical and food industries in importance (Abt, 1979). Many of these forested lands are classified as pine sites, but are presently stocked with previously high-graded hardwoods. Conversion to pine plantations by the forest industry and individual landowners is occurring at an increasing rate.

Loblolly pine (*Pinus taeda* L.) is the most important softwood species in the Southern region, representing slightly over one half of the total pine volume. Loblolly is particularly noted for its rapid growth on a variety of soils and for its wood quality valued for pulp and structural materials. Although native in Tennessee to only a few counties bordering Alabama, Mississippi, and Georgia, loblolly pine is being planted throughout Tennessee, northward into Kentucky and in southern portions of Illinois, Indiana and Ohio.

The first step in all breeding programs is to examine genetic differences among races for future use in breeding (Namkoong, 1979).

Breeding within an average seed source (provenance) may yield better trees than those existing in any unimproved provenance. However, if breeding is started within the best adapted provenances, the base population from which selections are made will provide an immediate improvement over the poor adapted provenances. Since most of Tennessee is located north of the species range, it is important to determine which loblolly pine provenances are best suited to the various physiographic regions of the state. Breeding the best trees of the best provenances offers an opportunity for substantial improvement of wood yield and quality. Consequently, the objectives of this study are:

1. To determine the phenotypic variation among and within provenances.

2. To determine the provenance best suited to particular physiographic regions of Tennessee.

CHAPTER II

LITERATURE REVIEW

I. Natural Variation

Loblolly pine (Pinus taeda L.) occurs naturally throughout the southeastern coastal plain from portions of Texas to southern New Jersey and extends into much of the adjoining piedmont as far as the southern border of Tennessee. Because of this extensive range loblolly pine is exposed to a wide variety of environmental conditions facilitating local site adaptation and hence, phenotypic variation. Such variation has been identified by comparing physical characteristics and differences in composition of various chemical constituents among sampled individuals. These efforts have resulted in the compilation of valuable information and records, the foundation from which future progeny testing and breeding programs can be built.

Tree Growth and Yield

Tree volume is a function of diameter, height and form class. The nature of these characteristics is such that their expressions are closely related to and often confounded by the site on which a given tree is growing. Consequently, growth rate and yield cannot be evaluated from natural variation surveys. Differences in the appearance and vigor of natural stands among areas throughout the range of loblolly pine led researchers to believe some of the variation to be genetic. Such was the case during the 1950's and

earlier. In Arkansas, visitors observing the vigorous, high quality stands of loblolly pine in the vicinity of Crossett frequently asked if these trees represented a superior geographic race (Grigsby, 1975). Subsequent provenance testing revealed that loblolly pine of other origins exhibited even faster growth rates and larger volumes than trees originating from Crossett area stands (Zarger, 1961; Rink and Thor, 1971; Grigsby, (1975).

Wood Properties

Of all the commercially important wood properties, specific gravity is considered by most authors to be the most valuable in terms of breeding. Van Buijtenen (1976) recently concluded that specific gravity is the only wood property of consideration that can be realistically modified by silvicultural and genetic means.

Although usually referred to as a single characteristic, specific gravity is actually a function of several variables such as percent summerwood, cell wall thickness and cell wall diameter (Zobel, 1961). Snyder and Hamaker (1970) found that 55% of the outerwood from natural stands of loblolly on moist sites in Mississippi is summerwood.

Many surveys concerning specific gravity and other wood properties have been conducted for all the commercially important southern pines. Zobel and McElwee (1958) studied natural variation in specific gravity of loblolly pine from Alabama to Virginia. They found a broad geographic trend in which average specific gravity decreased in a westward direction. In later surveys conducted throughout the entire range of loblolly pine, Zobel et al. (1960, 1972) found low values of specific gravity occurring in the Piedmont,

and the highest values in the Coastal Plain of the Carolinas and Georgia.

Specific gravity in general increases rapidly to about age 20-25 and more slowly thereafter (Zobel et al., 1972). Geographic differences are more noticeable at the edge of a species range but become less distinct when whole tree values of specific gravity are compared rather than increment core values. These patterns of variation in specific gravity are substantiated by findings reported in several studies (Mitchell, 1964; Saucier and Taras, 1967, 1969; Whitesell et al., 1966).

Zobel et al. (1965) reported that variation in site index in natural stands had very little effect on average tree specific gravity or percent corewood. Similarly the effect of stand density on specific gravity of wood produced in trees of all ages and on all sites encountered was found to be negligible. In studies by Zobel and McElwee (1958a) and Whitesell et al. (1966), multiple regressions of site, growth rate and age accounted for only a minor proportion of the variation in tracheid length and specific gravity observed. Most of the variation associated with specific gravity and tracheid length occurs among trees within plots and within individual trees (Zobel et al., 1960; Whitesell et al., 1966; Zobel and McElwee, 1958).

Cones, Seed and Needles

Thorbjornsen (1961) conducted an extensive collection of cone and twig material from 15 trees in each of 18 areas throughout the range of loblolly pine. Although 13 morphological characteristics were statistically significant, only a few were found to follow

independent regional variation patterns. Among the different areas surveyed, significant variation was observed in the following characteristics: needle length, stomatal frequency and serrations on needles. Only stomatal frequency showed a distinct regional pattern. Trees from sources west of the Mississippi River were found to have low stomatal frequencies while trees from eastern sources had high stomatal frequencies. The ratio of May to August precipitation over the average summer temperature was correlated with stomatal frequency ($r=.666$) with significant results. This indicates that the variation pattern shows some evidence of an adaptive clinal response to gradual changes in moisture supply.

Knauf and Bilan (1974) report similar results. Needles collected from loblolly pine seedlings in Bastrop County, Texas, appear to be adapted for survival in a dry climate, having thicker protective layers and fewer stomatal frequencies than those collected from seedlings in east Texas. After a few years however, differences between these adaptive characteristics of the western trees appeared to be lost after the seedlings became firmly established. More hypodermal cells, fewer stomates per unit length, greater cross-sectional needle area, and greater perimeter were characteristic of two year old loblolly pines of the "Lost Pines" region (Thames, 1963). These special characteristics were postulated as an adaptive means to conserve moisture by limiting transpiration. In addition, Hare and Switzer (1969) found loblollys west of the Mississippi River to have shorter needles and shorter fascicle sheaths.

Clinal variation patterns appear to be evident for seed coat thickness and seed form. Seeds possessing thin coats occur in

western portions of the range while thick seed coats are a characteristic of eastern localities. Seed coat thickness was highly correlated with a ratio of precipitation to evaporation. Thus, it was hypothesized that thinner seed coats facilitate water absorption and therefore, display an inherited adaptive value. Seed form, expressed as seed width in percent of seed length, exhibits a regional north-east to south-west pattern. Pointed seeds are common to western localities and rounded seeds to eastern areas of the species range (Thorbjornsen, 1961).

Cone size also demonstrates a regional variation pattern (Thorbjornsen, 1961). Small cones were consistently encountered in the "Lost Pines" and southeastern areas of the natural range, intermediate size cones in the northeastern part and large cones were found in the central portion of the species range. Local environments and edaphic conditions were attributed as factors influencing cone size. Introgression with shortleaf pine (Pinus echinata Mill) in the western part of the range was also suggested a cause for small cone size in that region (Thorbjornsen, 1961). Hybridization between loblolly and shortleaf might be responsible for a high degree of morphological variation within the loblolly pine species (Bilan, 1966).

Oleoresin

Of the many constituents of oleoresin, it is the steam-volatile portion, a diverse group of terpenes that has received the most attention in tree breeding research. Primarily due to the development of gas-liquid chromatography (GLC) during the 1950's, terpene research

was enhanced, specifically in the determination of the nature and composition of xylem and cortical monoterpenes.

All cortical monoterpenes in loblolly pine are remarkably consistent (Rockwood, 1973a; Squillace, 1976b; Gansel and Squillace, 1976). The composition of cortical monoterpenes in loblolly pine was found to be not appreciably influenced by tree age, local environment, edaphic conditions, seasonal effects or the position in the crown from which the sample was taken (Rockwood, 1973a).

The composition of terpenes in the oleoresin of slash pine was found to vary greatly among trees within stands and also among trees of different geographic sources (Squillace and Fisher 1966; Squillace, 1976a). Squillace (1976a) found cortex monoterpene composition to vary between plant tissues and organs. Considerable changes in monoterpene composition were also observed resulting from mechanical wounding, insect attacks and diseases.

The study of oleoresin can be a useful tool for identification of genetic differences among provenance groups. Most constituents were found to be strongly inherited. Some constituents appeared to be controlled mainly by a few genes, while others displayed polygenic inheritance (Squillace and Fisher, 1966). These results suggest that breeding for high or low amounts of myrcene, beta-pinene and beta-phellandrene could be successful.

Several other investigators have concentrated their efforts on determining the relationship of oleoresin composition to the degree of insect and disease resistance expressed by the tree. Hanover (1975) postulated that physical and/or chemical characteristics of the

oleoresin are responsible for resistance to insect attack. Smith (1966) found a difference in the monoterpene composition between healthy Ponderosa pine (Pinus ponderosa Laws) and those attacked by Dendroctonus brevicomis. Death to D. brevicomis was associated with resin vapors.

II. Provenance Test Variation

Studies of variation in trees are referred to as provenance, seed source or geographic variation research and involve the comparison of stands, progeny of trees in stands or both (Dorman, 1976). Genetic or genotypic differences occurring in different areas of a species range are referred to in broad terms as racial variation. Therefore, assuming racial variation exists in loblolly pine, provenance testing may indicate locations within the range in which selection would be more productive than in other areas.

Variation among areas is determined by collecting seed from native trees in different regions of the natural range and planting them in a common environment or several environments (Dorman, 1976). Through the use of pertinent experimental design, well planned data collection and analyses, genetic differences can then be identified. Therefore, a knowledge of the performance of trees away from their place of origin may be of greater importance in tree breeding than knowledge of performance in natural stands (Dorman, 1976).

Tree Growth and Yield

Provenance testing of nearly all the commercially important southern pines began during the 1950's and early 1960's. Many of

these consisted of loblolly pine seed sources, and every southeastern state from Maryland to Texas, and as far north as Ohio, could account for at least one study.

The oldest provenance test established in the South consisted of 4 seed sources planted in Louisiana in 1926. Bercaw (1955) reported results after 28 growing seasons and Wakeley and Bercaw (1965) after 35. They found trees of local sources producing 5 to 6 times the volume of trees from other sources (northern Georgia, north-central Arkansas and east Texas). In a test established in 1953, Crow (1964) found no significant differences among seed sources for height, dbh and volume, but growth trends indicated that the Arkansas source was growing consistently slower than trees from Louisiana. Ranking of sources did not change from the time of establishment (Crow, 1958a, 1958b, 1961). Zabala (1974) and others found no significant differences for any growth characteristics among sources when testing provenances whose origins were from within Louisiana.

A large test consisting of 36 seed sources established in 2 locations in southeastern Arkansas revealed somewhat different results (Grigsby, 1973). After 10 years, height and diameter were greatest in trees originating from southeastern Atlantic coastal areas. Seven of the top 10 producing provenances were from these areas, with a South Carolina source producing 30% more than all other sources. After 6 more growing seasons a change took place, and 7 of the 10 best sources originated from inland locations (Grigsby, 1977).

Testing a Crossett, Arkansas source against many other sources in 16 plantations in 6 southern states, Grigsby (1975) found trees of Crossett origin surviving better than those of all other sources.

When considering volume per plot, however, Crossett trees were often inferior even in plantations where they were the local source.

Provenance testing in Tennessee was initiated during the 1950's. Zarger (1961) reported loblolly pine from inland races survived the best, but found no significant differences in height growth among the 10 provenances tested. In a test planted in the lower elevations of the Cumberland Mountains, seedlings from the Alabama Piedmont and Georgia Piedmont had significantly fewer trees survive after 5 years than provenances representing areas from southeast Tennessee, North Carolina Piedmont and the North and South Carolina Coastal Plains (Thor and Brown, 1962). Trees of the North Carolina Piedmont source were significantly taller than trees from all other sources. At age 10, the North Carolina Piedmont source remained the tallest, while the ranking of all the other sources had changed between the fifth and tenth year, probably due to frost damage they suffered in the winter of 1962-1963 (Thor, 1967). An evaluation of 10 provenance tests of loblolly pines originating from throughout the range, revealed that trees from North Carolina, Virginia and Maryland were the best producers (Rink and Thor, 1971). Trees from those areas produced from 25-100% greater volumes and had superior survival compared to those of Deep South or South Carolina Coastal Plain origins.

Kraus (1967) found highly significant differences among trees from 3 broad areas in Georgia for height, dbh, and volume. Survival followed a decreasing pattern from the mountains in the north to the flatwoods in the south. The trend was reversed for the 3 growth characteristics above. Trees from Arkansas were unexcelled in all characteristics. LaFarge (1974) and Barber (1966) also showed significant

differences for the same traits and identified the same trends, but found survival to be the most important influence on total volume.

At age 7, a pattern of variation in North Carolina loblolly pine was determined by Lantz and Hofmann (1969). Overall performance of Coastal Plain trees was superior to that of Piedmont, Sandhills and Fall-line sources, producing up to 30% more volume and 12% taller trees. Goggans et al. (1972) found growth among Alabama trees to decrease in a south to north pattern within the state.

In southern Illinois, Woerheide (1959) found Maryland trees to rank first in height growth. Trees from a Virginia source ranked second and those from Arkansas third. In a Maryland provenance test, Little (1969) found trees of a local source to be tallest, producing the most volume, and incurring the least winter damage. Trees of a North Carolina Coastal Plain source ranked second. Both investigators reported similar results, finding that the form of loblolly pine where they were planted, to be so poor that only few high quality trees were present to produce saw logs or poles.

Trees from North Carolina produced 26% more volume than those of other sources when outplanted in western Virginia (Kormanik and Hoekstra, 1963). Trees from most sources were too poor in form for use as saw logs or poles. Trees of an Arkansas origin produced 15% complete forks, more than double that of all other sources.

The Southwide Pine Seed Source Study initiated in 1954 is the most extensive provenance test of southern pines. The loblolly pine plantings include 15 different seed sources replicated in 13 locations in 10 states. Wells and Wakeley (1966) reporting 10 year results

found trees from Livingston Parrish, Louisiana and Onslow County, North Carolina, made outstanding height growth in 9 plantations. Slower growth rates occurred from inland sources at all locations. Overall, provenances from east Texas and southwest Arkansas had about 10% better survival than all other sources. Local trees at the Maryland and west Tennessee plantations had superior height growth only on their respective sites. Collins (1964) reporting 10 year results of a "Southwide" loblolly pine planting in Dooly County, Georgia, found that height increased as seed origin became more southern. Based on 15 year results, Wells (1969) found no correlation among survival, rust resistance and height growth, all of which, along with diameter, influence volume yield. Thus he concluded that trees with genetic potential for superiority in each of these traits can be found throughout the natural range.

Many investigators have studied the apparent drought resistant loblolly pines of Texas origin. Seedlings from the "Lost Pines" area were found to survive consistently in greater numbers and exhibit better overall performance than those from more eastern areas (Zobel and Goddard, 1955; Cech and Goddard, 1957; Goddard and Brown, 1959).

Van Buijtenen (1966) tested the ability of trees, whose origins were west of the east Texas pine belt, to survive under droughty conditions. He found that more variation in drought resistance occurred among progenies of individual parent trees than among the seed sources. Long (1980) found that trees of non-local seed sources produced less average volume than those of local sources at the western extreme of the natural range. Dickerson (1971) reported that trees from the "Lost Pines" when planted on poor sites

in north Mississippi, failed to surpass loblolly pines from Mississippi or Alabama in either height or survival.

Wood Properties

An investigation of southern pine wood density by Zobel et al. (1972) revealed that in general the environment at the planting location has a greater effect on specific gravity than does the source of seed used. This was evident in North Carolina where Lantz and Hofmann (1969) found young tree specific gravity associated with location. Highest specific gravity was observed on the Coastal Plain (.39), lowest in the Sandhills (.33) and intermediate specific gravity (.36) occurred in the Piedmont location.

Jackson and Strickland (1962) found a highly significant linear relationship between latitude and wood specific gravity of loblolly pine. Trees from Florida, Georgia and South Carolina had lower specific gravities than those from Maryland and Virginia, ranging from .51 to .55. Saucier and Taras (1967) reported similar results. The percent summerwood and specific gravity increased from south to north and wood volume increased west to east. This suggested that trees producing the highest amount of dry weight originate in eastern and coastal areas. In a 5 year old test Thor and Brown (1962) found specific gravity to vary considerably within any given seed source. Trees of a Georgia Piedmont source produced a significantly lighter wood than those of southeast Tennessee, Alabama Piedmont, and North Carolina Coastal Plain sources. The faster growing trees possessed slightly heavier wood. After 10 years of growth, specific gravity in all trees was 10% higher, with the Georgia Piedmont trees (.372)

being significantly lower than trees from Alabama (.394) (Thor, 1967). Rink and Thor (1971) reported a trend where trees from northern sources had the highest observed specific gravity at 5 of 10 planting locations. In a west Tennessee plantation trees from a Virginia Piedmont source had significantly higher specific gravity than trees from all other sources. Trees of a southeast origin had significantly lower specific gravity than other sources. This trend, however, was not evident in some of the other provenance tests measured, where a southern source ranked high with regard to specific gravity in four locations. The authors concluded that the regional variation pattern of specific gravity determined from their study and previous work (Thor and Brown, 1962; Thor, 1967) is weak and not consistent with geographical patterns demonstrated for natural populations.

Oleoresin

The geographic variation of monoterpenes in cortical oleoresin of loblolly pine was thoroughly investigated by Squillace and Wells (1980) and Squillace et al. (1980). Approximately 2700 trees were sampled from 113 provenances in 9 provenance plantations and 1 natural stand. A total of 8 cortical monoterpenes was identified using gas-liquid chromatography. Alpha-pinene, beta-pinene, myrcene, limonene and beta-phellandrene were classified as major constituents. Minor constituents were camphene and alpha-phellandrene (up to 2%), and delta-3-carene was identified in relatively large amounts (up to 28%) in 3 trees.

Based on research by Squillace (1971), Gansel and Squillace (1976) and Squillace et al. (1980), in which beta-pinene, myrcene,

limonene, and beta-phellandrene, exhibited bimodality and simple inheritance, trees were classified as "high" or "low" for each of the 4 monoterpenes. Relatively little variation was found in beta-pinene, and no clear geographic trends were apparent. Myrcene was generally high in eastern localities and low in the west, with high and low patches occurring throughout the range. A definite east to west gradient was determined for limcnene. The percentage of trees sampled from eastern sources had 0% to 10% high amounts, while those in western localities had 80% to 100% high amounts. All trees sampled west of the Mississippi River had high beta-phellandrene, while east of the river the percentage of trees having high amounts average 91%. Coastal sources tended to have fewer trees with high beta-phellandrene than inland sources; a similar pattern of variation was found with limonene.

Alpha-pinene, not having a bimodal distribution, was examined on its average percent contribution to the total monoterpene composition within trees and provenances. Western sources were found to have the lowest average contents (15%), with contents increasing in an eastward direction. Average contents peaked in eastern Mississippi at about 40%, remaining relatively high in coastal areas, then decreasing towards the north and northwest.

Investigations of cortical monoterpene composition by Squillace (1971) and Squillace et al. (1980) and others indicated this characteristic would be useful as gene markers for study of population structure, seed certification and as a means of identifying geographic origin of seed.

Cronartium Resistance

Loblolly pine, over most of its natural range is susceptible to the fusiform rust fungus, Cronartium fusiforme (Hedgc. and Hunt. exCumm).

Many investigators have observed patterns of variation in loblolly to Cronartium resistance. It is well documented that trees in western portions of the natural range and of extreme northeastern origin retain their superior resistance to attack regardless of the planting site (Collins, 1964; Wells and Wakeley, 1966; Wells, 1969; Wells and Switzer, 1975; Grigsby, 1973, 1977). Apparently, a source from Livingston Parrish, Louisiana, consistently ranks the highest in resistance, but its tolerance of climates north of central Louisiana is low. It was recommended that a Maryland source be planted in the piedmont and upper-coastal plain regions of the south where the climate is too severe for the Livingston source (Wells and Switzer, 1975). In provenance tests planted in Tennessee, rust infestation was negligible (Rink and Thor, 1971).

Squillace (1980) and Rockwood (1973b, 1974) have found a relationship between cortex oleoresin and rust resistance. Apparently a few of the constituents are present in higher amounts in resistant trees than nonresistant trees.

Environmental Influence

Several investigators attempting to explain the characteristics that vary in loblolly pine have found that several geographic patterns are clinal. Significant relationships and trends of environmental

influence have been identified, but sound reasons as to why these occurred are not always evident.

Large fluctuations in temperature, length of growing season and variations in patterns of seasonal rainfall may exert quite strong influences in the development of racial strains over the entire range of loblolly pine (Dorman, 1976). Wells and Wakeley (1966) showed loblolly pine from Maryland and west Tennessee (areas of northern extremes of the species' natural range) to be superior in height only on those sites where they represented the local provenance. Postulating this relationship to be an adaptation of local populations to colder climates, a multiple regression of average minimum January temperature and average summer rainfall on height was developed. A highly significant association between climate and tree height existed at 7 of the 13 plantations. Trees from sources having high summer rainfall tended to grow faster than those from low rainfall provenances. Trees from sources with warm winters grew faster than those from cold winter origins. In Maryland and Tennessee plantings, however, where the coldest climates of the study were observed, the reverse was true. Grigsby (1973) found volume growth to follow a similar trend. Trees from low rainfall areas tend to survive better than those from high rainfall areas (Grigsby, 1977). Similar results are reported by Saucier and Taras (1969) and Wells and Wakeley (1966).

Zobel (1956) found the greatest variation in specific gravity to occur within each plot and the testable growth and environmental factors considered together accounted for only a small amount of this

variation. Results from a much larger study over a longer period of time revealed that the local environment has a greater effect on wood specific gravity than the influence of geographic difference in seed source (Zobel et al., 1972).

III. Variation Among Trees

In a Georgia provenance test of local sources, LaFarge (1974) found significant differences among seed sources for 6 characteristics. Significant differences among mother trees within provenance also occurred but for only 3 traits. Additive genetic variances for 7 characteristics based on mother trees without regard to provenance were 1.5 to 17 times greater than those based on mother trees within provenance. However, it is logical to expect variation within stands (provenance); geographic variation in a species could not evolve if inherent differences did not exist among individual trees (LaFarge, 1974).

The variation existing within a species of trees is generally determined for each commercially important characteristic by establishing and evaluating heritability tests. To evaluate inherent variation, narrow sense heritabilities are calculated for each of the traits. Narrow sense heritability (h^2) is that fraction of total variation in the expression of a trait due to genes with additive effects.

Stonecypher and Zobel (1966) report estimates of narrow sense heritabilities for several characteristics measured from 5-year-old progeny. For height growth and diameter at half-height, h^2 was

estimated to be .34 and .32, respectively. Narrow sense heritability estimates for volume growth per tree and stem diameter inside the bark were .23 and .28, respectively. Shelbourne and Stonecypher (1971) found bole straightness in young trees to be a heritable trait which becomes more strongly genetically controlled as the tree increases in age and height. At age 2 this h^2 was .20 and at age 5, .38. Sweep was generally much less heritable with values from .1 to .25 at age 5. Crook was more closely correlated with overall straightness than sweep.

Estimates of heritability on an individual tree basis for several other characteristics are reported by Stonecypher et al. (1973). Growth rate, tree form and rust resistance had h^2 values ranging from .1 to .3 and were considered to be under moderate genetic control. Selection of resistant trees in areas of high rust incidence can result in gains of 42%. Predicted gains for improvement in volume are 25% while height and basal area were considered to improve only moderately. Bole straightness and crown size are anticipated to show relatively low gains.

Several authors report heritabilities for specific gravity, tracheid length, compression wood and other wood properties. Early work by Van Buijtenen (1962) and Stonecypher et al. (1964, 1966) found specific gravity in young trees to be highly heritable, with estimates of h^2 ranging from .56 to .73. In more recent studies by Stonecypher et al. (1973) and Barefoot (1976) estimates are closer to .5. Specific gravity, therefore, appears to be under strong genetic control.

Van Buijtenen et al. (1974) found specific gravity to be the only wood property economically meaningful to the mills, since it

accounted for a major portion of the variation in wood quality encountered.

Squillace (1976a) found the volatile terpenes of pines, as a group, to be strongly inherited. The degree of cortex monoterpene inheritance in loblolly pine varies among constituents and among trees. The mode of monoterpenes inheritance varies within the oleoresin but is consistent within the species (Rockwood, 1973b).

Squillace et al. (1980) revealed evidence supporting single-gene inheritance of beta-pinene, myrcene, limonene, and beta-phellandrene. Genes coding the production of myrcene and limonene also were found to be closely linked and occurring at a low rate of recombination.

CHAPTER III

MATERIALS AND METHODS

I. Provenance Test Description

Ten loblolly pine provenance tests were established in the state of Tennessee over the 11 year period from 1950 to 1961 (Table 1). Recent inspection of these determined that only 6 plantations were of adequate stocking to warrant re-measurements. The remaining 4 plantations sustained damage from fires, ice, insects and other natural causes as well as partial cuttings which would invalidate the statistical analysis. Consequently, these 4 plantations were not included in this study.

