To the Graduate Council:

I am submitting herewith a dissertation written by George Francis Brown, Jr., entitled "Estimates of Genetic Gain and Selection Strategy for Virginia Pine Christmas Tree Characteristics." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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Edward R. Buckner, Major Professor

We have read this dissertation and recommend its acceptance:

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Vice Provost
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ESTIMATES OF GENETIC GAIN AND SELECTION STRATEGY FOR VIRGINIA PINE CHRISTMAS TREE CHARACTERISTICS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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George Francis Brown, Jr.

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ABSTRACT

Third-year data from half-sib progeny tests of Virginia pine located in north Alabama and central Tennessee were evaluated to determine the genetic and environmental sources of variation for characteristics potentially important to the production of quality Christmas trees. Each progeny test was composed of 20 families from the Kimberly-Clark Corporation seed orchard and 36 families from a previously established plantation at the Highland Rim Forestry Field Station, Tennessee.

No major differences were found between the two seed sources and the source x location and family-within-source x location interaction terms were not significant. Families from either source may be utilized as seed sources for either location. Estimates of heritabilities for each location are given. Based on these estimates and the relative contribution of each characteristic to the overall quality of a Christmas tree, height, branches per whorl, color, crook and rating were selected to evaluate trees to be included in a breeding program. Genetic gains are presented, resulting in an increase in height of 12 cm at age three and a 5 percent reduction in the number of cull trees.

To determine if any characteristics pertaining to seed, seedlings, first-year field performance or second-year field performance can be used to predict third-year performance, eight seeds were selected from each of 57 half-sib families of Virginia pine. Each seed was measured, planted and subsequently remeasured as a seedling. The seedlings were field-planted and measured annually. The two test planntations utilized to determine heritabilities were also measured annually. The linear relationship of each set of measurements to the next set was determined by use of canonical correlations.

Seed, seedling and first-year field measurements were not accurate predictors of third-year field performance. Second-year measurements had canonical correlations ranging from 0.85 to 0.90 with third-year measurements and explained between 58 and 71 percent of the variance in the third-year measurements. Only the first canonical variate explained more than 2 percent of the third-year variation. The primary components of the first canonical variate were height and diameter which can be used to cull up to 66 percent of the trees without reducing the number of select trees.

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CHAPTER I

INTRODUCTION

Historically, the Christmas tree industry was primarily located in northern states and in Canada. The vast majority of trees sold in the South were imported. During the seventies, several studies established that southern markets could support a southern Christmas tree industry (Murray, 1976; Whitfield, 1972). Parallel to these studies the grower interest in Christmas tree production increased and between 1960 and 1980 several state growers' associations were organized, signifying the establishment of the industry in the South. The primary species being utilized throughout the South is the Virginia pine (Pinus virginiana Mill.) (Davis et al., 1981; and Hu and Main, 1980). Current figures indicate that at least 10 million Virginia pines were planted across the South in the 1982-83 planting season (Murray, 1983). It is evident that Virginia pine has been accepted by consumers and growers alike and has become the foundation species for the industry.

Prior to this interest, the Virginia pine was not considered a commercially important species by the forest industries; therefore, little silvicultural or genetic information is available (Genys, 1966). Most of the planting stock available to growers is obtained from wild trees or from a limited number of orchard trees originally selected for pulpwood characteristics. Development of a genetically improved line of Virginia pine specifically selected for Christmas tree characteristics should increase the quality and decrease production costs. For example, improvement and selection efforts could result in improved needle color, shorter rotation cycles, and a greater proportion of merchantable trees per acre.

The first step in an improvement program based on tree selection is to determine if genetic gain is possible on the characteristics selected. This involves measuring two factors, the heritability of each characteristic selected and the amount of variation in a population. If there is no variation, or if it is not strongly controlled by genetics, then genetic improvement is improbable. The first objective of this study was to determine the amounts of genetic gain that could be realized on several characteristics of Virginia pine that are important to their quality as Christmas trees.

One goal of an efficient tree improvement program is to maximize genetic gains and to minimize the time and number of progenies in a genetic planting. Forest tree improvement is severely limited by two factors--time and numbers. It may take 20 to 30 years for a pulpwood rotation for any of the southern pines. It also takes a large acreage to grow the numbers of trees needed to provide a selection base. Both of these factors make conventional tree improvement work very expensive. Early selection, or selection before the end of the rotation, can only be accomplished if the expression of a trait at an earlier age can be used to reliably predict the trait at a given rotation age. Juvenile characteristics have generally not been shown to reliably predict mature characteristics. A general rule followed in many tree improvement programs is to wait until at least half of the rotation age before predicting characteristics at rotation age.