The 6 plantations analyzed were established on abandoned farm land. They are located across the state as shown in Figure 1. Additional characteristics of each plantation are presented in Table 2. The provenances represented at each location are listed in Table 3.

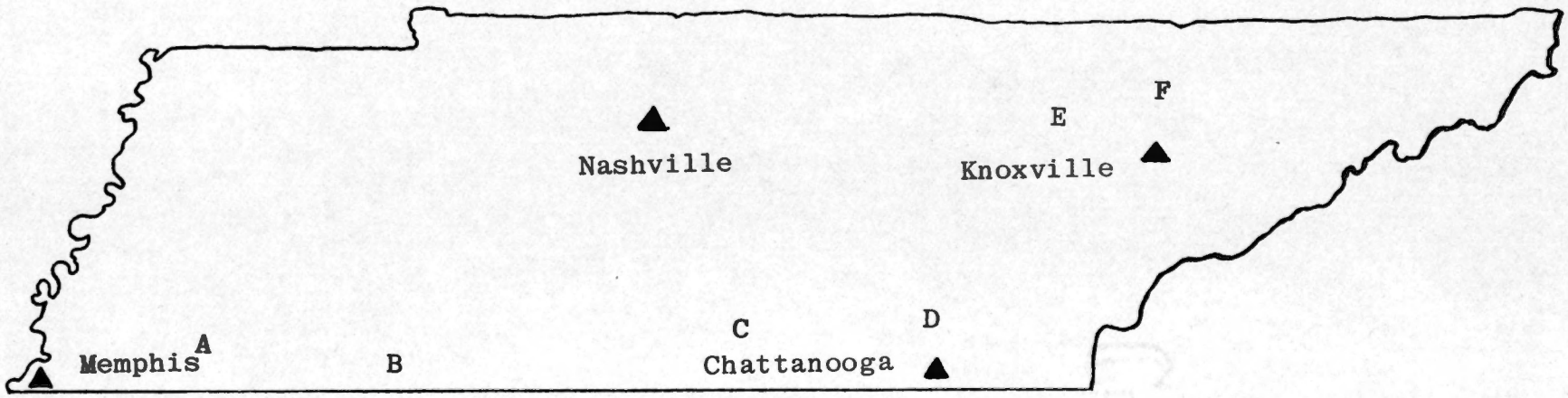
II. Measurements

All sample trees were measured for total height and for diameter at 1.4 meters (dbh). Height was measured to the nearest half meter using a Haga altimeter and dbh was determined to the nearest centimeter with a standard metric caliper. These measurements were then used to compute individual tree volumes up to an 8 cm top. The volume prediction equation used in this calculation was developed by

Table 1. Agencies Responsible for Establishment of the Ten Provenance Tests, Year of Establishment and Date of Measurement.

Plantation	Established By	Year Established	Date Measured
Ames	Univ. of Tennessee	1961	July, 1980
Chickasaw	U.S. Forest Service and Tenn. State Div. of Forestry	1952	*
Counce	Tenn. River Pulp & Paper Co. and Tenn. Valley Auth.	1960	August, 1980
Friendship	Univ. of Tennessee and Tenn. Valley Auth.	1954	Nov., 1980
Highland Rim	Univ. of Tennessee	1961	August, 1980
Norris	U.S. Forest Service and Tenn. Valley Auth.	1954	July, 1980
Norris-Loyston	Tenn. Valley Auth.	1950	*
Sewanee (A)	Univ. of the South and Tenn. Valley Auth.	1955	*
Sewanee (B)	Univ. of the South and Tenn. Valley Auth. and U.S. Forest Service	1956	*
Stephen's Switch	Univ. of Tennessee and Tenn. Valley Auth.	1956	July, 1980

*Provenance tests not measured because of insufficient stocking levels.



A = Ames Plantation
B = Counce
C = Highland Rim Forestry Sta.
D = Friendship Forest
E = Stephen's Switch
F = Norris

Figure 1. Location of Provenance Tests.

Table 2. Location of Provenance Test Plantations, Number of Provenances Represented, Age, Plot-size, and Spacing.

Plantation	Physiographic Region	County	Elevation (m)	Number of Provenances	Age	Trees/ Plot	Spacing (ft)
Ames	Coastal Plain	Fayette & Hardemann	153	10	19	25[a]	8x8
Counce	Coastal Plain	Hardin	122	9	20	25	6x6
Friendship	Ridge & valley	Hamilton	244	6	26	49	6x6
Highland Rim	Highland Rim	Franklin	305	6	19	25[a]	8x8
Norris	Ridge & valley	Anderson	305	6	26	25	6x6
Stephen's Switch	Cumberland Mountains	Morgan	458	6	24	49	6x6

[a]Mortality was replaced after the first growing season.

Table 3. Sources and Number of Replications Represented in Each Provenance Test Plantation.

Plantation	Sources Represented	Number of Replications
Ames	Virginia Coastal Plain Accomac, VA Virginia Piedmont Chilesburg, VA South Carolina Coastal Plain Georgetown, SC South Carolina Piedmont Johnston, SC Georgia Piedmont Griffin, GA north central Alabama Cullman, AL northeast Mississippi Coastal Plain Woodville, MS southeast Arkansas Crossett, AR Deep South (deep south Coastal Plain)[a]	4
Counce	Maryland Coastal Plain North Carolina Coastal Plain South Carolina Coastal Plain Horry County west central Georgia Heard County northwest Alabama southwest Alabama Clarke County northeast Mississippi Monroe County southeast Tennessee Hamilton County	3[b]
Friendship Forest[c]	Virginia Coastal Plain North Carolina Coastal Plain North Carolina Piedmont South Carolina Coastal Plain Georgia Piedmont Upson County Arkansas Howard County	4
Highland Rim	Virginia Coastal Plain Accomac, VA South Carolina Piedmont Johnston, SC Georgia Piedmont Griffin, GA	4

Table 3 (Continued)

Plantation	Sources Represented	Number of Replications
(Highland Rim)	north central Alabama Cullman, AL southeast Arkansas Crossett, AR Deep South (deep south Coastal Plain)[a]	
Norris[d]	North Carolina Coastal Plain South Carolina Coastal Plain north Georgia (lot 3) north Georgia (lot 6) northwest Georgia (lot 5) southeast Arkansas Crossett, AR	4
Stephen's Switch[e]	North Carolina Coastal Plain South Carolina Coastal Plain North Carolina Piedmont north Georgia Piedmont southeast Tennessee north Alabama	4

[a]Deep South sources at both Ames and Highland Rim consist of trees from southeast Texas, west central Louisiana, southeast Louisiana, southwest Georgia and northeast Florida. Due to poor first-year survival, trees of these sources were transplanted into the composite Deep South sources.

[b]Replication one was removed in 1971 to accommodate a holding pond.

[c]This plantation was row thinned several years ago. Because there is no record of the thinning, the methods are unknown.

[d]This plantation was selectively thinned in 1964; only slowest growing trees, diseased trees or trees with poor form were removed. The plantation is part of the Crossett-in-Reverse loblolly pine seed source study sponsored by the Southern Forest Experiment Station.

[e]A low thinning was performed in this plantation during the winter of 1970-1971. Plots were thinned to 25 trees, removing only the smallest trees of poor form.

Smalley and Bower (1968) which is applicable for loblolly pines grown in plantations located on abandoned fields.

$$V = 0.00003782 (D^2H) - 0.00297609$$

where

V = volume in cubic meters.

D = diameter at breast height (dbh) in centimeters.

H = total tree height in meters.

The conversion to this equation from the original formula which computed cubic foot volumes is presented in the Appendix (Table A-16).

Basal area was calculated from stem diameter using the following equation:

$$B.A. = 0.00007854 (D^2)$$

where

B.A. = basal area in square meters.

D = diameter at breast height (dbh) in centimeters.

In addition, the number of metric tonnes per hectare of wood fiber was computed on a per plot basis at both the Ames and the Highland Rim plantations as follows:

$$T = V (ESG)$$

where

T = tonnes per hectare.

V = volume per hectare in cubic meters.

ESG = extracted specific gravity.

Volume per hectare and basal area per hectare were determined by summing the individual tree volumes within each plot and adjusting

for the appropriate plot size. The plot sizes varied with respect to spacing and the presence or absence of border rows at each plantation (Appendix, Table A-17).

With one exception, wood cores and cortex resin samples were collected from 2 trees within each plot at both the Ames and Highland Rim plantations. Collections within the Deep South source plots included 2 samples from trees originating in southwest Texas, west-central Louisiana and southeast Louisiana. Dominant and codominant trees free from symptoms of disease and having no crooks or forks at or below breast height were selected.

An 11 mm increment borer was used to extract one core (bark to bark) at breast height from each sample tree. To minimize the amounts of compression wood, slight adjustments in the height of sample points were allowed to avoid obvious knots. All core samples were placed in labeled plastic tubes and stored in a freezer until specific gravities could be determined.

The annual growth rings for years 12 to 16 were cut transversely from both ends of the core. The specific gravity was estimated for each core sample on the basis of oven-dry weight and green volume. Volumes were calculated from the diameter and length of each core using the formula for determining the volume of a cylinder:

$$V = \pi r^2 L$$

where

V = volume of cylinder.

r = radius of transverse cross section.

L = length of the core.

Samples that were resin soaked or exhibiting a high proportion of compression wood or knotting were discarded and trees resampled to obtain more accurate specific gravity determinations. All acceptable samples of wood were dried for 2 days at 105° C and then cooled in a dessicator prior to determination of dry weights. All wood cores were weighed before and after extraction of non-fibrous matter to determine the unextracted and extracted wood specific gravities, respectively, and the amount of extractives.

The extraction was accomplished in 2 steps. First, the wood samples were soaked in water overnight, and then extracted in a Soxhlet apparatus with a mixture of benzene and 95% ethanol (2:1) for a period of 8 hours. This extract was drained and the cores were further extracted with pure 95% ethanol for 8 hours.

A sample of cortex resin was collected from each of the 2 sample trees per plot. These trees were climbed to the height where a branch in the upper crown could be cut with a pruning pole. The terminal bud was excised from the end of a twig, with the cut made at an angle in order to expose a large area of fresh tissue. Resin was allowed to form a droplet on the end of the twig, and then the end of the twig was immersed in about 5 ml of anhydrous ethyl ether in a screw-cap vial to dissolve the resin. Several crystals of pyrogallol, soluble in ether, were placed in each vial during preparation to prevent oxidation of the sample.

Cortex oleoresin samples dissolved in ether were analyzed on both a Varian Gas Chromatograph Model 1525-B and a Shimadzu GC-mini2 equipped with hydrogen ionization detectors. Temperatures of the

injection port and detector were 133°-135° C, and 150°-155° C, respectively, using the Varian chromatograph. With the Shimadzu chromatograph, the injection port and detector temperatures were 230° C. Helium was used as a carrier gas with a flow of 25 ml/minute. Samples of cortex resin were analyzed at 75° C constant temperature on an 8' x 1/8" stainless steel column packed with 10% B,B'oxydiproprionitrile on an 80/100 mesh chromosorb W support.

Qualitative identification of individual monoterpenes was made by comparing retention times with those of pure terpene standards analyzed under the same conditions. Because of the method in which resin was collected, the amount collected was not determined and no quantitative analysis was performed.

Percentage composition of each monoterpene on a total monoterpene basis of each resin sample was calculated by comparing the area under each monoterpene peak to the total area of monoterpenes. The area under each monoterpene peak was estimated by multiplying the height of the peak times its width at half peak height.

III. Statistical Analysis

Individual plantations were established in a randomized complete block design. An Analysis of Variance (ANOVA) was performed for each location on the characteristics of total tree height, dbh, volume per tree, volume per hectare and basal area per hectare. The total volume produced at Stephen's Switch includes the volume from thinning in 1971. The number of tonnes of wood fiber per hectare was computed for 10 provenances at Ames Plantation and for 6 provenances at Highland Rim. Volume per hectare, basal area per

hectare and tonnes of wood per hectare were computed on a per plot basis, thus precluding a within plot effect. The ANOVA procedure assumes that all errors are random, normally and independently distributed with a mean value of 0 and having a common variance. This may be expressed in the following linear model:

$$Yprw = M + Pp + Rr + PRpr + Ew$$

where

Yprw = individual observation.

M = mean.

Pp = provenance effect, with p = 1,2,3,...,i, and

i = number of provenances represented.

Rr = replication effect, with r = 1,2,3,...,j, and

j = number of replications represented.

PRpr = interaction effect of provenance and replication.

Ew = within plot effect (residual error), with w = number of individual trees per plot.

The ANOVA model used is presented in Table 4.

All calculations for these analyses were performed on an IBM 370 model 3031 computer at The University of Tennessee, Knoxville. The General Linear Models (GLM) procedure of the Statistical Analysis Program (SAS·79) formulated by Barr et al. (1979) was used. Mean separation of significant effects was determined by Duncan's New Multiple Range Test.

A combined location analysis of the Ames and Highland Rim plantations was possible for 6 of the provenances which were represented at both locations. Again, all effects were assumed to be random. The linear model for this analysis is as follows:

Table 4. Analysis of Variance, Expected Mean Squares, and Test of Hypothesis for Individual Location Analyses.

Source of Variation	d.f.	Expected Mean Squares[a]
Replications	r - 1	$\sigma^2_w + w\sigma^2_{RxP} + wp\sigma^2_R$
Provenance	p - 1	$\sigma^2_w + w\sigma^2_{RxP} + wr\sigma^2_P$
Replications x Provenance	(r-1) (p-1)	$\sigma^2_w + w\sigma^2_{RxP}$
Within Plot (=Residual)	(w-1)rp	σ^2_w

[a]Explanation of symbols:

σ^2_w = within plot variance component.

σ^2_{RxP} = variance component for interaction of replication with provenance.

σ^2_P = among provenance variance component.

σ^2_R = among replication variance component.

$$Y_{lprw} = M + L_l + RL/_{rl} + P_p + PL_{pl} + PR/L_{pr/l} + E_w$$

where

Y_{lprw} = individual observation.

M = mean.

L_l = location effect, with $l = 1,2,3,\ldots,q$, and

q = number of locations represented.

$RL/_{rl}$ = effect of replications within locations, with

$r = 1,2,3,\ldots,j$, and j = number of replications represented at a given location, and $l = 1,2,3,\ldots,q$, with q = number of locations represented.

P_p = provenance effect, with $p = 1,2,3,\ldots,i$, and

i = number of provenances represented.

PL_{pl} = interaction effect of provenance and location.

$PR/L_{pr/l}$ = effect of interaction of provenance and replication within location.

E_w = within plot effect (residual error), with

w = number of individual trees per plot.

The ANOVA model for this analysis is shown in Table 5.

Unextracted and extracted specific gravities and extractives were analyzed in a partially nested design according to the following linear model:

$$Y_{prt} = M + P_p + R_r + PR_{pr} + T/PR_{t/pr} + E_w$$

where

Y_{prt} = individual observation.

M = mean.

P_p = provenance effect, with $p = 1,2,3,\ldots,i$, and

i = number of provenances represented.

Table 5. Analysis of Variance, Expected Mean Squares, and Test of Hypothesis for the Combined Location Analysis of Six Provenances at Ames and Highland Rim Plantations.

Source of Variation	d.f.	Expected Mean Squares[a]
Locations	l-1	$\sigma^2_w + w\sigma^2_{RxP/L} + wr\sigma^2_{LxP} + wp\sigma^2_{R/L} + wpr\sigma^2_L$
Provenance	p-1	$\sigma^2_w + w\sigma^2_{RxP/L} + wr\sigma^2_{LxP} + wrl\sigma^2_P$
Locations x Provenance	(l-1) (p-1)	$\sigma^2_w + w\sigma^2_{RxP/L} + wr\sigma^2_{LxP}$
Replications within Location	(r-1)l	$\sigma^2_w + w\sigma^2_{RxP/L} + wp\sigma^2_{R/L}$
Replications x Provenance/ Location	(p-1)(r-1)l	$\sigma^2_w + w\sigma^2_{RxP/L}$
Within Plot (=Residual)	(w-1)rpl	σ^2_w

$-\sigma^2_w + w\sigma^2_{RxP/L}$

[a]Explanation of symbols:

σ^2_w = within plot variance component.

$\sigma^2_{RxP/L}$ = within location variance component for the interaction of provenance with replication.

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

σ^2_{LxP} = variance component for interaction of location with provenance.

σ^2_P = among provenance variance component.

σ^2_R = among replication variance component.

R_r = replication effect, with r = 1,2,3,...,j, and

j = number of replications represented.

PR_{pr} = interaction effect of provenance and replication.

$T/PR_{t/pr}$ = effect of tree with t = 1,2,3,...,k, and

k = number of trees represented, within provenance and replication.

E_w = within tree effect.

The ANOVA model for this analysis is given in Table 6.

Breeding values were calculated for each significant ($P < 0.05$) among provenance effect according to the methodology of Kung (1979). For those characteristics exhibiting heteroscedasticity (unequal variance within provenance) as determined by Bartlett's Test for Homogeneity of Variance (at the 0.05 significance level), the James and Stein (1961) estimator was used. The Box and Tiao (1973) estimator of breeding value was used for those characteristics having similar variance within provenances.

The breeding value of a provenance can be expressed as:

$$Z = \overline{Y} + C\ (Y-\overline{Y})$$

where

Z = among provenance characteristic estimated.

$\overline{Y}$ = plantation mean or average of all provenance means.

Y = provenance mean observed in a plantation.

C = shrinking factor.

The shrinking factor (estimator) reported by James and Stein (1961) is:

$$C = 1 - (K-3)\ D/S$$

Table 6. Analysis of Variance, Expected Mean Squares and Test of Effects for Unextracted Specific Gravity, Extracted Specific Gravity, and Extractives at Ames and Highland Rim Plantations.

Source of Variation	d.f.	Expected Mean Squares[a]
Replications	r-1	$\sigma^2_w + w\sigma^2_{T/RxP} + wt\sigma^2_{RxP} + wtp\sigma^2_R$
Provenances	p-1	$\sigma^2_w + w\sigma^2_{T/RxP} + wt\sigma^2_{RxP} + wtr\sigma^2_P$
Replications x Provenance	(r-1) (p-1)	$\sigma^2_w + w\sigma^2_{T/RxP} + wt\sigma^2_{RxP}$
Trees/Provenance and Replication	(t-1)rp	$\sigma^2_w + w\sigma^2_{T/RxP}$
Within Tree	(w-1)rtp	σ^2_w

[a]Explanation of symbols:

σ^2_w = within tree variance component.

$\sigma^2_{T/RxP}$ = among trees within provenance and replication variance component.

σ_{RxP} = variance component for interaction of replication with provenance.

σ^2_P = among provenance variance component.

σ^2_R = among replication variance component.

where

K = number of provenances.

D = estimated variance of the theoretical normal distribution of breeding values (calculated from the error variance divided by the number of observations within the provenance).

S = the summation of (provenance-plantation mean)^2.

The shrinking factor (estimator) reported by Box and Tiao (1973) is:

$$C = 1 - (1/F)$$

where

F = mean square among provenances divided by the mean square within provenances as defined by the ANOVA table.

Bimodal frequency distributions of beta-pinene, myrcene, limonene and beta-phellandrene was demonstrated by Squillace et al. (1980). These 4 constituents were shown by the authors to be monogenically inherited, with high amounts being dominant over low in each case. Therefore, their classification scheme was used to assign each tree as being "high" or "low" for each of the 4 monoterpenes found by them to be simply inherited, as described below:

Beta-pinene: Considered to be high when its content was greater than Y, where Y = 4.8 - .035X and X is the sum of limonene + beta-phellandrene contents, otherwise low.

Myrcene: Considered to be high when its content was greater than Y, where Y = 4.5 + .058X and X is content of limonene, otherwise low.

Limonene: Considered to be high when its content was 8 or more percent and low when 6 or less.

Beta-phellandrene: Considered to be high when its content was 3 or more percent and low when 1 or less.

Classifying each tree as being high or low for each of the 4 monoterpenes results in 16 possible phenotypes. Alpha-pinene, a major constituent of the oleoresin not shown to be monogenically inherited, was studied based on its mean percentage content.

IV. Plantation vs Seed Origin Environmental Interactions

Four environmental-source (E-S) variables were obtained for each provenance at the Ames and Highland Rim plantations (Thorbjornsen, 1961). They are:

NFFD - the number of frost free days at the origin of the source.

MARF - the mean annual rainfall at the origin of the source.

MJNT - the mean January temperature at the origin of the source.

MJLT - the mean July temperature at the origin of the source.

Factor analysis was applied to the 4 E-S variables to determine which would be the best predictors of 4 mean growth characteristics (height, dbh, volume/ha and basal area/ha) of each provenance at both locations. The principal axis method of the FACTOR procedure and the VARIMAX axis rotation and PLOT options were specified in SAS·79 to compute the analysis. Multiple regression equations and correlations of the best predicting E-S variables and the 4 mean growth characteristics of each provenance were computed using GLM of SAS·79. Linear and multiple regression equations (significant at $P < 0.05$), were introduced into a Hewlett-Packard computer via a patented program, and plotted.

CHAPTER IV

RESULTS

I. Individual Location Analysis

Significant differences among provenances for the growth characteristics measured were limited to 4 planting locations: Stephen's Switch, Highland Rim, Counce and Ames Plantation. Analysis of the Norris and Friendship data revealed no significant difference ($P < 0.05$) among provenances for any characteristic. Means are presented in the Appendix, Tables A-1 and A-2 for these plantations. Tables 7-10 present means for growth characteristics evaluated in the 4 plantations showing significant differences. In Table 10 the volume from thinning in 1971 is included.

Mean squares, degrees of freedom, and levels of significance for individual location analyses for Stephen's Switch, Highland Rim, Counce and Ames Plantation are presented in Tables 11-14. Mean separations by Duncan's New Multiple Range test were employed for those characteristics calculated on a per hectare basis at Stephen's Switch, Highland Rim, and Ames and are presented in Tables 15-17. Analysis of unextracted and extracted specific gravity and extractives revealed no significant differences among sources ($P < 0.05$); means for each provenance and the ANOVA tables are presented in Tables 18 and 19.

Table 7. Average Performance for Seven Growth Characteristics at Ames Plantation.

Seed Source	Height (m)	dbh (cm)	Surv. (%)	m^3/ Tree	m^3/ ha	m^2/ ha	Tonnes/ ha
Chilesburg, VA	16.5	22.1	58	.32	334	41.3	151
Accomac, VA	16.3	20.1	76	.27	391	48.1	174
Johnston, SC	16.1	20.4	66	.27	355	44.9	153
Tishomingo, MS	15.9	20.5	71	.28	411	52.1	194
Crossett, AR	15.9	21.3	57	.28	307	39.5	135
Griffin, GA	15.8	20.4	61	.26	278	36.0	121
Cullman, AL	15.6	21.5	54	.29	293	38.1	135
Georgetown, SC	14.2	19.2	58	.21	220	31.2	100
Woodville, MS	14.0	19.6	39	.22	185	26.7	82
Deep South	13.7	19.7	53	.22	222	32.4	97

Table 8. Average Performance of Seven Growth Characteristics at the Highland Rim Plantation.

Seed Source	Height (m)	dbh (cm)	Surv. (%)	m^3/ Tree	m^3/ ha	m^2/ ha	Tonnes/ ha
Accomac, VA	17.9	21.5	86	.32	514	59.8	236
Johnston, SC	17.5	21.1	77	.30	453	54.0	204
Griffin, GA	17.1	21.2	62	.30	354	42.8	211
Cullman, AL	17.0	21.7	61	.31	371	45.4	162
Crossett, AR	16.5	20.5	74	.27	389	49.3	179
Deep South	16.3	20.4	47	.27	263	33.3	114

Table 9. Average Performance of Six Growth Characteristics at the Counce Plantation.

Seed Source	Height (m)	dbh (cm)	Surv. (%)	m^3/ Tree	m^3/ ha	m^2/ ha
South Carolina Coastal Plain	18.3	22.3	28	.36	399	45.0
North Carolina Coastal Plain	17.3	18.5	46	.24	439	51.9
Maryland Coastal Plain	17.1	16.7	42	.19	316	38.4
South Alabama	16.9	19.8	28	.26	295	35.8
Northwest Alabama	16.7	17.5	39	.20	318	39.1
Georgia Piedmont	16.7	17.4	43	.20	350	42.8
South Mississippi	16.7	18.4	34	.24	323	38.8
Northeast Mississippi	16.5	16.5	41	.17	289	36.5
Southeast Tennessee	16.4	18.7	39	.22	355	44.4

Table 10. Average Performance of Six Growth Characteristics and the Number of Trees Measured for Six Seed Sources at Stephen's Switch.

Seed Source	Height (m)	dbh (cm)	# of Trees	m^3/ Tree	m^3/ ha	m^2/ ha	m^3 Produced/ ha[a]
North Carolina Coastal Plain	21.4	21.5	61	.39	361	34.8	378
North Carolina Piedmont	21.1	21.2	62	.37	353	34.5	391
South Carolina Piedmont	20.7	21.4	54	.38	313	30.9	331
Georgia Piedmont	20.5	22.1	40	.40	246	24.5	251
Southeast Tennessee	20.5	19.4	85	.31	405	40.5	443
North Alabama	20.3	19.7	77	.32	373	37.4	394

[a]Includes volume from thinning in 1971.

Table 11. Degrees of Freedom, Mean Squares, and Levels of Significance at Ames Plantation.[a]

Source of Variation	df	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha	Tonnes/ ha
Replication	3	19.4 (1)	30.6 (0)	2.5 (0)	2338 (0)	21 (0)	660 (0)
Provenance	9	52.7** (14)	52.0* (3)	6.9* (5)	22621** (46)	250** (41)	4992** (42)
Replication x Provenance	27	11.1* (9)	20.4 (0)	2.5 (5)	5145 (54)	66 (59)	1291 (58)
Within Plot	553	4.0 (76)	20.3 (97)	1.7 (89)	-	-	-

*P < 0.05.

**P < 0.01.

[a]Numbers in parentheses indicate percent variation based on variance component estimates. Cubic meter/tree presented times 100.

Table 12. Degrees of Freedom, Mean Squares, and Levels of Significance at the Highland Rim Plantation.[a]

Source of Variation	df	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha	Tonnes/ ha
Replication	3	24.4 (0)	28.5 (2)	1.8 (0)	316 (0)	3 (0)	884 (0)
Provenance	5	24.4* (17)	14.3 (1)	3.2* (3)	29646** (74)	339** (73)	7406** (63)
Replication x Provenance	15	6.0** (18)	6.3 (0)	0.8 (1)	2392 (26)	28 (27)	949 (37)
Within Plot	383	1.1 (65)	13.6 (97)	1.2 (96)	-	-	-

*P < 0.05.

**P < 0.01.

[a]Numbers in parentheses indicate percent variation based on variance component estimates. Cubic meter/tree presented times 100.

Table 13. Degrees of Freedom, Mean Squares, and Levels of Significance at Counce.[a]

Source of Variation	df	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha
Replication	2	39.1** (11)	149.4** (6)	17.2** (9)	1611* (24)	14* (20)
Provenance	8	9.4 (4)	106.1** (12)	9.2** (12)	1103 (16)	13.1 (20)
Replication x Provenance	16	5.7* (11)	25.2* (5)	2.4** (7)	3998 (60)	40 (60)
Within Plot	339	2.0 (74)	14.1 (77)	1.1 (72)	-	-

*P < 0.05.

**P < 0.01.

[a]Numbers in parentheses indicate percent variation based on estimates of variance components. Cubic meter/tree presented times 100.

Table 14. Degrees of Freedom, Mean Squares, and Levels of Significance for Six Characteristics Evaluated at Stephen's Switch.[a]

Source of Variation	df	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha	m^2 Produced/ ha[b]
Replications	3	5.0 (0)	38.6 (0)	6.4 (1)	2217 (0)	16 (0)	1725 (0)
Provenance	5	9.8 (4)	67.2* (5)	9.0 (3)	12299* (40)	124** (46)	17527** (51)
Replication x Provenance	15	4.1* (6)	23.4 (2)	3.7 (4)	3364 (60)	28 (54)	3349 (49)
Within Plot	355	2.1 (90)	17.6 (93)	2.7 (92)	-	-	-

*P < 0.05.

**P < 0.01.

[a]Numbers in parentheses indicate percent variation based on variance component estimates. Cubic meter/tree presented times 100.

[b]Includes volume from thinning in 1971.

Table 15. Duncan's New Multiple Range Test of Volume Per Hectare, Basal Area Per Hectare, and Tonnes Per Hectare for Ten Provenances at Ames Plantation.

Seed Source	m^3/ha[a]	m^2/ha[a]
Tishomingo, MS	411	52.1
Accomac, VA	391	48.1
Johnston, SC	355	44.9
Chilesburg, VA	334	41.3
Crossett, AR	307	39.5
Cullman, AL	293	38.1
Griffin, GA	278	36.0
Deep South	222	32.4
Georgetown, SC	220	31.2
Woodville, MS	185	26.7

	Tonnes/ha[a]
Tishomingo, MS	194
Accomac, VA	174
Johnston, SC	153
Chilesburg, VA	151
Crossett, AR	135
Cullman, AL	135
Griffin, GA	121
Georgetown, SC	100
Deep South	97
Woodville, MS	82

[a]Means connected with the same line are not significantly different from each other ($P < 0.05$).

Table 16. Duncan's New Multiple Range Test of Volume Per Hectare, Basal Area Per Hectare, and Tonnes Per Hectare for Six Provenances at the Highland Rim Plantation.

Seed Source	m^3/ha[a]	m^2/ha[a]
Accomac, VA	514	59.8
Johnston, SC	453	54.0
Crossett, AR	389	49.3
Cullman, AL	371	45.4
Griffin, GA	354	42.8
Deep South	263	33.3

	Tonnes/ha[a]
Accomac, VA	236
Griffin, GA	211
Johnston, SC	204
Crossett, AR	179
Cullman, AL	162
Deep South	114

[a]Means connected with the same line are not significantly different from each other ($P < 0.05$).

Table 17. Duncan's New Multiple Range Test of Volume Per Hectare, Total Volume Produced Per Hectare and Basal Area Per Hectare for Six Provenances at Stephen's Switch.

Seed Sources	m^3/ha[a]	m^2/ha[a]
southeast Tennessee	405	40.5
north Alabama	373	37.4
North Carolina Coastal Plain	361	34.8
North Carolina Piedmont	353	34.5
South Carolina Coastal Plain	313	30.9
Georgia Piedmont	246	24.5

	m^3 Produced/ha[a,b]
southeast Tennessee	443
north Alabama	394
North Carolina Piedmont	391
North Carolina Coastal Plain	378
South Carolina Coastal Plain	331
Georgia Piedmont	251

[a]Means connected with the same line are not significantly different from each other ($P < 0.05$).

[b]Includes volume from thinning in 1971.

Table 18. Degrees of Freedom, Mean Squares, and Levels of Significance for Unextracted and Extracted Specific Gravity and Extractives at Ames and the Highland Rim.[a]

Source of Variation	Ames df	Ames Unextracted Specific Gravity	Ames Extracted Specific Gravity	Ames Extractives	Highland Rim df	Highland Rim Unextracted Specific Gravity	Highland Rim Extracted Specific Gravity	Highland Rim Extractives
Replication	3	20.79 (0)	20.26 (0)	.17 (0)	3	48.43 (0)	52.86 (2)	.11 (0)
Provenance	11	40.87 (2)	42.51 (2)	.25 (4)	7	58.48 (4)	48.40 (2)	.70 (9)
Replication x Provenance	33	35.57 (22)	36.44* (24)	.19 (9)	21	46.37** (45)	41.89** (43)	.39* (24)
Tree/Replication and Provenance	48	21.70** (59)	21.12** (56)	.15** (53)	32	14.35** (31)	13.73** (31)	.19** (23)
Within Tree	96	2.76 (17)	2.88 (18)	.04 (34)	64	3.39 (19)	3.63 (22)	.09 (44)

*P < 0.05.

**P < 0.01.

[a]Numbers in parentheses indicate percent variation based on variance component estimates. Mean squares presented times 10,000.

Table 19. Mean Values of Each Provenance for Unextracted Specific Gravity, Extracted Specific Gravity and Extractives at Ames and the Highland Rim.

Provenance	Ames			Highland Rim		
	Unextracted Specific Gravity	Extracted Specific Gravity	Extractives	Unextracted Specific Gravity	Extracted Specific Gravity	Extractives
Rusk, TX	.445	.427	.018	.457	.436	.021
Hornbeck, LA	.485	.471	.014	.471	.450	.021
Walker, LA	.434	.419	.015	.431	.412	.019
Woodville, MS	.456	.441	.016	-	-	-
Crossett, AR	.462	.445	.016	.487	.462	.025
Tishomingo, MS	.486	.470	.016	-	-	-
Cullman, AL	.474	.460	.014	.458	.436	.022
Griffin, GA	.447	.432	.014	.485	.463	.022
Georgetown, SC	.475	.460	.015	-	-	-
Johnston, SC	.459	.443	.016	.473	.450	.023
Accomac, VA	.457	.443	.014	.484	.460	.024
Chilesburg, VA	.463	.447	.016	-	-	-

Height Growth

Differences among provenances were significant at the 1% level at Ames (Table 11, page 45) and at the 5% level at the Highland Rim Plantation (Table 12, page 46). The tallest trees at Ames and the Highland Rim are from a Virginia Coastal Plain source and from the Virginia and South Carolina Piedmont regions. Trees of intermediate heights have origins from the upper-Coastal Plain regions of Arkansas, Mississippi, Alabama and Georgia. The slowest growing trees originated from the South Carolina and Deep South Coastal Plains.

Diameter

Analyses of variance indicate significant differences among sources at Ames, Counce and Stephen's Switch provenance tests. At Ames largest diameter growth was obtained by trees from the Virginia Piedmont, north-central Alabama and southeast Arkansas. Slower diameter growth was common among trees from Deep South Coastal Plain regions and the South Carolina Coastal Plain (Table 11). In the Counce plantation, trees from the South Carolina Coastal Plain were largest in diameter, while trees from northeast Mississippi and the Maryland Coastal Plain had the slowest diameter growth (Table 13, page 47). At Stephen's Switch trees from North and South Carolina Coastal Plain sources and those from the North Carolina Piedmont had the best diameter growth. Trees from north Alabama and southeast Tennessee had the slowest diameter growth (Table 17, page 51).

Survival

Results from the Ames, Highland Rim and Counce provenance tests indicate that trees from the Deep South Coastal Plain and South Carolina Coastal Plain have the poorest survival, while those from northeastern and inland localities have higher survival. At both Ames and the Highland Rim, a Virginia Coastal Plain source had the highest survival (Tables 7 and 8, pages 41 and 42, respectively). Trees from the North Carolina Coastal Plain had the highest survival at Counce (Table 9, page 43).

Volume Per Tree

Common to the Ames, Highland Rim and Counce plantations was a significant difference among provenances for volume of individual trees. At Ames and the Highland Rim, volume growth was best in trees originating from the Virginia Piedmont and Coastal Plain (Tables 11 and 12, pages 45 and 46, respectively). At Ames, trees from the north-central Alabama, northeast Mississippi, South Carolina Piedmont and southeast Arkansas rank high; the same sources including a northeast Georgia source are also among the largest at the Highland Rim. Trees from the Deep South and South Carolina Coastal Plain are consistently smaller. At Counce, trees from the South Carolina Coastal Plain grew largest in diameter, while those from northeast Mississippi grew the least in diameter (Table 13, page 47).

Volume Per Hectare and Basal Area Per Hectare

Significant differences among sources were found at the Ames, Highland Rim and Stephen's Switch provenance tests (Tables 15-17, pages 49, 50, and 51, respectively). At Ames, trees from northeast

Mississippi performed the best on a per hectare basis, followed by those from Virginia Coastal Plain and Piedmont, South Carolina Piedmont and southeast Arkansas. Similarly, at the Highland Rim loblolly pines from the Virginia Coastal Plain, and South Carolina Piedmont had greater volumes per hectare. Trees of intermediate production originate from north Georgia and north-central Alabama while the poorest producing trees are from the South Carolina Coastal Plain and the Deep South at both locations. Southeast Tennessee trees out produced all others at Stephen's Switch. Trees from north Alabama and those of North Carolina Coastal Plain and Piedmont origins were intermediate; trees from South Carolina Coastal Plain and Georgia Piedmont regions had the lowest yield per hectare.

Wood Properties

Analysis of variance disclosed no significant differences among sources for unextracted or extracted specific gravity or extractives (Table 18). A weak pattern seems to be evident, however, with high values found in trees from northeast Piedmont and Coastal Plain regions, and decreasing in trees from inland and southwest origins (Table 19, page 53; Appendix, Figure A-1). High values occurred in north Mississippi, southeast Arkansas and southwest Louisiana. No trend was evident regarding extractives.

Significant differences among sources were present for tonnes of wood produced per hectare at Ames and the Highland Rim (Tables 15 and 16, pages 49 and 50, respectively). At Ames, trees from the north Alabama source had the highest wood production per hectare while those of a southern Mississippi source had the lowest. In the

Highland Rim plantation Virginia Coastal Plain trees had the highest wood production, while those from the Deep South had the lowest. Trees of high wood production also originate from the Piedmont of South Carolina and Virginia, while intermediate producers occur from inland locations at both plantations.

II. Combined Location Analysis--Ames Plantation and Highland Rim

Six common seed sources were subject to combined analyses of 6 growth characteristics, and 8 seed sources common to both locations were used in analyses of 3 wood properties. Means are presented in Tables 20 and 21. Significant differences between locations were determined for height, tree volume, volume per hectare, basal area per hectare and tonnes of wood produced per hectare (Table 22). For each characteristic, trees at the Highland Rim were superior. Significant differences among seed sources were evident for those characteristics calculated on a per hectare basis. Trees from the Virginia Coastal Plain and South Carolina Piedmont are significantly different from all others in volume per hectare. Trees of these 2 sources also have the highest basal area and tonnes of wood per hectare (Table 23). Intermediate producers originate from southeast Arkansas, north-central Alabama and north Georgia, while poor yields are common among trees originating from the Deep South.

Trees at the Highland Rim produced significantly greater amounts of extractives, whereas a difference in specific gravity was not evident. No significant differences among seed sources were determined for the 3 wood properties (Table 24).

Table 20. Means of Seven Growth Characteristics Determined in the Combined Analysis of Six Provenances Common to Ames Plantation and the Highland Rim.

Seed Source	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha	Tonnes/ ha
Accomac, VA	17.1	21.8	.32	453	54.0	205
Johnston, SC	16.8	20.7	.29	404	49.5	178
Crossett, AR	16.2	20.9	.28	348	44.4	157
Griffin, GA	16.4	20.8	.28	316	39.4	166
Cullman, AL	16.3	21.6	.30	332	41.7	148
Deep South	15.0	20.0	.24	243	32.9	107

Table 21. Means of Unextracted Specific Gravity, Extracted Specific Gravity and Extractives Determined in the Combined Analysis of Six Provenances Common to Ames Plantation and the Highland Rim.

Seed Source	Unextracted Specific Gravity	Extracted Specific Gravity	Extractives
Accomac, VA	.471	.452	.019
Johnston, SC	.466	.446	.019
Crossett, AR	.474	.453	.021
Griffin, GA	.466	.448	.018
Cullman, AL	.466	.448	.018
Walker, LA	.432	.415	.017
Hornbeck, LA	.478	.460	.018
Rusk, TX	.451	.432	.019

Table 22. Degrees of Freedom, Mean Squares, and Levels of Significance for Combined Analysis of Two Locations for Six Characteristics Evaluated.[a]

Source of Variation	df	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha	Tonnes/ ha
Locations	1	374.8* (29)	27.4 (0)	11.5* (2)	82983** (29)	697** (38)	28141** (36)
Provenance	5	59.8 (0)	29.0 (0)	4.6 (0)	42258** (39)	446** (23)	8769* (26)
Replication/ Locations	6	7.5 (0)	21.2 (0)	1.6 (0)	2881 (0)	34 (0)	1225 (1)
Provenance x Locations	5	13.2 (0)	22.0 (1)	2.2 (1)	1460 (0)	28 (0)	1368 (3)
Provenance x Replication Within Location	30	9.4** (0)	12.8 (0)	1.6 (1)	3847 (32)	48 (39)	1038 (34)
Within Plot	726	2.5 (71)	16.7 (99)	1.5 (96)	-	-	-

*P < 0.05.

**P < 0.01.

[a]Numbers in parentheses indicate percent variation based on variance component estimates. Cubic meter/tree presented times 100.

Table 23. Duncan's New Multiple Range Test of Volume Per Hectare, Basal Area Per Hectare, and Tonnes Per Hectare for the Combined Analysis of Two Locations.

Seed Source	m^3/ha[a]	m^2/ha[a]
Accomac, VA	452	54.0
Johnston, SC	404	49.5
Crossett, AR	348	44.4
Cullman, AL	332	41.7
Griffin, GA	316	39.4
Deep South	243	32.9

	Tonnes/ha[a]
Accomac, VA	205
Johnston, SC	178
Griffin, GA	166
Crossett, AR	157
Cullman, AL	148
Deep South	106

[a]Means connected with the same line are not significantly different from each other ($P < 0.05$).

Table 24. Degrees of Freedom, Mean Squares, and Levels of Significance for Combined Analysis of Two Locations for Unextracted and Extracted Specific Gravity, and Extractives.[a]

Source of Variation	df	Unextracted Specific Gravity	Extracted Specific Gravity	Extractives
Locations	1	67.98 (1)	7.9 (0)	29.54** (58)
Provenance	7	70.22 (1)	65.28 (0)	0.54 (0)
Replications/ Locations	7	31.47 (0)	29.78 (3)	0.53 (0)
Provenance x Locations	6	45.38 (0)	48.59 (0)	0.11 (4)
Provenance x Replication within Location	42	38.85** (48)	36.85** (46)	0.30** (13)
Within Plot	192	8.06 (50)	7.97 (51)	0.10 (25)

*P < 0.05.

**P < 0.01.

[a]Numbers in parentheses indicate percent variation based on variance component estimates. Mean squares presented times 10,000.

Breeding Values

Since homogeneous variances had been determined for all means from which breeding values were to be calculated, the methodology of Box and Taio (1973) was used to estimate all breeding values (Appendix, Tables A-3 through A-6). Ranking the breeding values of each characteristic in descending order did not deviate from the rank originally assigned to means. The result is a "shrinkage" of the distribution of means by a common denominator (Fisher's F statistic) so comparisons of provenance yields may be made more accurately.

III. Oleoresin Analyses

Major monoterpenes found were the same as those reported by Squillace and Wells (1980): alpha-pinene, beta-pinene, myrcene, limonene and beta-phellandrene. Minor constituents were camphene, occurring up to 4%, and delta-3-carene found in trace amounts in 2 trees (Tables 25-27).

Frequency distributions (Appendix, Figures A-2 through A-8) for the five major constituents were similar to those reported by Squillace et al. (1980). Beta-pinene, myrcene, limonene and beta-phellandrene showed bimodality while the alpha-pinene data had normal distribution.

At Ames Plantation 9 of 16 possible phenotypes resulted from classifying each tree as being "high" or "low" for each of the 4 monoterpenes showing bimodality; 10 phenotypes were found at the Highland Rim (Tables 28 and 29). The most frequent phenotypes occurring at both plantations were BMLP, BMlP, BmLP, BmlP and bMlP.

Table 25. Mean Percentage Composition and Rank of Six Monoterpenes for Twelve Provenances at Ames Plantation.

Provenance	α-pinene		Camphene		β-pinene		Myrcene		Limonene		β-phellandrene	
	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank
Rusk, TX	15.8	11	2.8	1	12.6	11	6.3	12	27.5	1	34.9	3
Hornbeck, LA	21.0	9	1.8	4	20.0	4	10.6	10	18.5	3	27.9	5
Crossett, AR	12.6	12	1.1	7	11.5	12	12.5	9	23.1	2	38.9	2
Woodville, MS	18.5	10	1.5	5	14.6	10	15.8	7	13.3	4	36.3	1
Walker, LA	32.1	6	2.6	2	15.9	9	30.8	2	7.6	5	11.1	11
Tishomingo, MS	24.1	8	0.9	10	24.5	1	23.5	4	1.3	9	25.9	7
Cullman, AL	36.4	4	2.5	3	19.3	5	19.4	5	6.6	6	16.0	10
Griffin, GA	33.4	5	1.0	8	24.4	2	13.8	8	0.4	11	26.8	6
Johnston, SC	30.6	7	0.0	12	18.5	7	32.4	1	2.4	7	16.1	9
Georgetown, SC	43.6	2	1.0	8	17.8	8	18.9	6	2.4	7	16.5	8
Chilesburg, VA	44.1	1	0.5	11	21.8	3	24.6	3	0.3	12	8.8	12
Accomac, VA	41.8	3	1.3	6	18.6	6	9.8	11	0.6	10	28.0	4

Table 26. Mean Percentage Composition and Rank of Six Monoterpenes for Eight Provenances at the Highland Rim.

Provenance	α-pinene		Camphene		β-pinene		Myrcene		Limonene		β-phellandrene	
	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank
Rusk, TX	15.9	6	2.4	5	33.8	2	5.0	8	18.1	2	26.4	2
Hornbeck, LA	11.8	8	4.1	3	35.5	1	13.1	5	11.6	4	23.6	4
Crossett, AR	14.5	7	0.5	8	13.8	8	15.3	4	18.6	1	37.6	1
Walker, LA	26.1	3	4.9	1	28.8	4	11.6	6	13.1	3	16.3	8
Cullman, AL	21.0	4	4.9	1	18.1	6	31.4	1	3.8	6	16.9	7
Griffin, GA	40.4	1	2.0	6	25.9	5	9.6	7	6.7	5	18.4	6
Johnston, SC	20.3	5	2.6	4	32.6	3	21.4	3	3.3	7	20.0	5
Accomac, VA	30.5	2	1.9	7	17.3	7	25.4	2	0.4	8	24.6	3

Table 27. Mean Percentage Composition and Rank of Six Monoterpenes for Eight Provenances Common to Ames Plantation and the Highland Rim.

Provenance	α-pinene		Camphene		β-pinene		Myrcene		Limonene		β-phellandrene	
	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank
Rusk, TX	15.9	7	2.6	4	23.2	4	5.7	8	22.8	1	30.7	2
Hornbeck, LA	16.4	6	3.0	3	27.8	1	11.9	6	15.1	3	25.8	4
Crossett, AR	13.6	8	0.8	8	12.7	8	13.9	5	20.9	2	38.3	1
Walker, LA	29.1	3	3.8	1	22.4	5	21.2	3	10.4	4	13.7	8
Cullman, AL	28.7	4	3.7	2	18.7	6	25.4	2	5.2	5	16.5	7
Griffin, GA	36.9	1	1.5	6	25.2	3	11.7	7	3.6	6	22.6	5
Johnston, SC	25.5	5	1.3	7	25.6	2	26.9	1	2.9	7	18.1	6
Accomac, VA	36.2	2	1.6	5	18.0	7	17.6	4	0.5	8	26.3	3

Table 28. Sums and Average Content of Major Monoterpenes in Branch Cortical Oleoresin of Sixteen Loblolly Pine Phenotypes Representing Twelve Provenances Sampled at Ames Plantation.

Phenotype[a]	Trees (Number)	Composition[b] α-pinene Σ	α-pinene X̄%	β-pinene Σ	β-pinene X̄%	Myrcene Σ	Myrcene X̄%	Limonene Σ	Limonene X̄%	β-phellandrene Σ	β-phellandrene X̄%
BMLP	6	127	21.2	88	14.7	122	20.3	99	16.5	149	24.8
BMLp	-	-	-	-	-	-	-	-	-	-	-
BMlP	40	1155	28.9	835	20.9	1188	29.7	24	.6	782	19.6
BMlp	4	219	54.8	75	18.8	94	23.5	0	0	0	0
BmLP	24	454	18.9	398	16.6	88	3.7	661	27.5	747	31.1
BmLp	-	-	-	-	-	-	-	-	-	-	-
BmlP	12	426	35.5	298	24.8	38	3.2	14	1.2	390	32.5
Bmlp	1	47	47.0	48	48.0	0	0	0	0	0	0
bMLP	-	-	-	-	-	-	-	-	-	-	-
bMLp	-	-	-	-	-	-	-	-	-	-	-
bMlP	5	161	32.2	8	1.6	203	40.6	1	.2	121	24.2
bMlp	-	-	-	-	-	-	-	-	-	-	-
bmLP	1	16	16.0	1	1.0	4	4.0	32	32.0	46	46.0
bmLp	-	-	-	-	-	-	-	-	-	-	-
bmlP	3	228	76.0	4	1.3	8	2.7	0	0	61	20.3
bmlp	-	-	-	-	-	-	-	-	-	-	-
Total	96										

[a]B, M, L and P represent high amounts of β-pinene, myrcene, limonene, and β-phellandrene, respectively, while lower case letters represent low amounts.

[b]Small amounts of camphene were also found in most trees and trace amounts of delta-3-carene in 2 trees.

Table 29. Sums and Average Content of Major Monoterpenes in Branch Cortical Oleoresin of Sixteen Loblolly Pine Phenotypes Representing Eight Provenances Sampled at the Highland Rim.

Phenotype[a]	Trees (Number)	Composition[b] α-pinene Σ	α-pinene X̄%	β-pinene Σ	β-pinene X̄%	Myrcene Σ	Myrcene X̄%	Limonene Σ	Limonene X̄%	β-phellandrene Σ	β-phellandrene X̄%
BMLP	8	101	12.6	179	22.4	140	17.5	173	21.6	180	22.5
BMLp	-	-	-	-	-	-	-	-	-	-	-
BMlP	29	694	23.9	659	22.7	781	26.9	39	1.3	662	22.8
BMlp	-	-	-	-	-	-	-	-	-	-	-
BmLP	14	264	18.9	339	24.2	43	3.1	321	22.9	406	29.0
BmLp	2	40	20.0	110	55.0	0	0	50	25.0	0	0
BmlP	2	50	25.0	31	15.5	4	1.3	3	1.5	70	35.0
Bmlp	4	118	29.5	271	67.8	3	.8	4	1.0	0	0
bMLP	1	10	10.0	0	0	28	28.0	14	14.0	49	49.0
bMLp	-	-	-	-	-	-	-	-	-	-	-
bMlP	2	49	24.5	3	1.5	59	29.5	1	1.5	86	43.0
bMlp	1	45	45.0	18	18.0	33	33.0	0	0	0	0
bmLP	-	-	-	-	-	-	-	-	-	-	-
bmLp	-	-	-	-	-	-	-	-	-	-	-
bmlP	1	72	72.0	2	2.0	0	0	0	0	17	17.0
bmlp	-	-	-	-	-	-	-	-	-	-	-
Total	64										

[a]B, M, L and P represent high amounts of β-pinene, myrcene, limonene, and β-phellandrene, respectively, while lower case letters represent low amounts.

[b]Small amounts of camphene were also found in most trees. Trace amounts of delta-3-carene were not found in this plantation.

Ninety-one percent of the trees at Ames and 86% of the trees at the Highland Rim fell into these 5 classes. Combining the data from the 2 plantations reveals 12 of 16 possible phenotypes, with BMlP occurring nearly twice as often as BmLP (Table 30). Eighty-nine percent of the trees are found in the 5 most frequent phenotypes. Four trees which lack genes coding for high amounts of beta-pinene, myrcene and limonene average 75% alpha-pinene. Trees having the phenotypes mL and Ml occur much more frequently than expected from random pairing of these alleles, while ML and ml types have considerably lower frequencies. It is believed that the two genes are closely linked (Squillace and Wells, 1980).

Using combined data, little variation among seed sources was evident for beta-pinene (Table 31, Figure 2). Percentages of high amounts varied from 76% to 100%. Percentages of trees having high myrcene varied from 25% to 75%, with high amounts occurring more frequently in trees from eastern origins (Table 31, Figure 3). The percentage of trees having high limonene increased from east to west (Table 31, Figure 4). Loblolly pines from South Carolina and Virginia had 0% to 13% high amounts and those from southwest Mississippi, Arkansas, Louisiana and Texas had 44% to 88% high amounts of limonene. Trees from inland areas had high amounts ranging from 13% to 31%. The percentage of trees having high beta-phellandrene varied from 81% to 100% (Table 31, Figure 5). It appears that more trees from the western portion of the species range had high beta-phellandrene than those from the east.

Average content of alpha-pinene was lowest (13% to 19%) in trees of western origins, intermediate in trees from inland

Table 30. Sums and Average Content of Major Monoterpenes in Branch Cortical Oleoresin of Sixteen Loblolly Pine Phenotypes Representing Combined Data from Ames and the Highland Rim.

Phenotype[a]	Trees (Number)	Composition[b] α-pinene Σ	α-pinene X%	β-pinene Σ	β-pinene X%	Myrcene Σ	Myrcene X%	Limonene Σ	Limonene X%	β-phellandrene Σ	β-phellandrene X%
BMLP	14	228	16.3	267	19.1	262	18.7	272	19.4	329	23.5
BMLp	-	-	-	-	-	-	-	-	-	-	-
BMlP	69	1849	26.8	1494	21.7	1969	28.5	63	.9	1444	20.9
BMlp	4	219	54.8	75	18.8	94	23.5	0	0	0	0
BmLP	38	718	18.9	737	19.4	131	3.4	982	25.8	1153	30.3
BmLp	2	40	20.0	110	55.0	0	0	50	25.0	0	0
BmlP	14	476	34.0	329	23.5	42	3.0	17	1.2	460	32.9
Bmlp	5	165	33.0	319	63.8	3	.6	4	.8	0	0
bMLP	1	10	10.0	0	0	28	28.0	14	14.0	49	49.0
bMLp	-	-	-	-	-	-	-	-	-	-	-
bMlP	7	210	30.0	11	1.6	262	37.4	2	.3	207	29.6
bMlp	1	45	45.0	18	18.0	33	33.0	0	0	0	0
bmLP	1	16	16.0	1	1.0	4	4.0	32	32.0	46	46.0
bmLp	-	-	-	-	-	-	-	-	-	-	-
bmlP	4	300	75.0	6	1.5	8	2.0	0	0	78	19.5
bmlp	-	-	-	-	-	-	-	-	-	-	-
Total	160										

[a]B, M, L and P represent high amounts of β-pinene, myrcene, limonene, and β-phellandrene, respectively, while lower case letters represent low amounts.

Table 31. Percent High and Low Content of Four Simply Inherited Monoterpenes for Twelve Provenances at Ames and the Highland Rim.

Provenance	Percent							
	β-pinene		Myrcene		Limonene		β-phellandrene	
	Low	High	Low	High	Low	High	Low	High
Rusk, TX	0	100	75	25	12	88	6	94
Hornbeck, LA	6	94	56	44	37	63	6	94
Crossett, AR	12	88	56	44	18	82	0	100
Woodville, MS	12	88	24	76	50	50	0	100
Walker, LA	6	94	38	62	56	44	12	88
Tishomingo, MS	0	100	24	76	86	12	0	100
Cullman, AL	12	88	25	75	81	19	6	94
Griffin, GA	18	82	37	63	94	6	19	81
Johnston, SC	0	100	18	82	88	12	12	88
Georgetown, SC	12	88	50	50	87	13	12	88
Chilesburg, VA	24	76	24	76	100	0	12	88
Accomac, VA	12	88	31	69	100	0	6	94

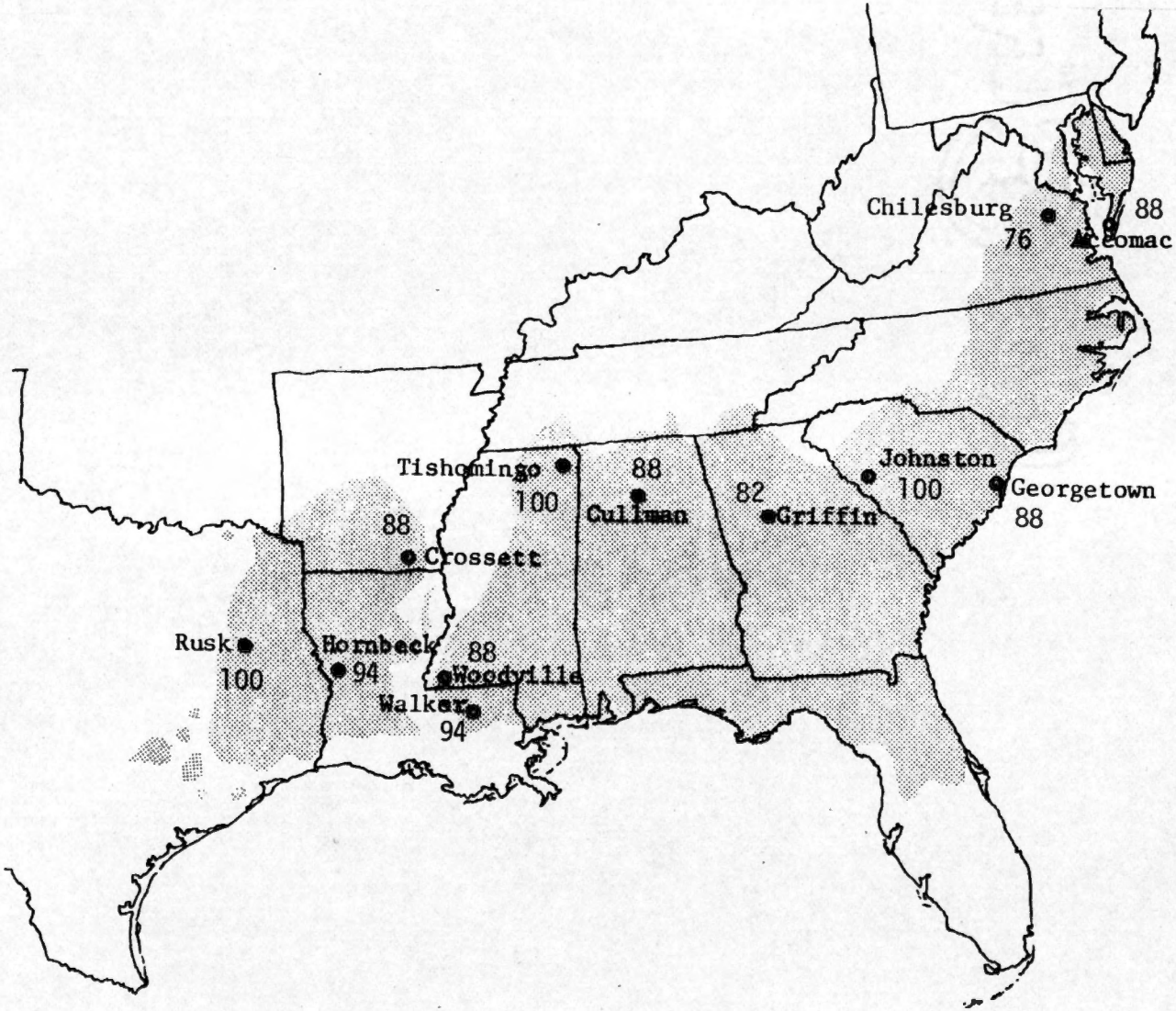


Figure 2. The Origin and the Percentage of Trees Having High Beta-pinene at Ames and the Highland Rim.

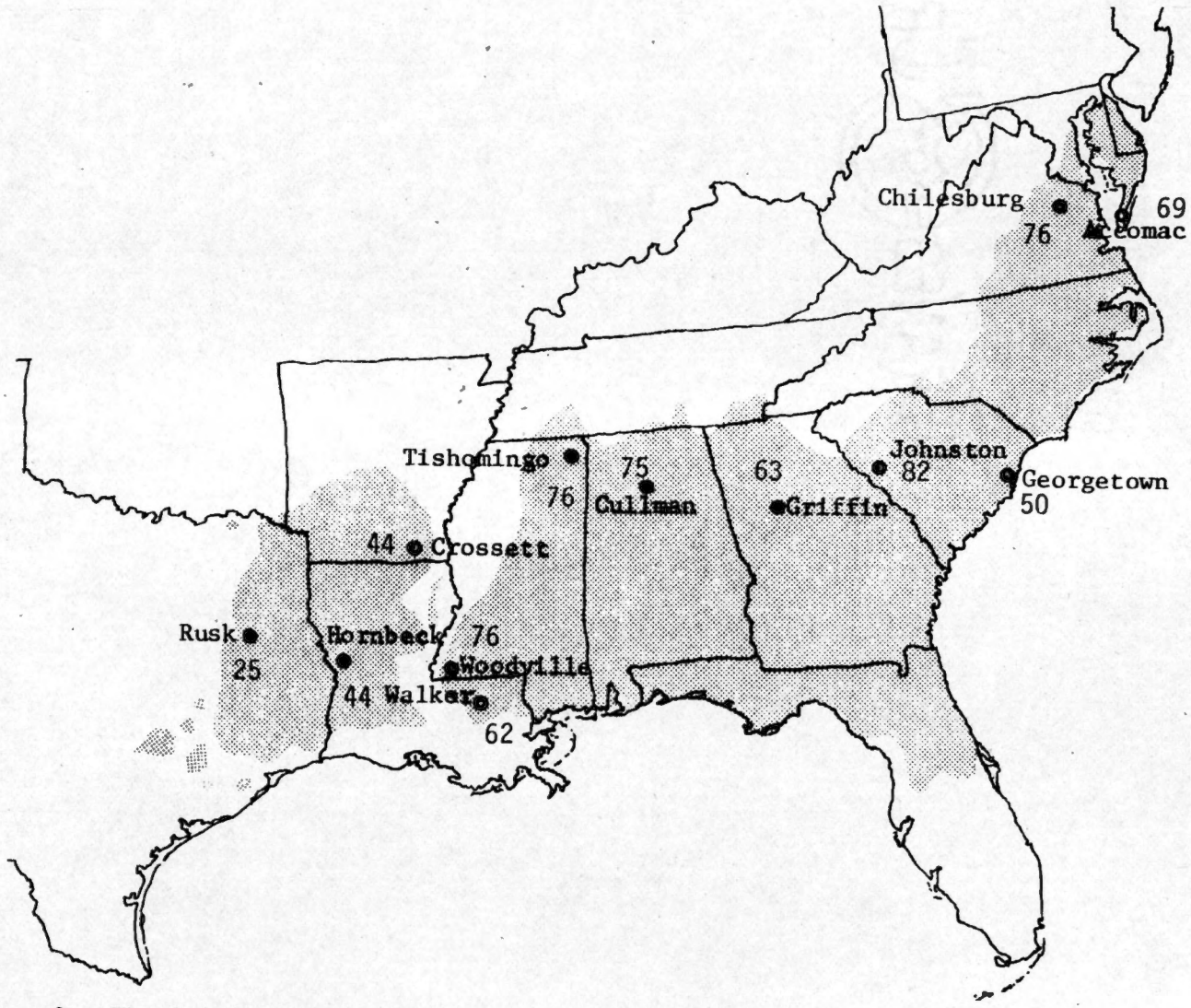


Figure 3. The Origin and the Percentage of Trees Having High Myrcene at Ames and the Highland Rim.

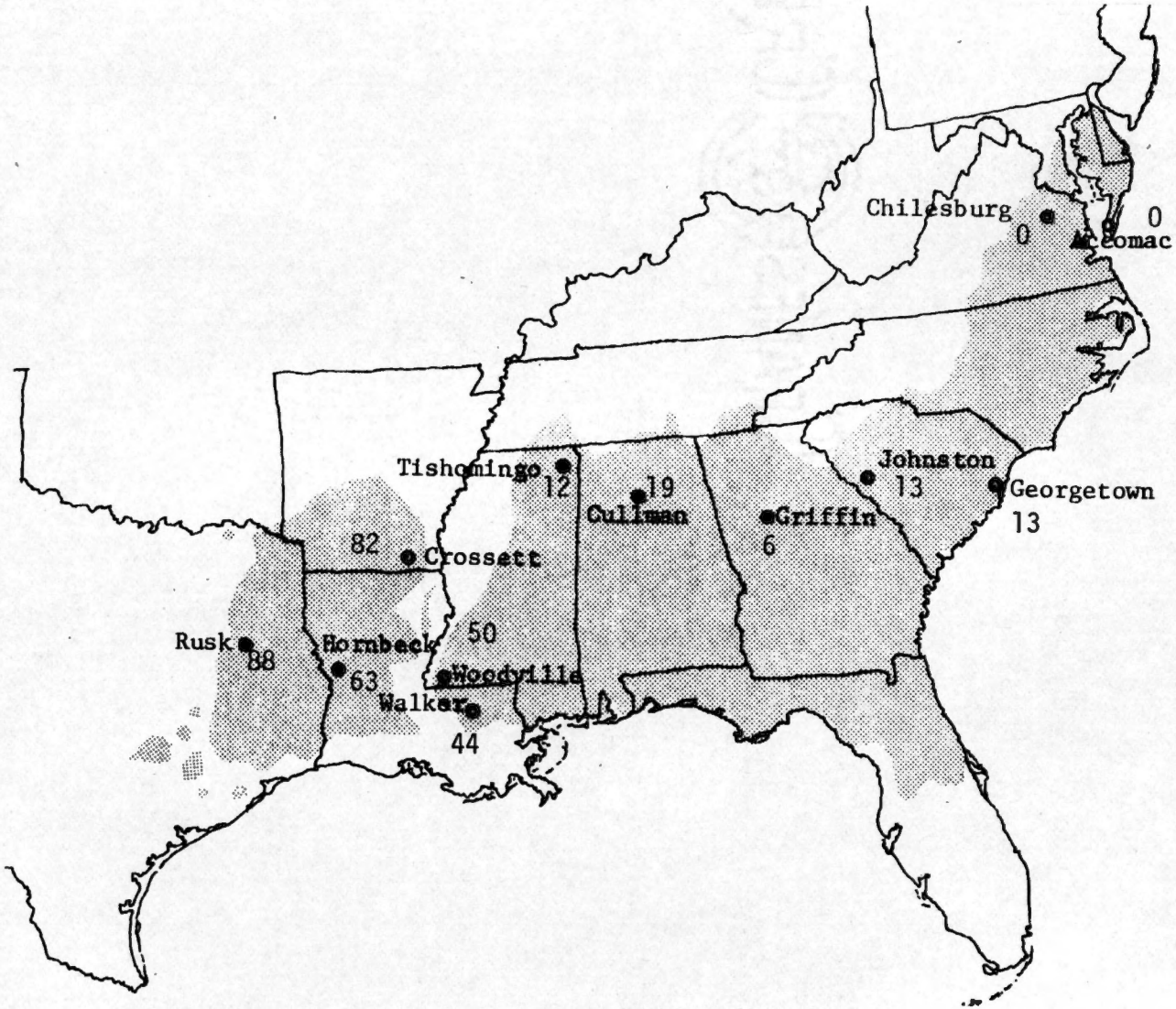


Figure 4. The Origin and the Percentage of Trees Having High Limonene at Ames and the Highland Rim.

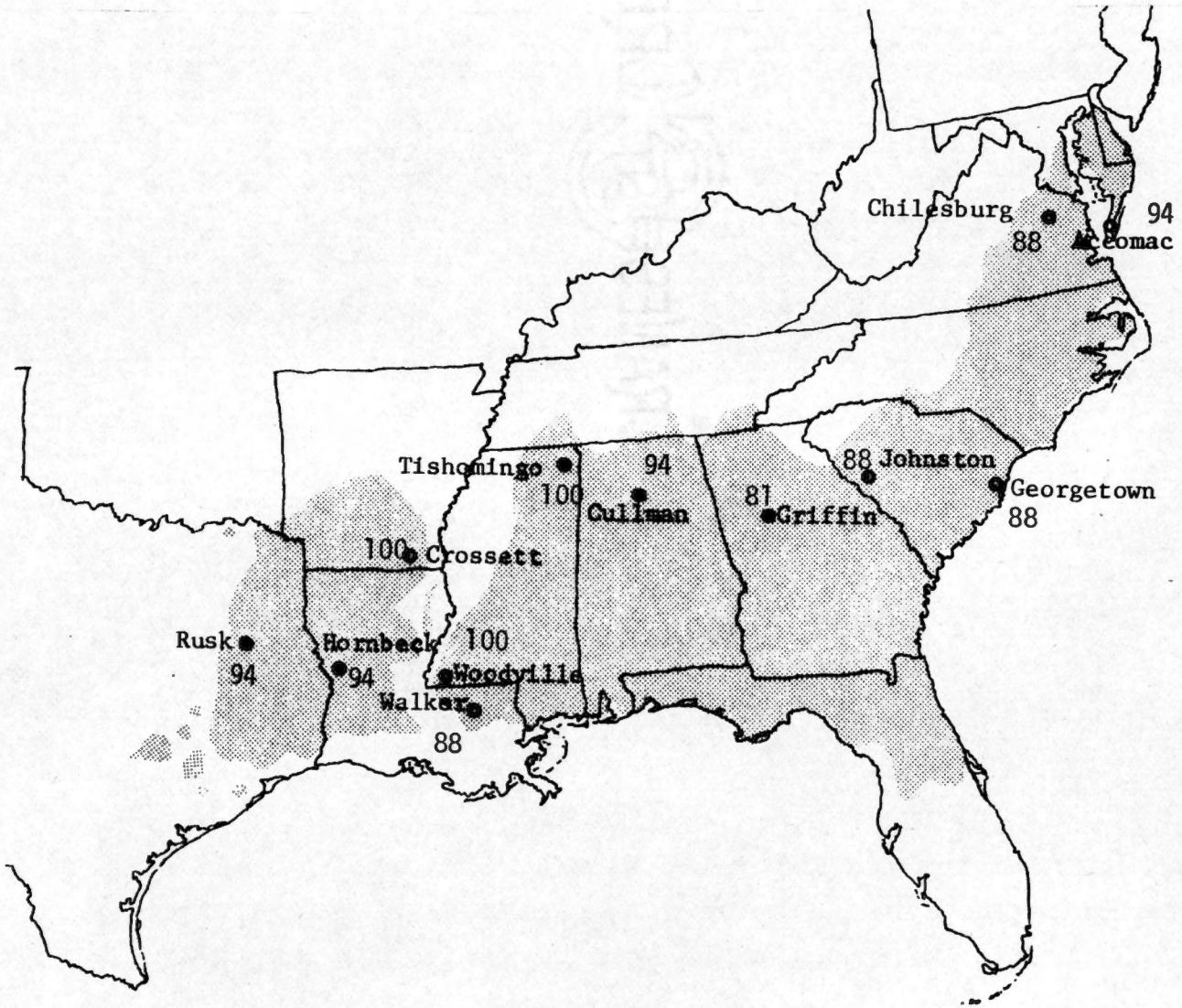


Figure 5. The Origin and the Percentage of Trees Having High Beta-phellandrene at Ames and the Highland Rim.

locations (19% to 37%) and highest (36% to 44%) in Atlantic Coastal Plain trees (Table 32, Figure 6).

The average percent of phenotypes occurring in each provenance at Ames and the Highland Rim plantations, and the combined data are presented in the Appendix, Tables A-7 through A-9.

IV. Environmental Interactions

Five regressions with a single independent environmental variable were significant at Ames (Table 33, Figures 7-11). No significant linear equations were found at the Highland Rim. All 5 regression equations express the same relationship; yield decreases as the climate at the provenance origin, expressed as mean January temperature (MJNT) and number of frost free days (NFFD), increases. Sources from South Carolina Coastal Plain and Mississippi Coastal Plain represent areas of the longest growing seasons (272 and 245 frost free days, respectively) among all provenances tested, and their yields are consistently the lowest (Table 34). In general, trees whose environmental origins typify the environment at Ames yield the most wood.

At both locations, factor analysis revealed that the number of frost free days (NFFD) and mean annual rainfall (MARF) at the origin of each provenance are the most useful environmental variables in multiple regression equations to predict the variation in yields (Tables 35 and 36). One significant equation was evident at each location using height growth of trees at Ames Plantation and diameter growth of trees at the Highland Rim (Table 33). Figures 12 and 13 show the response of height and diameter to an increase in NFFD and

Table 32. Average Percentage Content of Alpha-pinene for Twelve Provenances at Ames and the Highland Rim.

Provenance	α-pinene (%)
Chilesburg, VA	44.1
Georgetown, SC	43.6
Griffin, GA	36.9
Accomac, VA	36.2
Walker, LA	29.1
Cullman, AL	28.7
Johnston, SC	25.5
Tishomingo, MS	24.1
Woodville, MS	18.5
Hornbeck, LA	16.4
Rusk, TX	15.9
Crossett, AR	13.6

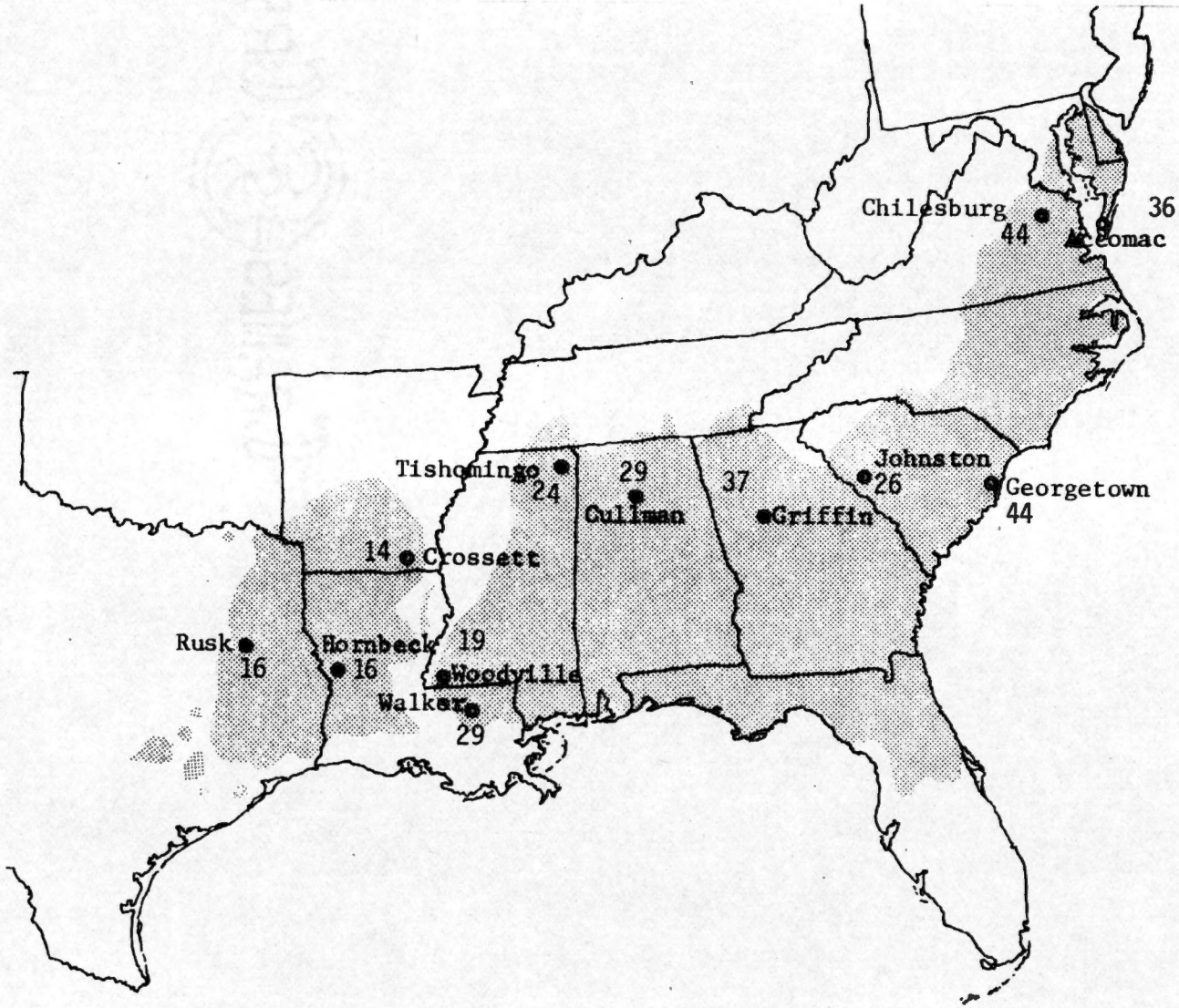


Figure 6. The Origin and Mean Percentage Alpha-pinene Content in Trees at Ames and the Highland Rim.

Table 33. Significant Linear and Multiple Regression Equations of Yield and Environmental-Source Variables at Ames and the Highland Rim.

Equation		Location	R^2
		Ames Plantation	
dbh	=	28.1596 - 0.0330 NFFD[a]	.71
height	=	21.3170 - 0.0249 NFFD	.44
height	=	22.2163 - 0.1476 MJNT[a]	.62
BA/ha	=	92.1476 - 1.1655 MJNT	.54
Vol/ha	=	838.4230 - 11.7027 MJNT	.48
height	=	25.8601 - 0.0253 NFFD - 0.0913 MARF[a]	.75
		Highland Rim	
dbh	=	-38.6551 + 0.3067 NFFD + 1.4115 MARF - 0.0072 NFFD * MARF	1.00

[a]These variables are defined on page 39.

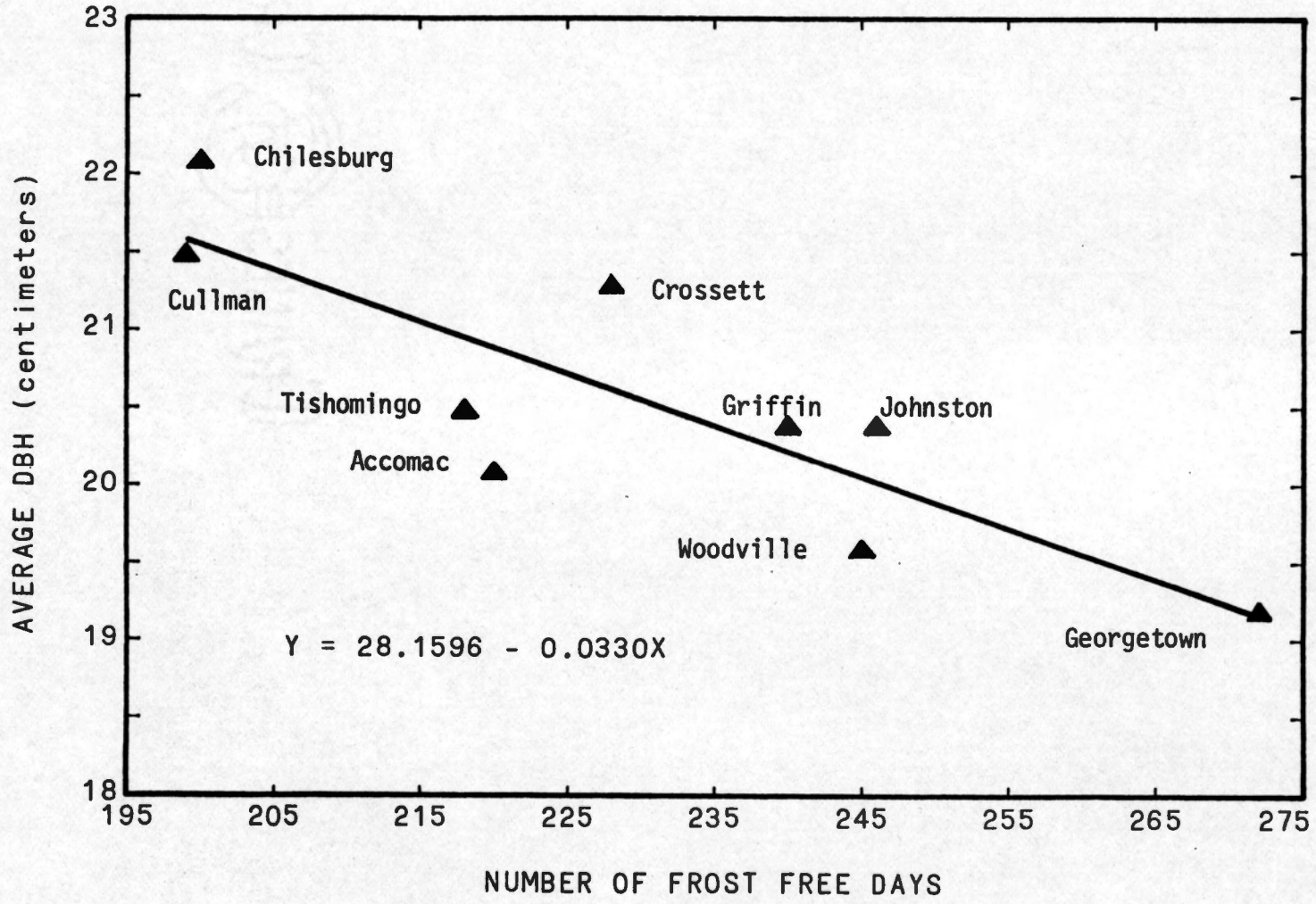


Figure 7. Average dbh Growth at Ames Plotted Against Number of Frost Free Days of the Provenance.

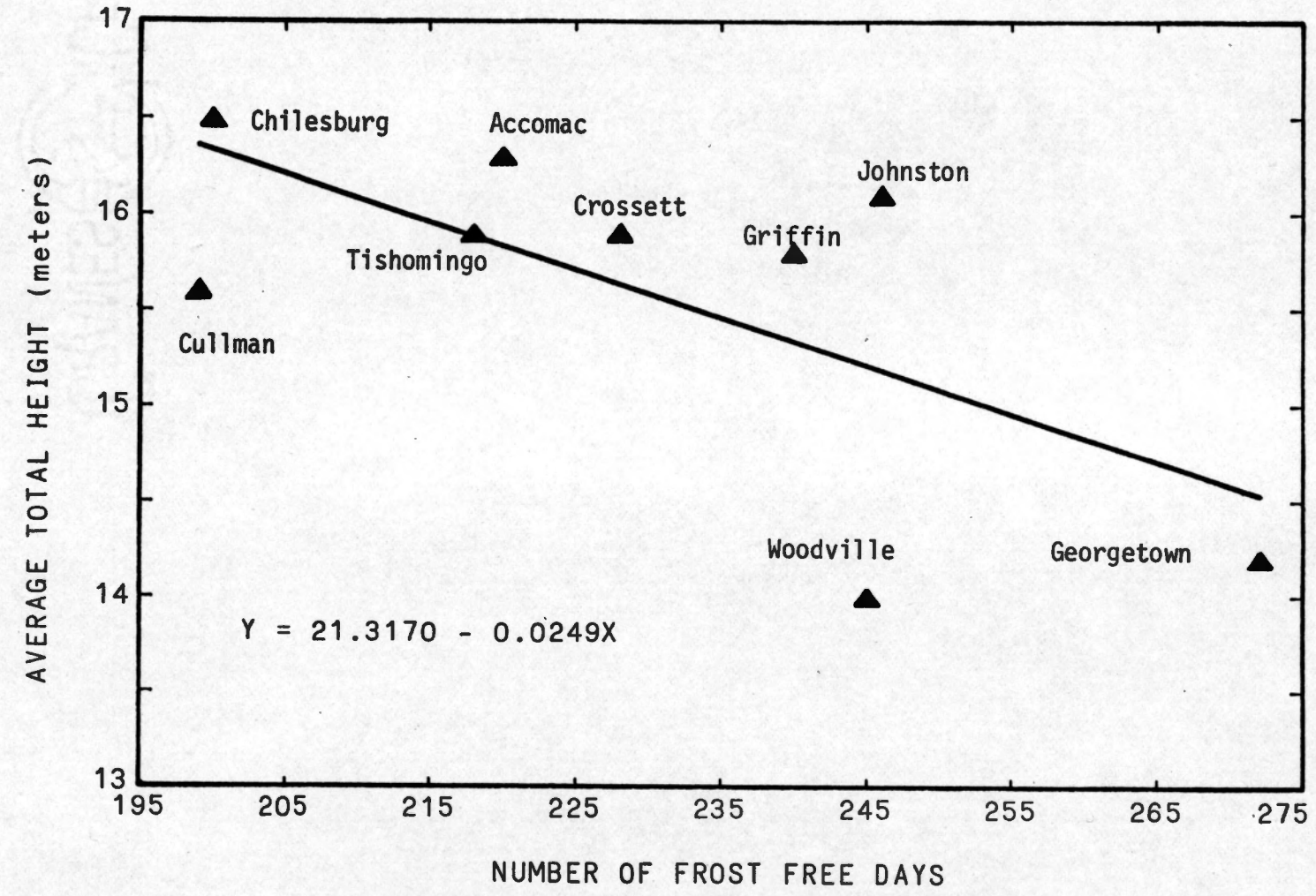


Figure 8. Average Total Height Growth at Ames Plotted Against Number of Frost Free Days of the Provenance.

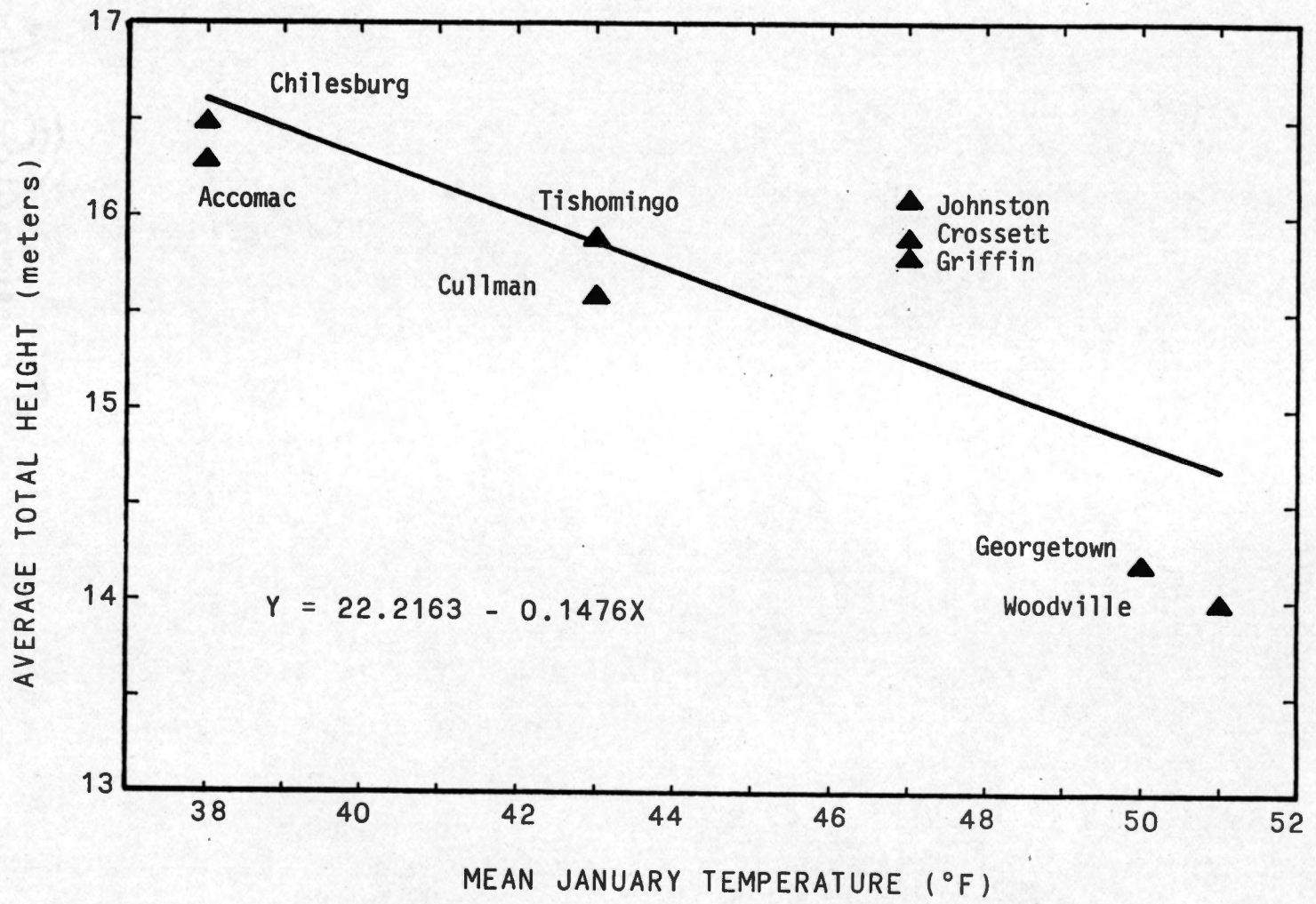


Figure 9. Average Total Height at Ames Plotted Against Mean January Temperature of the Provenance.

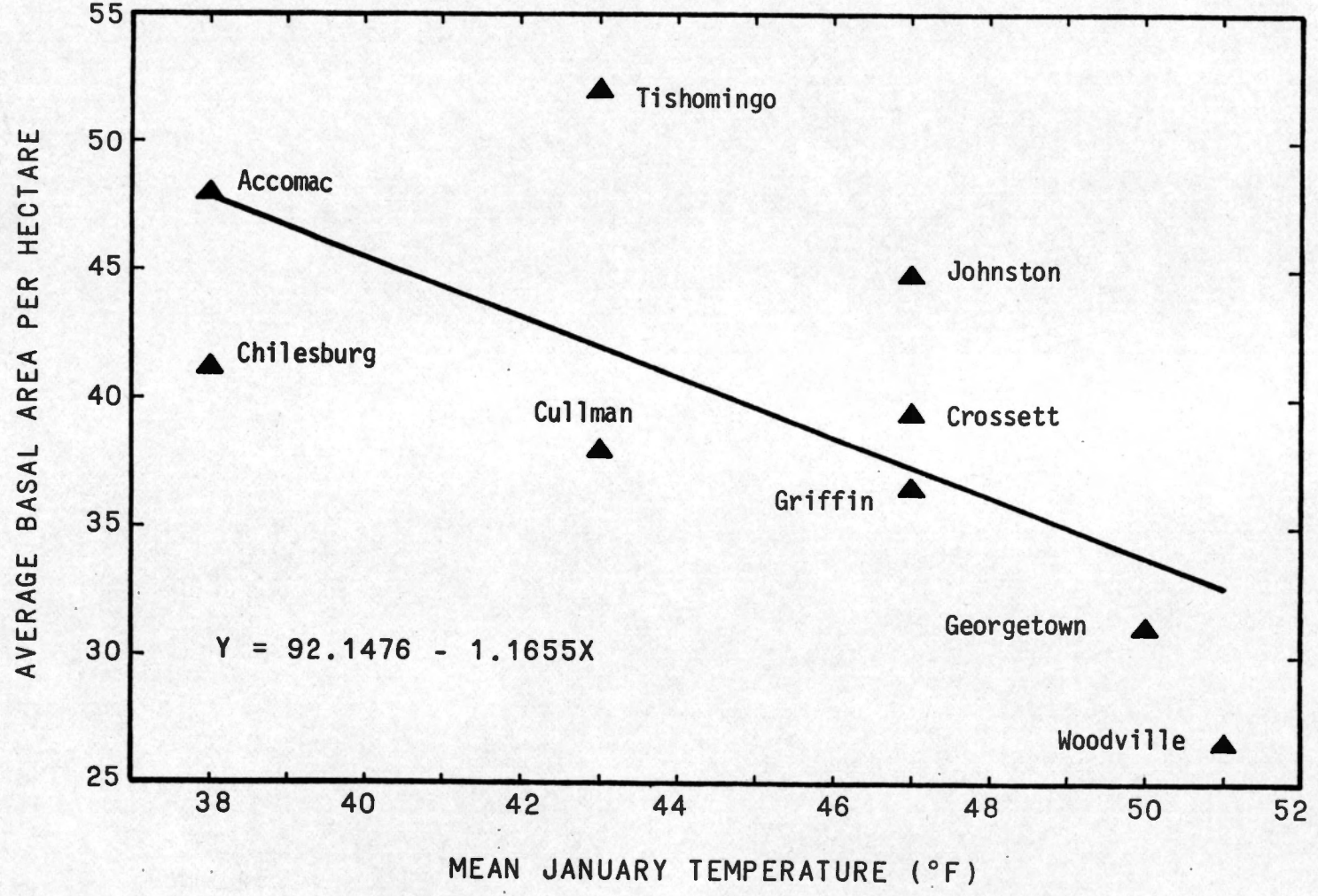


Figure 10. Average Basal Area/ha at Ames Plotted Against Mean January Temperature of the Provenance.

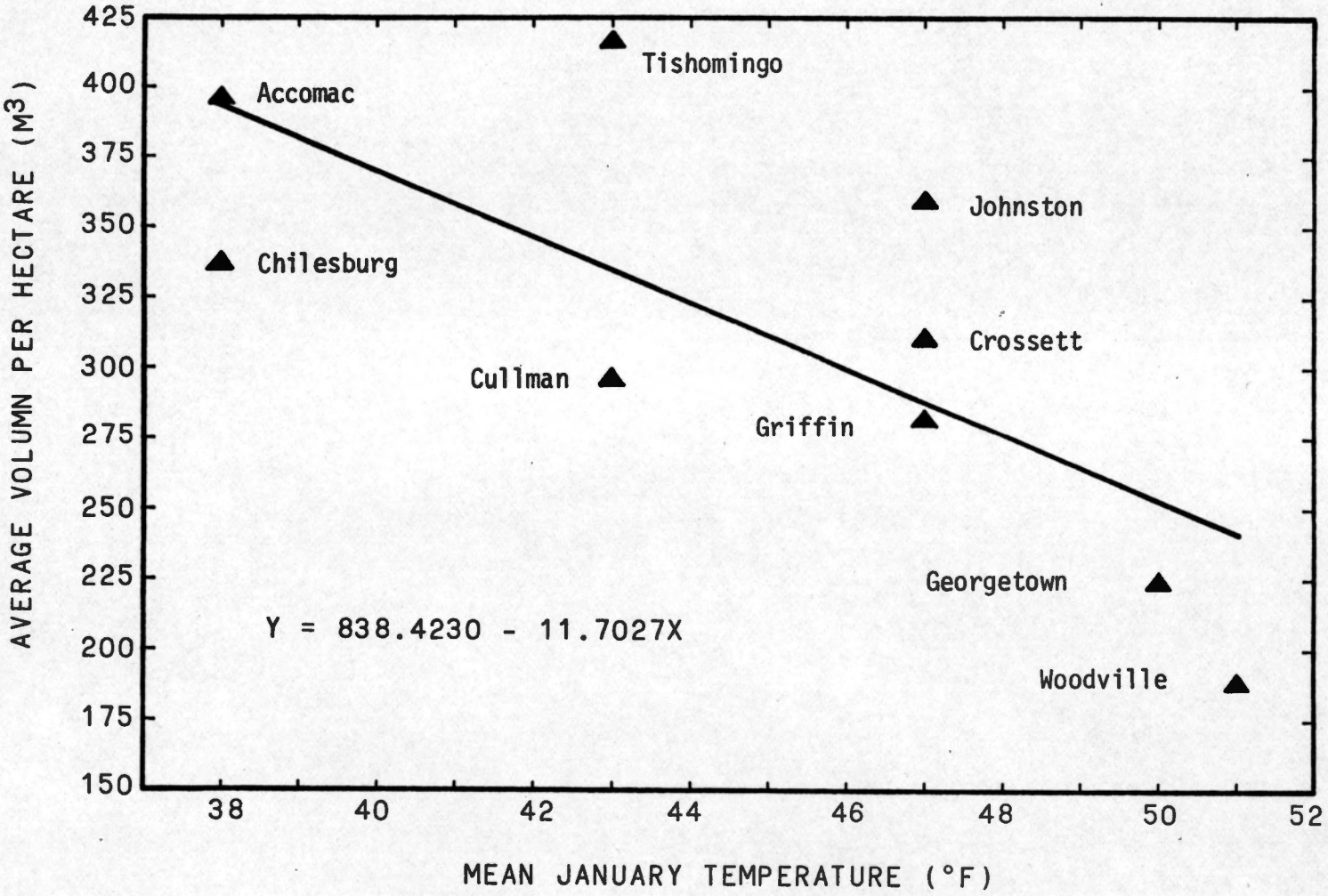


Figure 11. Average Volume/ha at Ames Plotted Against Mean January Temperature of the Provenance.

Table 34. Means of Four Yield Variables for Each Provenance and Their Associated Environmental Variables at Ames and the Highland Rim.

Location/ Provenance	Height (m)	dbh (cm)	m^3/ ha	m^2/ ha	NFFD	MARF[a] (In.)	MJNT[a] °F	MJLT[a] °F
Ames Plantation					200	52	41	79
Crossett, AR	15.9	21.3	307	39.5	228	49	47	82
Woodville, MS	14.0	19.6	185	26.7	245	56	51	82
Tishomingo, MS	15.9	20.5	411	52.1	218	55	43	80
Cullman, AL	15.6	21.5	293	38.1	199	55	43	79
Griffin, GA	15.8	20.4	278	36.0	240	45	47	81
Georgetown, SC	14.2	19.2	220	31.2	272	48	50	80
Johnston, SC	16.1	20.4	355	44.9	246	45	47	81
Accomac, VA	16.3	20.1	391	48.1	220	45	38	78
Chilesburg, VA	16.5	22.1	334	41.3	200	41	38	77
Highland Rim					196	55	40	77
Crossett, AR	16.5	20.5	389	49.3	228	49	47	82
Cullman, AL	17.0	21.7	371	45.4	199	55	43	79
Griffin, GA	17.1	21.2	354	42.8	240	45	47	81
Johnston, SC	17.5	21.1	453	54.0	246	45	47	81
Accomac, VA	17.9	21.5	514	59.8	220	45	38	78

[a]These variables are defined on page 39.

Table 35. Factor Analysis of Four Environmental-Source Variables for Ames Plantation.

	NFFD[a]	MARF[a]	MJNT[a]	MJLT[a]
Eigenvalues	2.653	1.027	0.263	0.057
Portion	0.663	0.257	0.066	0.014
Cumulative Portion	0.663	0.920	0.986	1.000

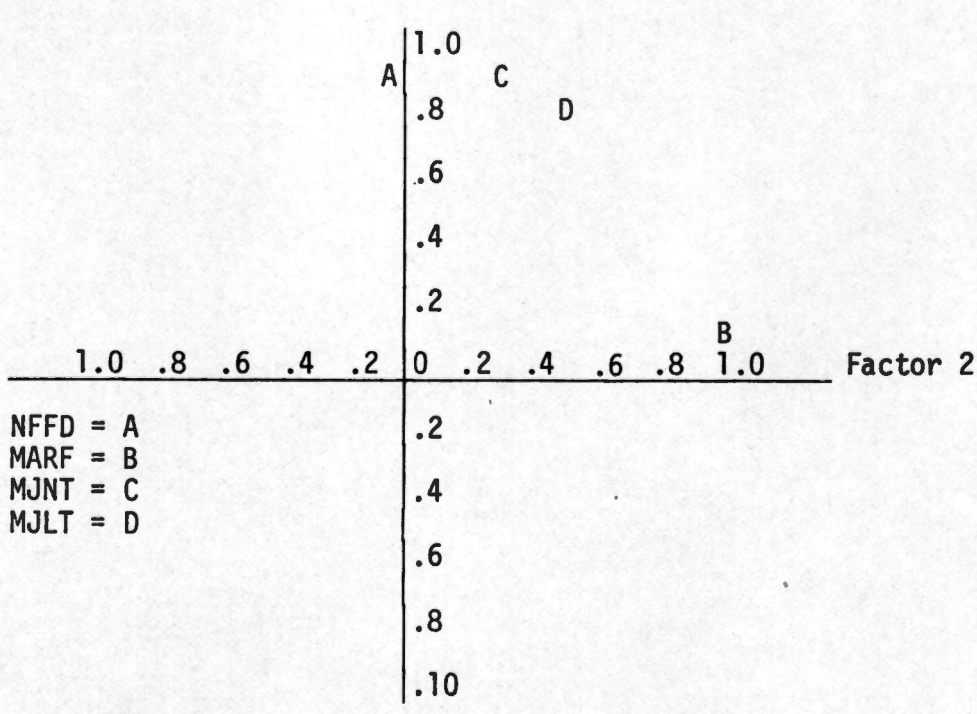
Factor Pattern

	#1	#2
NFFD	0.797	-0.525
MARF	0.463	0.860
MJNT	0.980	-0.064
MJLT	0.919	0.090

Rotated Factor Pattern

	#1	#2
NFFD	0.937	-0.178
MARF	0.096	0.972
MJNT	0.929	0.318
MJLT	0.814	0.437

Plot of Factor 1 with Factor 2



[a]These variables are defined on page 39.

Table 36. Factor Analysis of Four Environmental-Source Variables for the Highland Rim Plantation.

	NFFD[a]	MARF[a]	MJNT[a]	MJLT[a]
Eigenvalues	2.659	1.272	0.063	0.006
Portion	0.665	0.318	0.016	0.002
Cumulative Portion	0.665	0.983	0.998	1.000

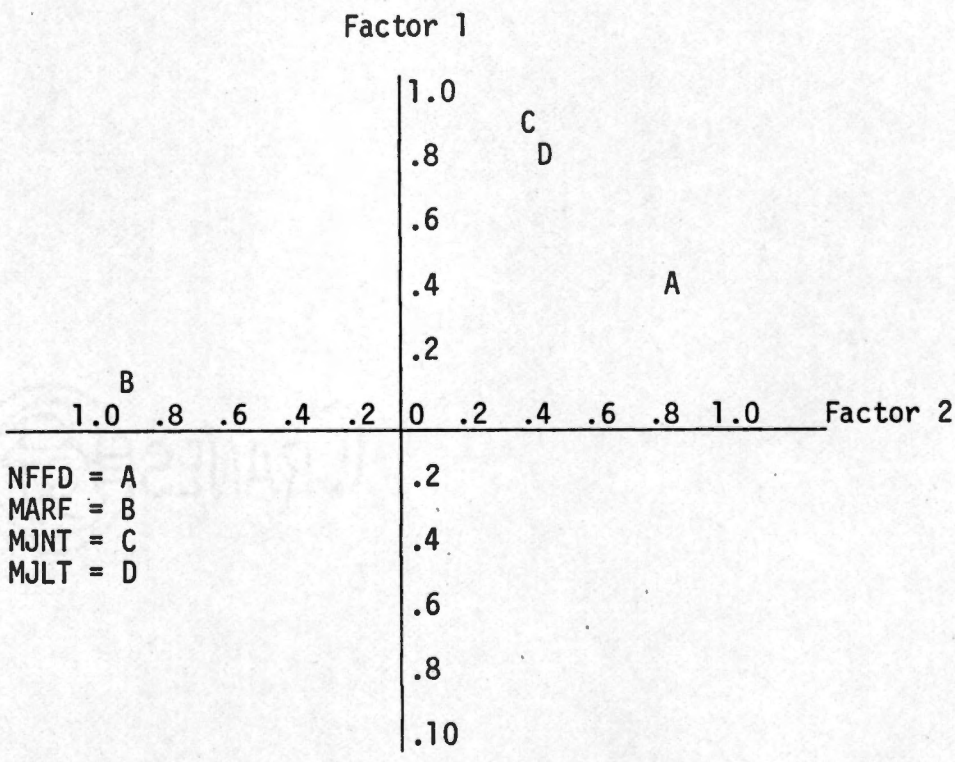
Factor Pattern

	#1	#2
NFFD	0.918	-0.383
MARF	-0.577	0.814
MJNT	0.839	0.525
MJLT	0.883	0.432

Rotated Factor Pattern

	#1	#2
NFFD	0.503	0.859
MARF	0.029	-0.997
MJNT	0.986	0.085
MJLT	0.965	0.186

Plot of Factor 1 with Factor 2



[a]These variables are defined on page 39.

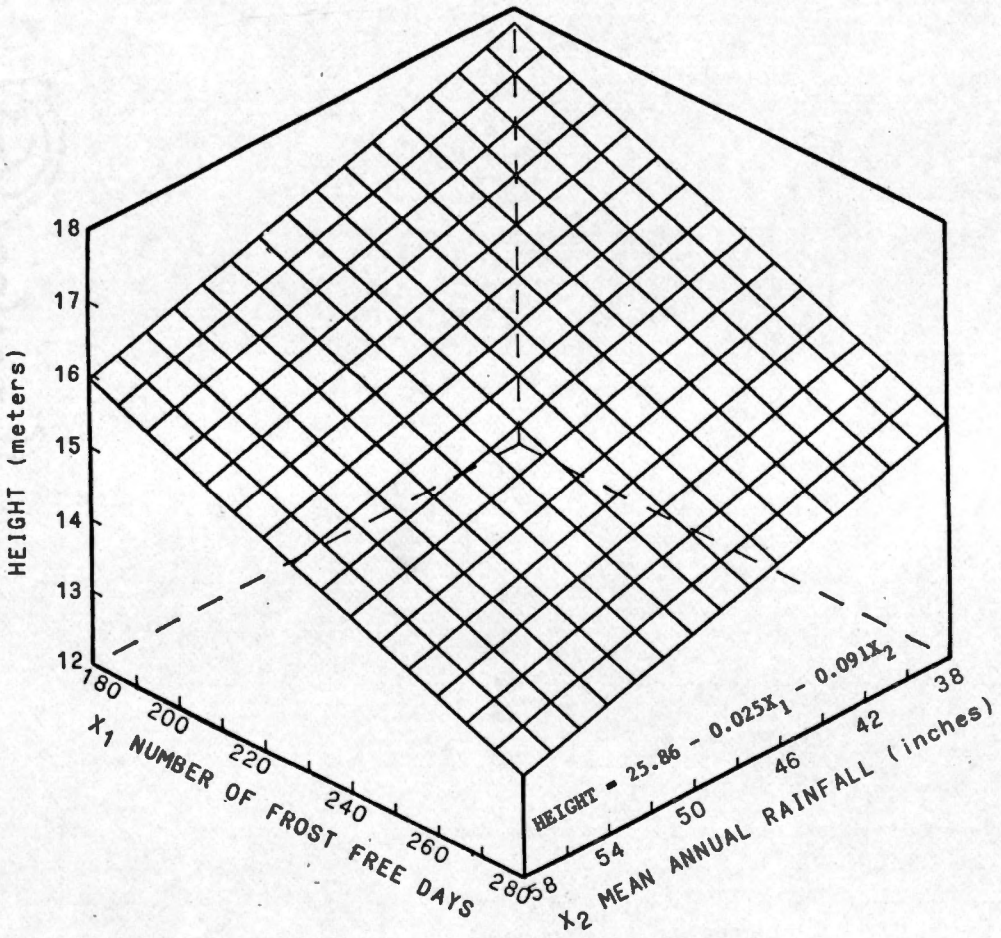


Figure 12. Average Height Growth at Ames Plotted Against Number of Frost Free Days and the Mean Annual Rainfall of the Provenance.

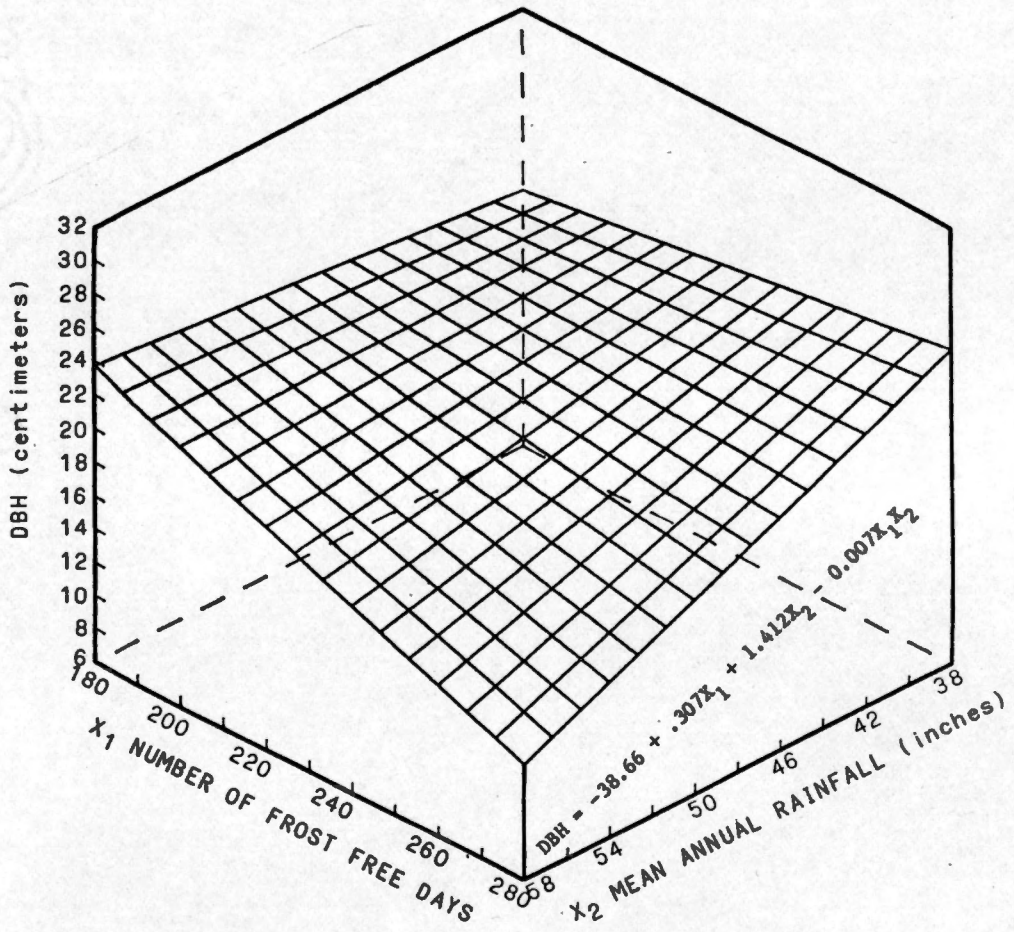


Figure 13. Average Diameter Growth at HRF Plotted Against Number of Frost Free Days and the Mean Annual Rainfall of the Provenance.

MARF at both planting locations. The "bend" in Figure 13 is the result of a NFFD-by-MARF interaction. In both cases South Carolina Coastal Plain and Mississippi Coastal Plain trees produce the least yield, but originate from areas of high rainfall and the longest growing seasons. Sources from Virginia Coastal Plain, Virginia and South Carolina Piedmonts and upper-Coastal Plain of Mississippi are consistently the 4 best producers; they also average the lowest NFFD and MARF (Table 34, page 85).

CHAPTER V

DISCUSSION AND CONCLUSIONS

Evaluation of provenance tests of loblolly pine in Tennessee reported before the current investigation involved trees that were relatively young. Although growth data were recorded at regular intervals since establishment, the stability of the provenances tested has not yet been confirmed. Stability refers to the consistency with which a given seed source performs on different sites. Thus, highly consistent seed sources may be regarded as having "good stability."

Comparisons of height growth in provenances common to the Ames Plantation and the Highland Rim plantation (see Table 37) reveal the stability of these provenances. Since the 5th growing season, sources from northeastern Coastal Plain and Piedmont provenances produced the tallest trees. Trees from inland provenances were uniformly intermediate, while trees from South Carolina Coastal Plain and the Deep South consistently ranked among the shortest.

This pattern of height growth was found among sources planted at Stephen's Switch (Table 38). Although rankings have changed considerably during the last 10 years, trees from Atlantic Coastal Plain areas are currently tallest at Counce. Similar patterns of height growth among provenances are reported by Rink and Thor (1971), Thor (1967), Thor and Brown (1962), Woerheide (1959), and Little (1969).

Table 37. Height Growth and Percent Survival of Trees Planted at the Ames and Highland Rim Plantations Since Establishment.

Provenance	1962 Height (m)	1962 Surv. (%)	1963[a] Height (m)	1963[a] Surv. (%)	1965 Height (m)	1965 Surv. (%)	1969 Height (m)	1969 Surv. (%)	1979 Height (m)	1979 Surv. (%)
Ames Plantation										
Chilesburg, VA	0.5	55	1.0	62	4.6	62	7.6	62	16.5	58
Accomac, VA	0.5	73	1.0	96	4.5	96	7.7	95	16.3	76
Johnston, SC	0.5	78	0.9	98	4.3	97	7.3	97	16.1	66
Tishomingo, MS	0.4	84	1.0	99	4.2	94	7.1	91	15.9	71
Crossett, AR	0.4	67	1.0	67	4.3	66	7.1	66	15.9	57
Cullman, AL	0.5	49	0.9	66	4.0	63	7.0	63	15.6	54
Griffin, GA	0.5	64	1.0	73	4.4	71	7.1	71	15.8	61
Georgetown, SC	0.4	78	0.8	96	3.9	93	6.3	92	14.2	58
Woodville, MS	0.4	28	0.7	55	3.4	55	6.0	54	14.0	39
Deep South	0.3	100	0.7	82	3.1	77	5.5	76	13.7	53
Highland Rim										
Accomac, VA	0.5	87	1.0	100	4.2	99	7.9	98	17.9	86
Johnston, SC	0.5	86	0.9	98	3.9	98	7.2	96	17.5	77
Crossett, AR	0.4	95	1.0	100	3.7	100	7.2	99	16.5	74
Cullman, AL	0.5	61	0.9	71	3.8	71	7.1	72	17.0	61
Griffin, GA	0.6	79	1.0	86	3.9	86	7.1	86	17.1	62
Deep South	0.4	100	0.7	83	3.1	70	6.3	70	16.3	47

[a]Mortality was replaced after the first growing season.

Table 38. Height Growth and Percent Survival of Trees at Stephen's Switch During the Last Twenty Years and at Counce During the Last Ten Years.

Seed Source	1960 Height (m)	1960 Surv. (%)	1965 Height (m)	1965 Surv. (%)	1969 Height (m)	1969 Surv. (%)	Trees Cut in Thinning	1975 Height (m)	1975 Surv. (%)	1979 Height (m)	1979 Surv. (%)
Stephen's Switch											
southeast Tennessee	3.1	96	8.1	92	12.2	83	63	17.4	48	20.5	43
Alabama Piedmont	3.1	82	8.6	74	13.0	66	30	17.2	49	20.3	39
Georgia Piedmont	3.3	84	8.0	71	12.8	53	12	17.6	38	20.5	20
North Carolina Piedmont	3.6	94	9.2	90	13.5	78	52	18.5	48	21.1	32
North Carolina Coastal Plain	3.1	91	8.5	81	13.2	66	30	18.0	46	21.4	31
South Carolina Coastal Plain	3.2	91	8.0	80	12.1	70	37	17.0	43	20.7	28
Counce											
South Carolina Coastal Plain					8.7	44				18.3	28
North Carolina Coastal Plain					9.7	63				17.3	46
Maryland Coastal Plain					9.0	67				17.1	42
southwest Alabama					8.7	53				16.9	28
northwest Alabama					8.7	76				16.7	39
Georgia Piedmont					8.8	68				16.7	43
south Mississippi					8.1	53				16.7	34
northeast Mississippi					8.9	79				16.5	41
southeast Tennessee					8.0	62				16.4	39

An interesting effect common to each of the Ames, Highland Rim, Counce, and Stephen's Switch plantations is the significant replication-by-height interaction effect. Apparently, height growth within provenances varies among replications at each of the test plantations; this variation may be due to microsite influences. Perhaps more replications would preclude this effect.

The largest proportion of variation associated with individual tree height, diameter and volume at each location is within experimental plots (Tables 11-14, pages 45-48, respectively). This result implies that considerable variation is present within the population (stand) from which the seed was collected.

Observations of individual trees during measurements suggest that trees from southeast Arkansas have a higher frequency of forked stems. This undesirable trait was also observed by Kormanik and Hoekstra (1961) among southeast Arkansas loblolly pines planted in Virginia. Planting trees of this seed source north of its origin may result in frost damage to the meristem, forcing lateral buds to grow vertically, and thus forming "forks."

At Ames Plantation, loblolly pines from Virginia and South Carolina had 4% better survival than those from inland sources and 19% better than trees from the Deep South. This same trend is evident at the Highland Rim plantation. This pattern was found earlier by Rink and Thor (1971).

Percent survival ultimately has the greatest impact upon total volume per hectare produced by trees from a given seed source (Figure 14). Percent survival, however, and its associated random spatial influence upon individual tree growth is confounded with the

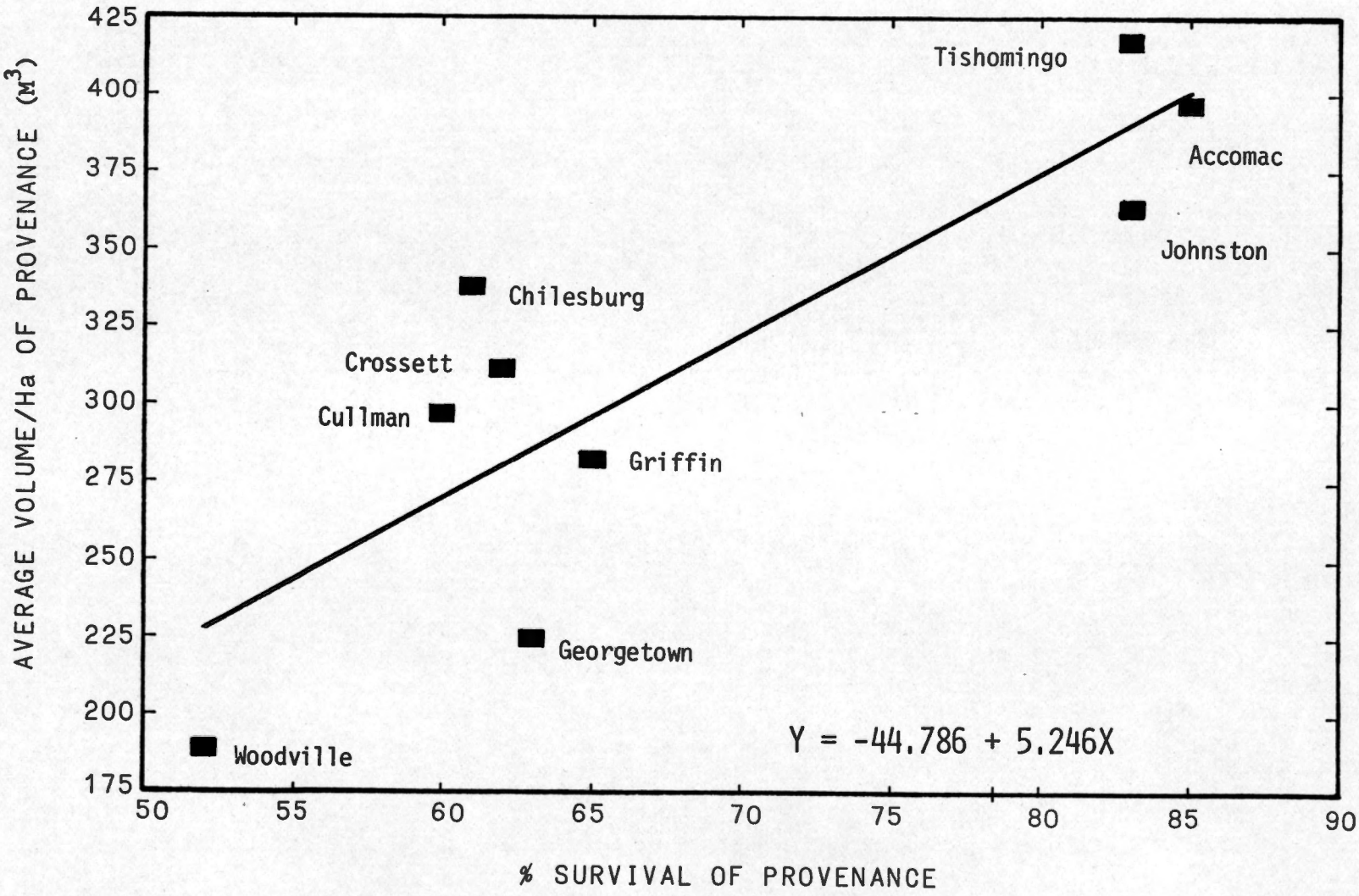


Figure 14. Volume/ha vs % Survival of Each Provenance at Ames.

genetic potential of seed source. As seen in Table 39, those trees at the Ames and Highland Rim plantations which produce the greatest volume per hectare also maintain the highest survival percentage. They are not necessarily, however, the largest trees in the plantations. This relationship is also evident at Stephen's Switch; trees from southeast Tennessee which occur in greater numbers rank last in diameter and volume and second to last in height growth. Nevertheless, total volume production is 49 cubic meters more per hectare for those trees than the second ranked north Alabama trees (Table 10, page 44). LaFarge (1974) and Barber (1966) reported a similar trend among 3 broad physiographic regions in Georgia where survival was found to be the major influence on total volume production.

The combined location analyses of the Ames and Highland Rim plantations revealed some interesting results. The provenance-by-planting location interaction was found not to be statistically significant for any characteristic (Table 22, page 60). This result implies that provenances tested at both locations will perform similarly on similar sites in Tennessee, and may be regarded as another measure of provenance stability. Namkoong (1979) describes the provenance-by-planting location interaction as follows: "To the extent that each site has unique optimal sources, the site-by-source interaction can be expected to be high. To the extent that sources perform consistently over different sites, the provenance source will have a large effect at the expense of the interaction component."

Individual tree height and volume, and volume, basal area and tonnes of wood per hectare were significantly greater at the Highland Rim than at Ames Plantation. Greenwald (1973) reported that best

Table 39. Percent Contribution of Six Seed Sources to Each of Seven Growth Characteristics Common to Ames Plantation and the Highland Rim Forest.

Seed Source	Height (m)		dbh (cm)		m^3/ Tree		m^3/ ha		m^2/ ha		Tonnes/ ha		Surv. (%)	
	Ames	HRF	Ames	HRF	Ames	HRF	Ames	HRF	Ames	HRF	Ames	HRF	Ames	HRF
Accomac, VA	105	105	98	103	100	109	131	127	123	126	130	128	128	127
Johnston, SC	104	103	100	100	100	102	119	112	115	114	114	111	111	114
Crossett, AR	103	97	104	97	106	92	103	96	101	104	101	97	96	91
Griffin, GA	102	100	100	101	98	102	93	87	92	90	90	114	103	90
Cullman, AL	101	100	105	103	109	106	98	91	98	96	101	88	91	110
Deep South	88	96	96	97	83	92	74	65	83	70	72	62	89	69

growth was exhibited by loblolly pine seedlings exposed to mild day temperatures (23° C) and cool night temperatures (17° C). Under these conditions photosynthates were produced in excess of that required for respiration. As seen in Table 34, page 85, trees on the Highland Rim may have benefitted by increased growth rates since annual rainfall is greater and mean July temperature is less here than at the origin of each provenance. Greenwald (1973) also found that oleoresin production increased as the amount of photosynthates produced exceeded that consumed in respiration. This may explain the significantly greater amount of extractives found in trees planted on the Highland Rim as compared to Ames Plantation.

In general, yield is greater in those trees whose environmental origin is similar to that of the planting site. This relationship appears typical in provenance tests located in the northeastern and northwestern extremes of the species range (Wells and Wakeley, 1966). At the Ames Plantation trees of a northeastern Mississippi source produced the greatest total volume. At Stephen's Switch southeast Tennessee trees produced the greatest volume. Evidently, when trees are planted further south, those of warm winters and high rainfall origins survive the best (Wells and Wakeley, 1966; Grigsby, 1977, 1973; Collins, 1964).

Specific gravity did not vary significantly among provenances or between locations. Rink and Thor (1971) reported that trees at the Ames Plantation from the Virginia Piedmont source had significantly greater extracted specific gravity. They also identified a weak trend among 5 provenance tests where trees from the northeast portion of the species range had the highest specific gravities. This trend

may still be evident with Atlantic Coastal Plain trees having higher unextracted and extracted specific gravities than most trees from inland and western origins. Still, trees from north Mississippi, southeast Arkansas and southwest Louisiana rank among the highest.

The statistically significant ($P < 0.05$) replication-by-provenance and tree-within-replication effects at both locations indicate that a considerable amount of variation in specific gravity is among and within plots (Table 18, page 52). The provenance-by-replication within location effect in the combined analysis was also significant ($P < 0.01$) accounting for about 47% of the variation in specific gravity. Within plot effects accounted for approximately 51% (Table 23, page 61). Quite similar results are reported by Zobel et al. (1972) finding the environment at the planting location to have greater effect on specific gravity than the source of seed.

Wood production expressed as tonnes per hectare followed a pattern very similar to volume and basal area growth per hectare. An exception to the pattern was trees from northwest Georgia at the Highland Rim Plantation that ranked second in wood production but only fifth in volume and basal area per hectare (Table 16, page 50). At the Ames Plantation, trees of the same source ranked seventh in all 3 characteristics (Table 15, page 49).

Estimates of volume, basal area and tonnes of wood per hectare may be higher than that produced in average forest plantations. The proportional increase in yield per plot to yield per hectare is in some cases 100 fold. This estimate assumes that tree size, spatial distribution among trees and various microsite influences on

the few trees in an experimental plot are the same as in an area the size of a hectare.

Although oleoresin sampling by Squillace and Wells (1980) was considerably more intensive, results of the monoterpene analysis here paralleled their findings. This is attributed to the broad representation of the species range present in the provenance tests sampled. An east-to-west gradient was observed in limonene, myrcene and alpha-pinene, while trees containing high beta-phellandrene originated from the northwestern and southeastern portions of the species range. Distribution of beta-pinene was patchy, and no clear trend could be identified. It appears that cortical monoterpene composition patterns can be useful for identifying the seed origin of trees planted in commercial plantations. Identification of provenance origin would be an added benefit, if not necessary, where phenotype selection in commercial plantations is carried out for breeding purposes.

Factor analysis was applied to the environmental-source (E-S) variables to eliminate variate redundancies. Each variable was standardized by factor weighting to make them dimensionless and interpretable. Two factors were calculated for each E-S variable at the Ames and Highland Rim plantations because there were 2 eigenvalues greater than 1 (Tables 35 and 36, pages 86 and 87, respectively). Jeffers (1964) recommended choosing eigenvalues (variances) which are equal to or greater than 1 as the basis for determining the number of factors to be calculated for biological data. This procedure is somewhat analogous to choosing the probability level that one wishes to operate at in a routine analysis of variance (Isebrands and Crow,

1975). By using a minimum eigenvalue of 1, mean July temperature (MJLT) and mean January temperature (MJNT) were eliminated from further analyses (Tables 35 and 36, pages 86 and 87, respectively). These were considered redundant variables and not necessary in subsequent multiple regression equations involving number of frost free days (NFFD) and mean annual rainfall (MARF). Factors were then plotted in order to achieve more interpretability (Tables 35 and 36).

Analysis of biologically related systems by simple linear regression may not be an adequate statistical treatment of the relationships among the variables in question. As is the case here, the E-S variables do not act independently on yield but act rather as a collective, yet dynamic, influence on tree growth. A multivariate analysis, therefore, would better predict the relationships among the variables involved. Response surfaces, however, involving variables of many different units of measure such as tree diameter, height and volume could not be drawn. Therefore, when response surfaces are desired, multiple regression analysis is employed to estimate E-S variable interactions on a single parameter.

At Ames Plantation the influences of the number of frost free days (NFFD) and the mean annual rainfall (MARF) at the seed origin affect height growth equally (Figure 12, page 88). Slow growth can be attributed to trees whose NFFD and MARF at the origin are high. Diameter growth at the Highland Rim plantation appears to decrease as NFFD and MARF at seed origin increase (Figure 13, page 89). The fact that there is an interaction between these 2 variables and a resulting R^2 of 1.0 indicates that optimum growth may be obtained

by trees from origins of short growing seasons and low rainfall. Overall, trees from provenances of longer growing seasons and generally warmer winters and more annual rainfall did not grow well at Ames or the Highland Rim plantations. Results of the analysis of variance verify conclusions made from interpreting the response surfaces.

In retrospect, the use of factor analysis to eliminate redundancies is usually reserved for problems involving many more variables. Because the E-S variables applied in this study were few, a stepwise regression analysis would have yielded the same results. The advantage of factor analysis, however, is the multivariate "weighting method" used to select the most meaningful E-S variables. Perhaps in future analyses of this type more appropriate E-S variables to include would be seasonal rainfall, seasonal temperatures, seasonal evapotranspiration and other quantitative seasonal environments.

CHAPTER VI

SUMMARY AND RECOMMENDATIONS

Six loblolly pine (Pinus taeda L.) provenance test plantations distributed across Tennessee (ages 19 to 26 years from planting) were evaluated on an individual tree basis for total height, dbh, volume and basal area. In addition, wood specific gravity and percentage composition of cortical monoterpenes were evaluated at the Ames Plantation in west Tennessee and the Highland Rim Forestry Field Station near Tullahoma. Significant differences among provenances were found at Ames Plantation, the Highland Rim Forestry Field Station, the Counce plantation in west Tennessee and the Stephen's Switch plantation in the lower elevations of the Cumberland Mountains.

At the Stephen's Switch plantation, trees originating from southeast Tennessee, north Alabama and the North Carolina Piedmont and Coastal Plain produce significantly more volume and basal area on a per hectare basis than trees originating from the Georgia Piedmont or the South Carolina Coastal Plain. At the Ames Plantation, trees from Tishomingo, MS (upper-Coastal Plain), Accomac, VA (eastern shore), Johnston, SC (Piedmont), Chilesburg, VA (Piedmont) and Crossett, AR (upper-Coastal Plain) are consistently producing the most volume per hectare, basal area per hectare, and tonnes of wood per hectare. Intermediate production is attained by trees originating from Griffin, GA and Cullman, AL, both of the upper-Coastal Plain region. Low production is associated with provenances that originate near Georgetown, SC (Coastal Plain) and in Gulf Coastal Plain localities.

Results from identical provenances planted at the Highland Rim follow quite closely the pattern of response found at Ames. Trees in the Counce plantation varied significantly only in diameter and volume per tree. Trees from the South Carolina Coastal Plain, south Alabama and the North Carolina Coastal Plain were largest in diameter and volume, while those from the Georgia Piedmont, Maryland Coastal Plain and northeast Mississippi were smallest.

Poorly adapted trees to Tennessee growing conditions were consistently from southern origins within the species natural range. In some cases, individual tree size of southern trees was greater than those from northern origins. However, by not maintaining a high survival percentage total production per hectare by southern trees was less.

No significant differences among provenances for unextracted and extracted specific gravity, or extractives were evident at either Ames Plantation or the Highland Rim. However, extractives were produced at the Highland Rim in significantly greater amounts than at Ames. With one exception, a general pattern of decreasing specific gravity from the Atlantic Coastal Plain (.475 to .471), inland into the Piedmont region (.466 to .463) was evident.

Considerable variation was found in cortical monoterpene composition; beta-pinene, myrcene, limonene, and beta-phellandrene showed bimodality, while the alpha-pinene data had normal distribution. Combined data from the Ames and Highland Rim plantations revealed that 12 of 16 possible phenotypes occurred when classifying each tree as being "high" or "low" for each of the 4 monoterpenes showing bimodality. High amounts of limonene and beta-phellandrene occurred in greater

percentages in trees of western origins, while high amounts of myrcene were frequently found in eastern trees. Distribution of beta-pinene was patchy and no trend was identified. A trend of increasing percent alpha-pinene content in a southwest to northeast pattern was indicated.

Based on the results of this investigation, trees best suited to west Tennessee include those from Virginia, the Carolina Piedmonts and north Mississippi. Loblolly pine plantations on the Highland Rim should consist of trees from Virginia and the Carolina Piedmonts. Trees from southeast Tennessee, north Alabama and the North Carolina Piedmont are recommended for planting in the lower elevations of the Cumberland Mountains. Loblolly pines whose origins have the lowest annual rainfall and the shortest growing season within the natural range of the species appear to be better adapted to Tennessee growing conditions.

Future measurements of the provenance tests at the Friendship Forest and Norris are not recommended. The 1964 selection thinning at Norris plantation most likely eliminated whatever growth differences were present in that provenance test. Trees row thinned at the Friendship Forest probably produced the same result.

Low thinnings were performed in the Counce, Ames and Highland Rim provenance tests in the Fall of 1980. Trees were thinned to 12 trees per plot (10 trees per plot at Counce) removing only the smallest trees of poor form. The number of trees cut and means of 5 growth characteristics are presented in the Appendix, Tables A-10 through A-12. Those trees left standing (crop trees) are presented in the Appendix, Tables A-13 through A-15.

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APPENDIX

Table A-1. Average Performance of Five Growth Characteristics and the Number of Trees Measured at Norris.

Seed Source	Height (m)	dbh (cm)	No. of Trees	m^3/ Tree	m^3/ ha	m^2/ ha
North Carolina Coastal Plain	22.3	21.4	31	.40	367	34.2
South Carolina Coastal Plain	21.8	21.0	30	.37	330	31.4
North Georgia (Lot 6)	21.7	21.6	35	.39	410	39.1
North Georgia (Lot 3)	21.5	20.3	39	.35	405	38.8
Northwest Georgia (Lot 5)	21.2	20.9	35	.36	378	36.9
Crossett, Arkansas	21.0	19.6	41	.31	385	38.0

Table A-2. Average Performance of Five Growth Characteristics and the Number of Trees Measured at Friendship Forest.

Seed Source	Height (m)	dbh (cm)	No. of Trees	m^3/ Tree	m^3/ ha	m^2/ ha
Virginia	20.1	20.7	34	.34	344	34.9
Arkansas	20.1	20.3	34	.33	336	34.2
South Carolina	20.0	21.4	36	.36	345	35.3
Central North Carolina	19.9	19.8	36	.31	329	34.0
Georgia	19.8	20.3	35	.32	342	35.3
Eastern North Carolina	19.8	20.4	36	.33	348	35.9

Table A-3. Breeding Values and Ranks for Those Growth Characteristics Determined Significantly Different at Ames Plantation.

Seed Source	Height (m)	Rank	dbh (cm)	Rank	m^3/ Tree	Rank	m^3/ ha	Rank	m^2/ ha	Rank	Tonnes/ ha	Rank
Chilesburg, VA	16.3	1	21.5	1	.32	1	326	4	40.7	4	147	4
Accomac, VA	16.1	2	20.3	7	.27	5	370	2	45.7	2	164	2
Johnston, SC	16.0	3	20.4	6	.27	5	342	3	43.3	3	148	3
Tishomingo, MS	15.8	4	20.5	5	.28	3	386	1	48.7	1	179	1
Crossett, AR	15.8	4	21.0	3	.28	3	305	5	39.4	5	135	5
Griffin, GA	15.7	6	20.4	4	.26	7	284	7	36.8	7	125	7
Cullman, AL	15.6	7	21.1	2	.29	2	294	6	38.3	6	135	5
Georgetown, SC	14.5	8	19.7	10	.21	10	238	9	33.3	9	109	8
Woodville, MS	14.3	9	20.0	8	.22	8	211	10	29.9	10	95	10
Deep South	14.1	10	20.0	8	.22	8	239	8	34.1	8	107	9

Table A-4. Breeding Values and Ranks for Those Growth Characteristics Determined Significantly Different at Counce.

Seed Source	dbh (cm)	Rank	m^3/ Tree	Rank
South Carolina Coastal Plain	21.3	1	0.32	1
south Alabama	19.4	2	0.26	2
southeast Tennessee	18.6	3	0.23	5
North Carolina Coastal Plain	18.5	4	0.24	3
south Mississippi	18.4	5	0.24	3
northwest Alabama	17.7	6	0.21	6
Georgia Piedmont	17.6	7	0.21	6
Maryland Coastal Plain	17.1	8	0.20	8
northeast Mississippi	16.9	9	0.19	9

Table A-5. Breeding Values and Ranks for Those Growth Characteristics Determined Significantly Different at the Highland Rim.

Seed Source	Height (m)	Rank	m^3/ Tree	Rank	m^3/ ha	Rank	m^2/ ha	Rank	Tonnes/ ha	Rank
Accomac, VA	17.7	1	.32	1	504	1	58.1	1	229	1
Johnston, SC	17.4	2	.30	3	448	2	49.8	2	202	3
Cossett, AR	17.1	3	.28	5	389	3	48.2	3	180	4
Griffin, GA	16.6	5	.30	3	357	5	43.2	5	208	2
Cullman, AL	17.0	4	.31	2	373	4	45.6	4	165	5
Deep South	16.5	6	.28	5	273	6	34.5	6	123	6

Table A-6. Breeding Values and Ranks for Those Growth Characteristics Determined Significantly Different at Stephen's Switch.

Seed Source	dbh (cm)	Rank	m^3/ ha	Rank	m^2/ ha	Rank	m^3 Produced/ ha[a]	Rank
southeast Tennessee	19.8	6	388	1	39.0	1	443	1
north Alabama	20.0	5	365	2	36.6	2	394	2
Georgia Piedmont	21.6	1	272	6	26.6	6	251	6
North Carolina Piedmont	21.0	4	350	4	34.3	3	391	3
North Carolina Coastal Plain	21.2	3	356	3	34.6	4	378	4
South Carolina Coastal Plain	21.5	2	321	5	31.6	5	331	5

[a]Includes volume from thinning in 1971.

Table A-7. Percent of Sixteen Possible Phenotypes Determined from Four Simply Inherited Cortical Monoterpenes in Each Provenance at Ames Plantation.

Phenotype	Trees (Number)	Provenance (By Percent)											
		Rusk, TX	Hornbeck, LA	Crossett, AR	Woodville, MS	Walker, LA	Tishomingo, MS	Cullman, AL	Griffin, GA	Johnston, SC	Georgetown, SC	Chilesburg, VA	Accomac, VA
BMLP	6	25			25	12					12		
BMLp													
BM1P	40		25	25	50	38	75	50	50	88	25	50	25
BM1p	4					12					12	12	12
BmLP	24	75	63	75	12	25	12	25		12			
BmLp													
Bm1P	12		12				12	12	25		38	12	38
Bm1p	1								12				
bMLP													
bMLp													
bM1P	5					12		12	12			12	12
bM1p													
bmLP	1				12								
bmLp													
bm1P	3										12	12	12
bm1p													
Total	96												

Table A-8. Percent of Sixteen Possible Phenotypes Determined from Four Simply Inherited Cortical Monoterpenes in Each Provenance at the Highland Rim.

Phenotype	Trees (Number)	Provenance (By Percent)							
		Rusk, TX	Hornbeck, LA	Crossett, AR	Walker, LA	Cullman, AL	Griffin, GA	Johnston, SC	Accomac, VA
BMLP	8		38	38	12		12		
BMLp									
BMlP	29	25	25		38	75	38	75	88
BMlp									
BmLP	14	63	25	38	25	12		12	
BmLp	2	12			12				
BmlP	2				12				12
Bmlp	4		12				25	12	
bMLP	1			12					
bMLp									
bMlP	2			12			12		
bMlp	1					12			
bmLP									
bmLp									
bmlP	1						12		
bmlp									
Total	64								

Table A-9. Percent of Sixteen Possible Phenotypes Determined from Four Simply Inherited Cortical Monoterpenes in Each Provenance at Ames and the Highland Rim.

Phenotype	Trees (Number)	Provenance (By Percent)											
		Rusk, TX	Hornbeck, LA	Crossett, AR	Woodville, MS	Walker, LA	Tishomingo, MS	Cullman, AL	Griffin, GA	Johnston, SC	Georgetown, SC	Chilesburg, VA	Accomac, VA
BMLP	14	12	19	19	25	12			6		12		
BMLp													
BMlP	69	12	25	12	50	38	75	63	44	82	25	50	56
BMlp	4					6					12	12	6
BmLP	38	69	44	56	12	25	12	19		12			
BmLp	2	6				6							
BmlP	14		6			6	12	6	12		38	12	25
Bmlp	5		6						19	6			
bMLP	1			6									
bMLp													
bMlP	7			6		6		6	12			12	6
bMlp	1							6					
bmLP	1				12								
bmLp													
bmlP	4								6		12	12	6
bmlp													
Total	160												

Table A-10. Means of Five Characteristics and the Number of Trees Thinned in 1979 at Ames Plantation.

Seed Source	No. of Trees	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha
Deep South	9	11.1	15.2	.10	28.7	4.8
Crossett, AR	13	15.4	18.6	.21	50.4	6.7
Woodville, MS	2	11.0	15.5	.11	5.8	1.1
Tishomingo, MS	29	14.3	16.0	.14	82.3	12.0
Cullman, AL	11	13.2	14.9	.12	22.3	3.4
Griffin, GA	17	15.6	17.5	.19	55.3	7.2
Georgetown, SC	12	12.2	13.1	.08	16.1	2.8
Johnston, SC	25	14.7	16.5	.16	75.5	10.9
Chilesburg, VA	11	15.1	17.1	.18	37.3	5.0
Accomac, VA	30	14.7	15.6	.15	80.3	11.1

Table A-11. Means of Five Characteristics and the Number of Trees Thinned in 1979 at the Highland Rim.

Seed Source	No. of Trees	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha
Deep South	8	14.5	14.5	.12	20.5	2.9
Crossett, AR	29	16.4	18.3	.21	117.9	15.1
Cullman, AL	17	16.3	17.4	.19	60.8	7.8
Griffin, GA	18	16.0	16.8	.17	62.0	8.1
Johnston, SC	32	17.0	18.6	.23	141.7	17.4
Accomac, VA	41	17.6	18.6	.23	178.2	21.1

Table A-12. Means of Five Characteristics and the Number of Trees Thinned in 1979 at Counce.

Seed Source	Height (m)	dbh (cm)	No. of Trees	m^3/ Tree	m^3/ ha	m^2/ ha
Northwest Alabama	15.3	12.3	3	.09	10	1.4
Southeast Tennessee	15.1	16.0	4	.15	24	3.3
Northeast Mississippi	15.7	12.6	5	.09	18	2.5
South Mississippi	12.0	13.8	3	.07	9	1.4
South Alabama	0	0	0	0	0	0
Georgia Piedmont	15.1	13.0	7	.09	26	3.7
South Carolina Coastal Plain	0	0	0	0	0	0
North Carolina Coastal Plain	15.4	13.1	10	.10	40	5.4
Maryland Coastal Plain	15.8	12.3	6	.09	22	2.9

Table A-13. Means of Five Characteristics and the Number of Crop Trees Standing at Ames Plantation.

Seed Source	No. of Trees	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha
Deep South	44	14.1	20.6	.24	193	27.6
Crossett, AR	44	16.0	22.1	.31	256	32.8
Woodville, MS	37	14.2	19.9	.22	179	25.6
Tishomingo, MS	42	17.0	23.6	.37	329	40.1
Cullman, AL	43	16.1	23.2	.33	271	34.6
Griffin, GA	44	15.9	21.5	.29	223	28.8
Georgetown, SC	46	14.7	20.7	.25	204	28.4
Johnston, SC	41	16.9	22.7	.34	279	34.0
Accomac, VA	47	17.3	22.8	.35	310	37.0
Chilesburg, VA	46	16.8	23.5	.36	297	36.3

Table A-14. Means of Five Characteristics and the Number of Crop Trees Standing at the Highland Rim.

Seed Source	No. of Trees	Height (m)	dbh (cm)	m^3/ Tree	m^3/ ha	m^2/ ha
Deep South	39	16.6	21.6	.30	243	30.4
Crossett, AR	45	16.6	22.0	.30	271	34.3
Cullman, AL	44	17.3	23.4	.36	310	37.5
Griffin, GA	44	17.5	22.9	.35	292	34.7
Johnston, SC	45	17.8	22.9	.35	311	36.6
Accomac, VA	45	18.2	24.1	.40	336	38.7

Table A-15. Means of Five Characteristics and the Number of Crop Trees Standing at Counce.

Seed Source	Height (m)	dbh (cm)	No. of Trees	m^3/ Tree	m^3/ ha	m^2/ ha
Northwest Alabama	16.8	17.9	36	.21	308	37.6
Southeast Tennessee	16.6	19.1	35	.24	331	41.1
Northeast Mississippi	16.6	17.0	36	.19	271	34.0
South Mississippi	17.0	19.1	31	.25	314	37.4
South Alabama	16.9	19.8	28	.26	295	35.7
Georgia Piedmont	17.0	18.3	36	.23	324	39.1
South Carolina Coastal Plain	18.3	22.3	28	.36	399	45.0
North Carolina Coastal Plain	17.8	20.1	36	.28	400	46.4
Maryland Coastal Plain	17.5	17.4	36	.21	294	35.5

Table A-16. Conversion of Volume Equation to Compute Volume in Metric Units.

Equation		Calculations
$Vol\ (ft^3)$	=	$a + b(D_{in})^2\ (H_{ft})$
$D_{(in)}$	=	$D_{cm} / 2.54$
$D_{(ft)}$	=	$H_m * 3.28084$
$Vol\ (ft^3)$	=	$a + b\ (D_{cm} / 2.54)^2\ (H_m * 3.28084)$
$Vol\ (ft^3)$	=	$a + (b * 3.28084/2.54^2)\ (D_{cm})^2\ (H_m)$
$Vol\ (m^3)$	=	$0.0283168 * Vol\ (ft^3)$
$Vol\ (ft^3)$	=	$35.3198 * Vol\ (m^3)$
$Vol\ (m^3) * 35.3198$	=	$a + (b * 3.28084/2.54^2)\ (D_{cm})^2\ (H_m)$
$Vol\ (m^3)$	=	$[(a * 0.0283168) + (b * 3.28084 * 0.0283168/ (2.54)^2)\ (Dcm)^2\ (Hm)]$
IF a	=	$-.1051^a$ b = $.0026271^a$
Then a'	=	-.00297609 b' = .00003782
Hence		
$Vol\ (m^3)$	=	$.00003782\ (D^2H) - .00297609$

[a]From Smalley and Bower (1968), Table 9, page 10, outside bark volume to a 3.0 inch top.

Table A-17. Plot Size Calculations for Each Plantation.

Location	Spacing	Plot Size	ft^2	m^2
Ames and Highland Rim	8x8	25 tree plot	1600	148.64
		20 tree plot	1280	118.91
		16 tree plot	1024	95.13
Counce and Norris	6x6	25 tree plot	900	83.61
Friendship Forest and Stephen's Switch	6x6	49 tree plot	1764	163.89

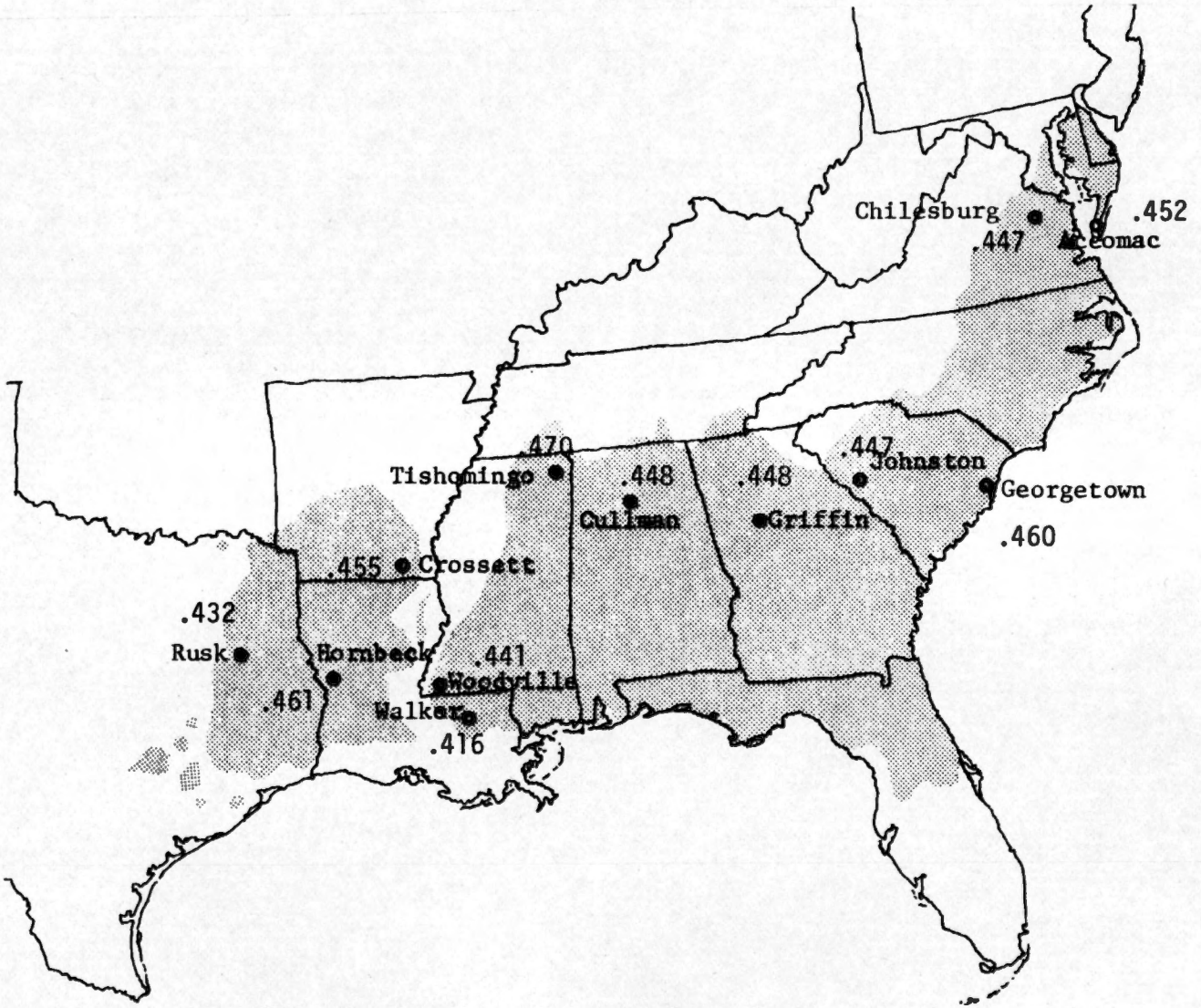


Figure A-1. The Origin and Mean Extracted Specific Gravity of Trees at Ames and the Highland Rim.

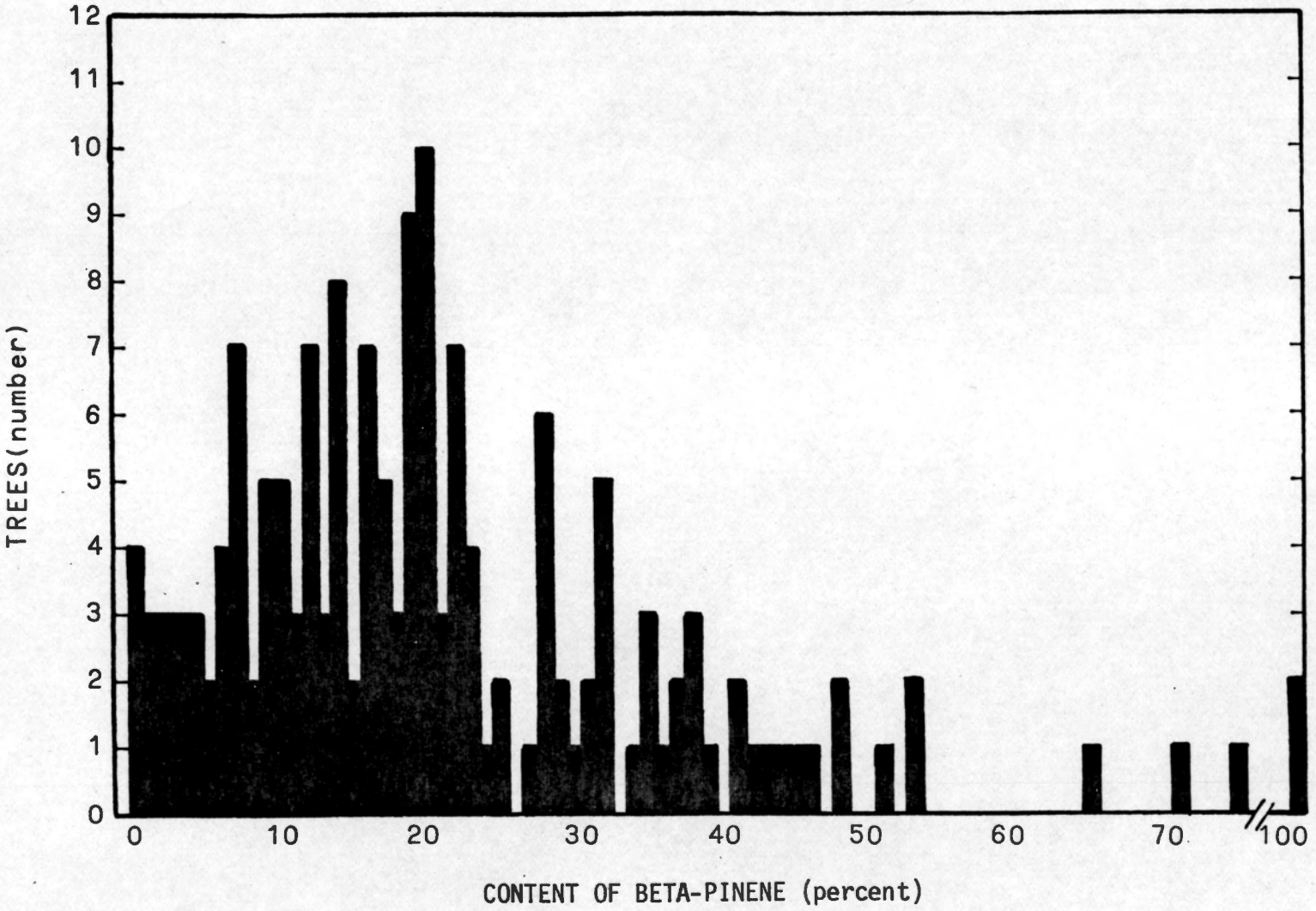


Figure A-2. Frequency Distribution for the Percentage Content of Beta-pinene in the Cortex Oleoresin of Trees at Ames and the Highland Rim.

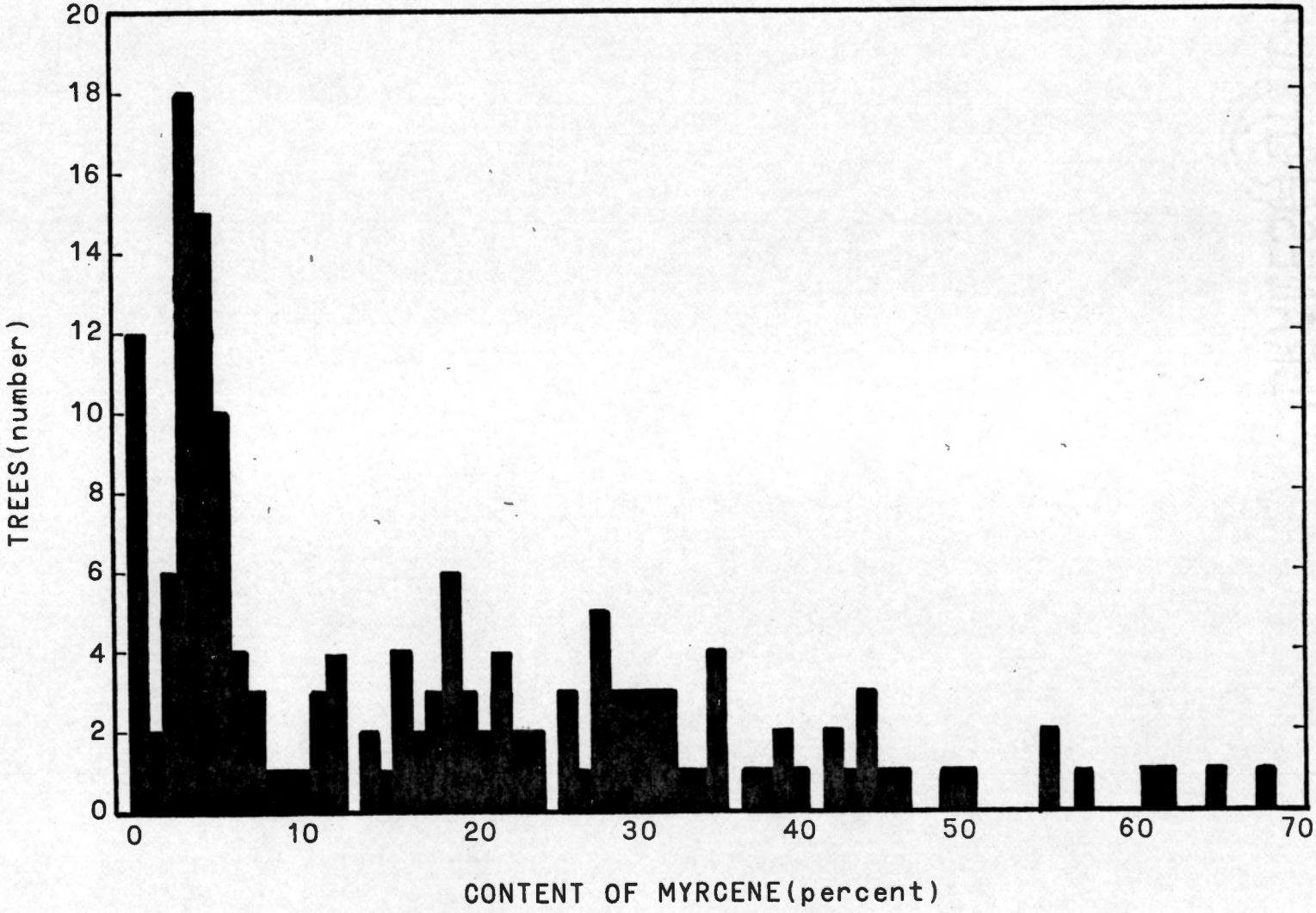


Figure A-3. Frequency Distribution for the Percentage Content of Myrcene in the Cortex Oleoresin of Trees at Ames and the Highland Rim.

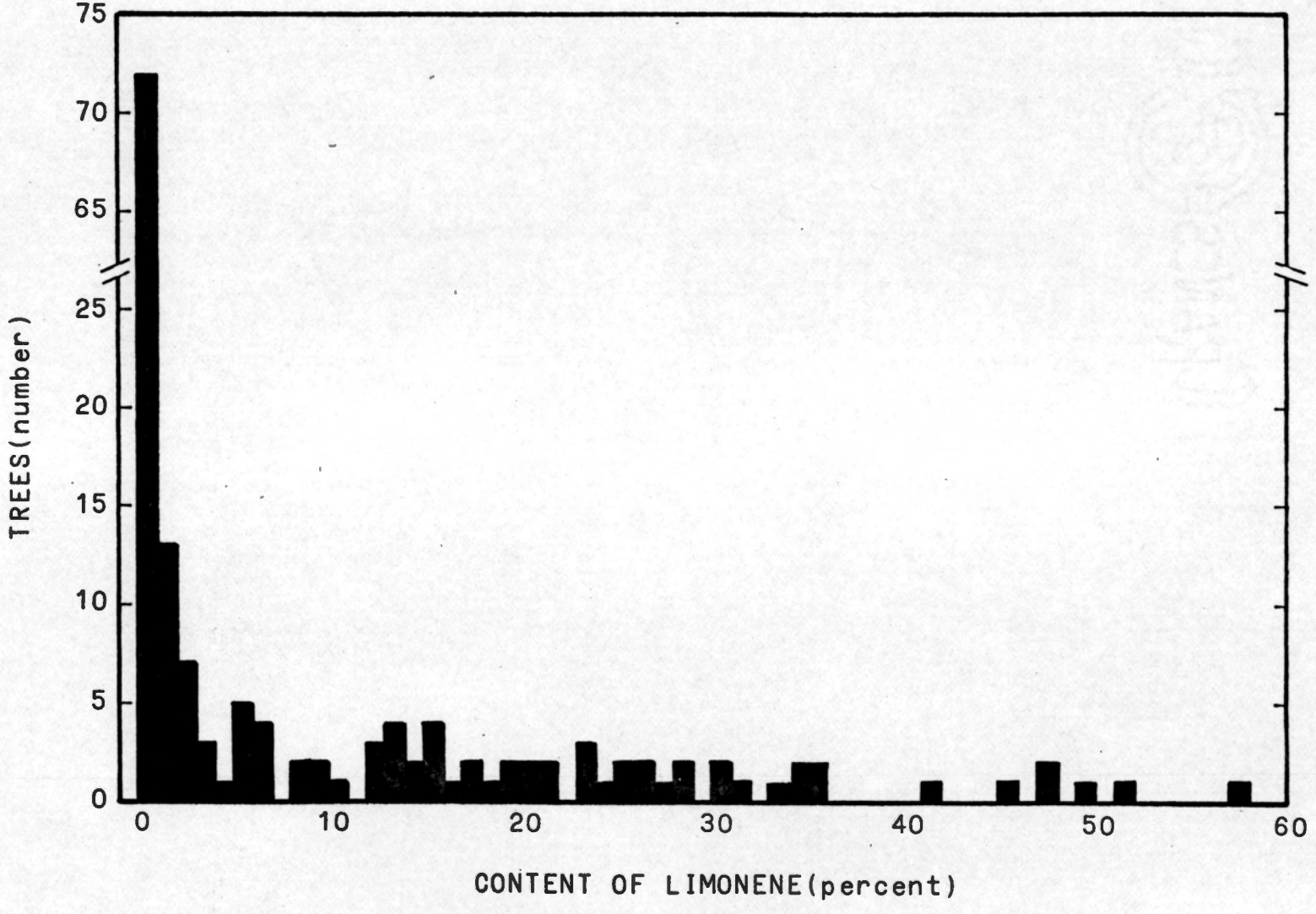


Figure A-4. Frequency Distribution for the Percentage Content of Limonene in the Cortex Oleoresin of Trees at Ames and the Highland Rim.

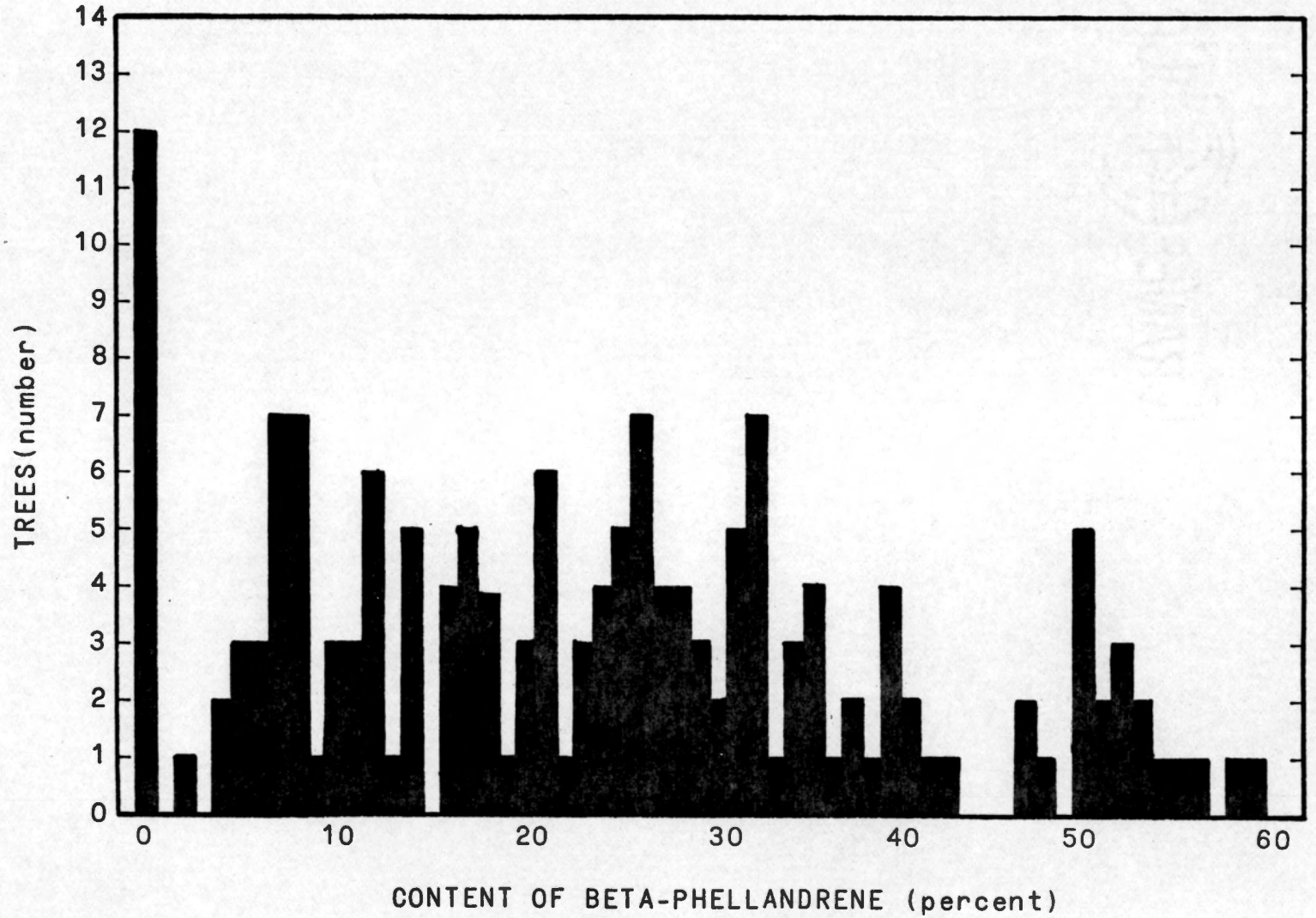


Figure A-5. Frequency Distribution for the Percentage Content of Beta-phellandrene in the Cortex Oleoresin of Trees at Ames and the Highland Rim.

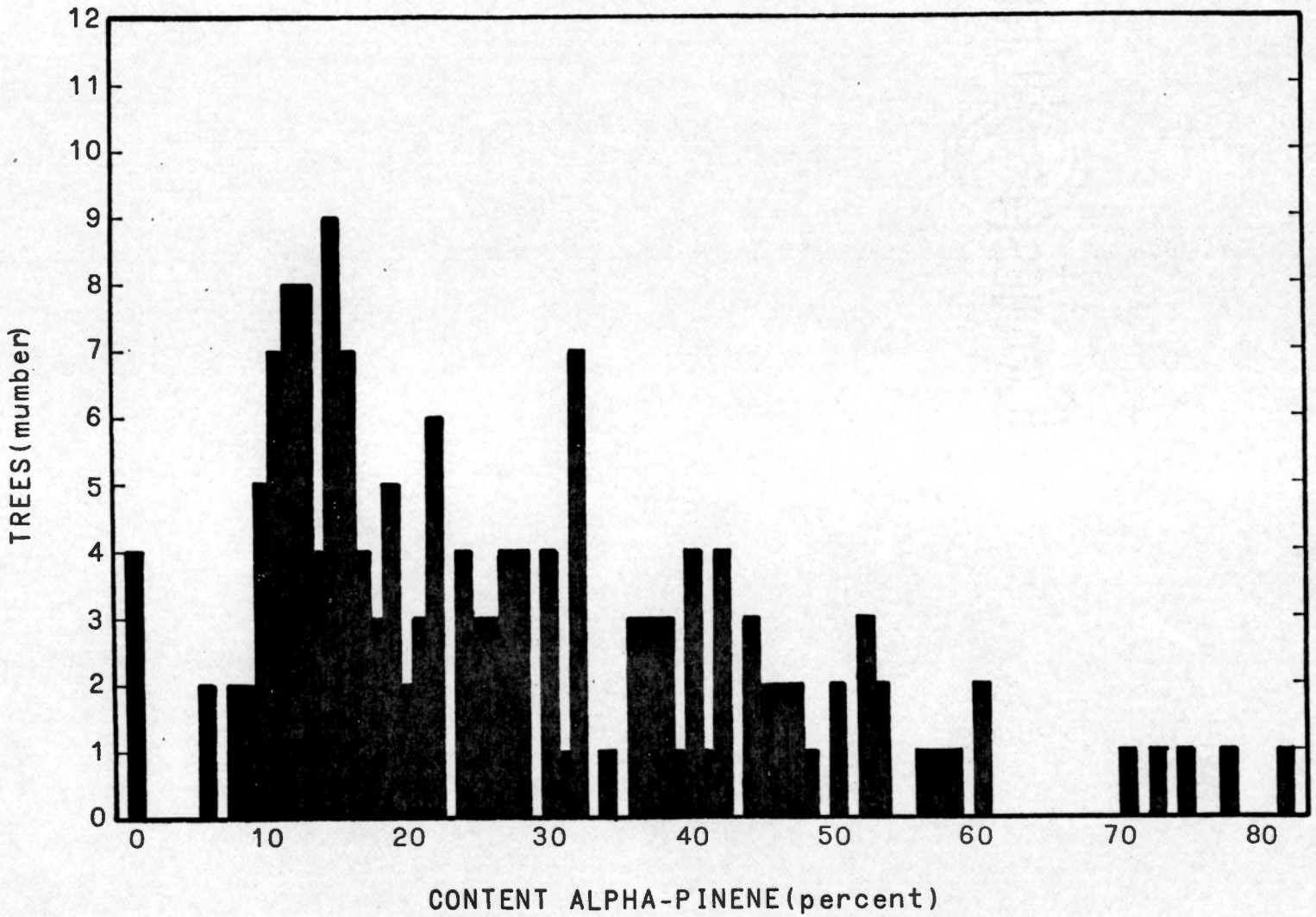


Figure A-6. Frequency Distribution for the Percentage Content of Alpha-pinene in the Cortex Oleoresin of Trees at Ames and the Highland Rim.

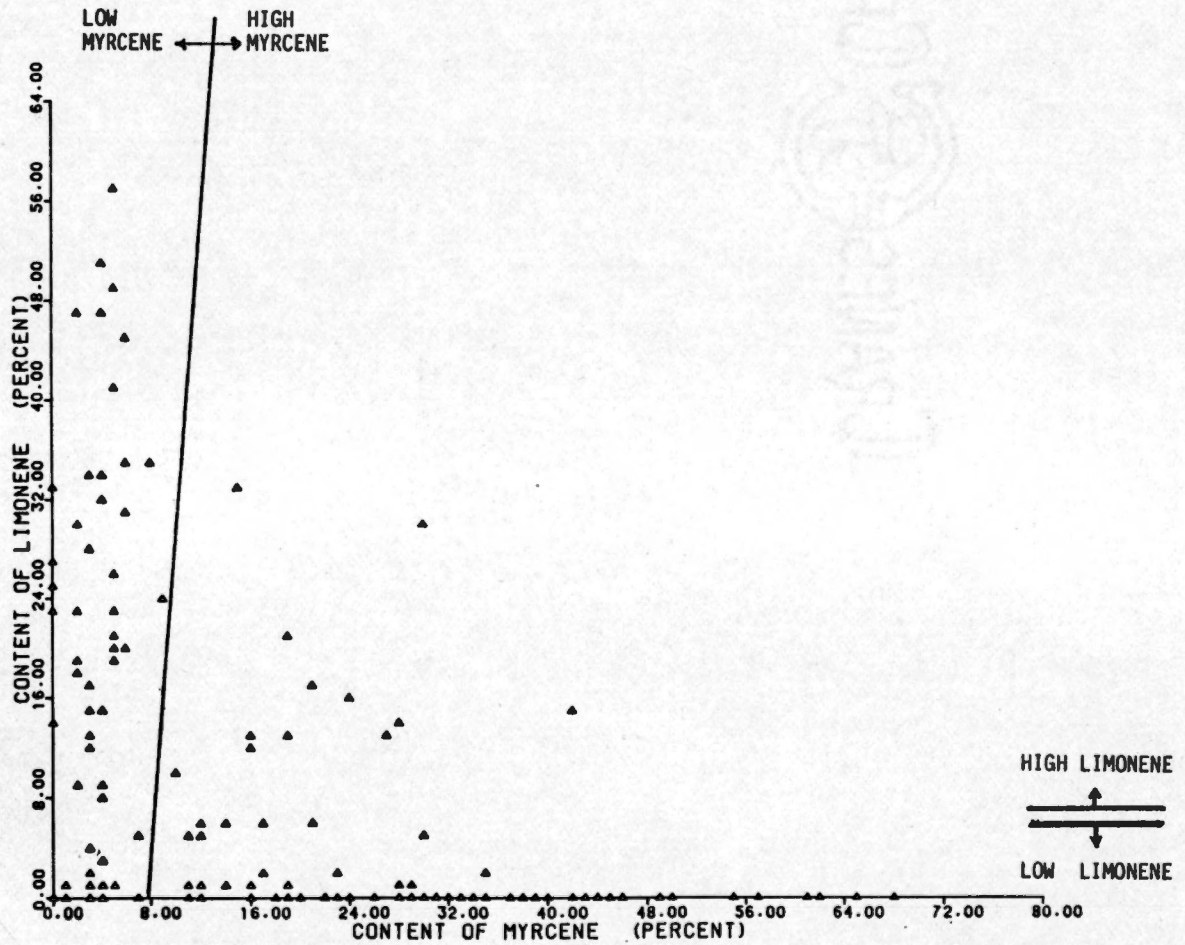


Figure A-7. Scatter Diagram of the Percentage Contents of Limonene over Myrcene.

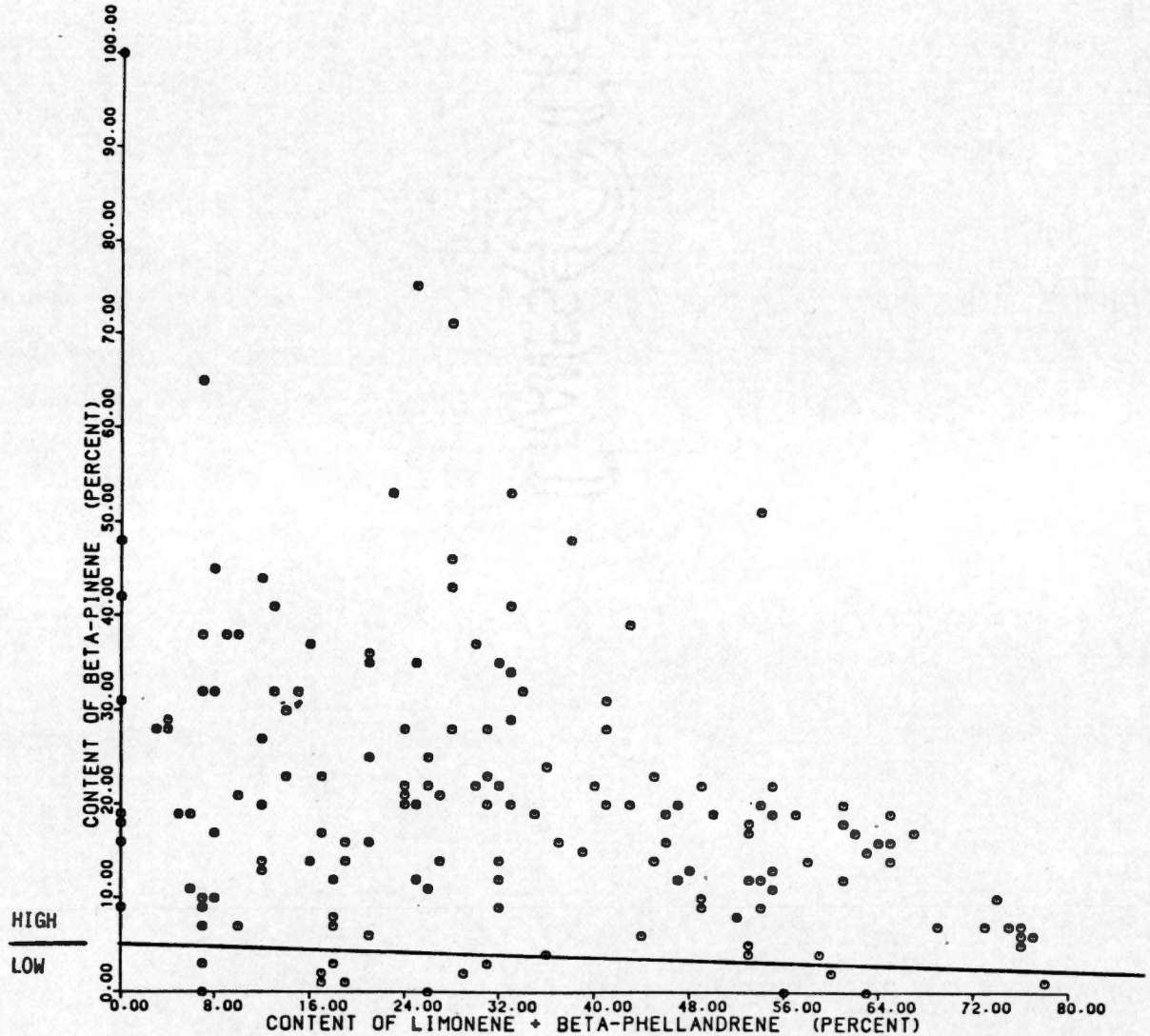


Figure A-8. Scatter Diagram of the Percentage Contents of Beta-pinene over Limonene + Beta-phellandrene.

VITA

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