The improvement of Virginia pine Christmas trees differs from a conventional tree improvement program in several ways. Rotation age is generally only five or six years. Mature parent trees cannot be selected unless it is known how their progeny will perform. Virginia pine often begin to produce flowers by age four, which allows the selection of superior crop trees directly from a progeny test. There are also differences in the economic aspects. An acre of properly managed Christmas trees has a much higher economic value than an acre of pine plantation for other forest crops. However, it also requires a higher investment to produce the Christmas tree.

A conventional tree improvement program requires several acres in order to grow a few thousand trees. Virginia pine Christmas trees require up to four years of intensive cultural practices. Most tree improvement programs are considered to be successful if 10 to 20 unrelated "select" trees for a future breeding program are identified. If desirable trees could be selected at an earlier age or undesirable trees screened and eliminated early in the test, then potential gains could accrue more rapidly and program costs reduced. Therefore, the second objective of this study was to determine if the canonical correlations statistical technique would provide an efficient selection strategy for the evaluation of relevant characteristics at an earlier age.

Objectives

The objectives of this study were:

1. To determine the amounts of genetic gain that could be realized on several characteristics of Virginia pine that are important to their quality as Christmas trees.

2. To determine if the canonical correlations statistical technique would provide an efficient selection strategy.

CHAPTER II

REVIEW OF LITERATURE

Ecology of the Species

The native range of Virginia pine is from the southern tip of New York to the northern third of Alabama in a band approximately 400 miles wide (Dorman, 1976). Throughout its range, Virginia pine occurs as a pioneer species, being the first pine species to colonize severely disturbed sites. It can grow on a wide variety of sites but does best on clay, loam and sandy-loam soils (Fowells, 1965). It requires a moderate to well-drained soil and does not do well on wet sites.

Virginia pine is intolerant to competition and requires full sunlight. On better sites it is usually quickly replaced by hardwoods (Fowells, 1965). Large Virginia pines are usually restricted to the poorest sites where hardwood invasion is slow. Because its growth and form on these sites is relatively poor, Virginia pine has earned a reputation as a scrub species best adapted to the most impoverished sites.

However, Virginia pine surviving where other trees cannot, does not mean that it will not grow better on good sites as southern Christmas tree growers have been demonstrating for the past several years. Research has shown that certain soil fertility levels can affect tree growth (Brown, 1983). Most of the Christmas tree plantations now being established in the South are on lands that were previously used for agricultural crops. These are commonly productive sites that are being converted to this new crop and not the eroded "old fields" earlier described as the typical Virginia pine site. Recommended practices for the production of Virginia pine Christmas trees include the selection of well-drained sites, cultivation of the soil prior to planting, fertilization if needed, and the control of competition by use of herbicides and mowing (Holemo and Brown, 1979).

Genetic Improvement

The general practice and procedures for tree improvement have been well developed in such texts as Wright's "Forest Genetics" (1976) and the FAO-North Carolina State Forest Tree Improvement Training Centre "Lecture Notes" (1969). More specifically, work with the southern pines is comprehensively covered in Dorman's "Genetics and Breeding of Southern Pines" (1976). It has been accepted that properly conducted tree improvement programs can yield significant gains at reasonable costs. Use of seed from current first generation orchards are expected to increase wood yields 10 to 20 percent. Preliminary results indicate that even greater gains will result from second and third generation orchards (Dorman, 1976).

One of the primary steps for beginning a tree improvement program involves selection of the best seed source (based on provenance tests). Genys (1966) established a Virginia pine provenance test in 1955 that included 17 provenances outplanted in Pennsylvania, Maryland, and Tennessee. Trees from the southern sources had much higher mortality on the northern planting locations. The Atlantic coastal plain and

Tennessee sources provided better growth on the Maryland and Tennessee locations after seven years. After 15 years (Genys et al., 1974), the northern sources were growing below the average rate at the southern locations. At the northern sites the southern sources grew at average or above average rates.

In a more recent study 15 seed sources of Virginia pine grown in Lee County, Alabama, exhibited significant differences for all measured traits except limb diameter. (Warlick, Duba and Goggans, 1985) The five most northern sources consistently performed poorest with respect to growth-related traits such as height, diameter and internodal length. This is consistent with earlier findings from provenance studies. Northern sources were adapted to shorter growing seasons and usually grew less than comparable southern sources. Southern sources usually suffered higher mortality rates when planted north of their native sites because they were not adapted to the environmental conditions. Research has demonstrated that seed for Virginia pine Christmas trees grown in Alabama and Tennessee should come from the southern half of its range.

The methods for conducting progeny tests to determine basic genetic information was comprehensively presented by Wright (1976). From such progeny tests the total amount of variation of a trait can be estimated along with the amount of variation due to families. These estimates are then used to calculate the portion of the total genetic variance (the heritability), the difference between the average and selected trees (the selection differential), and finally the genetic gain, which is the selection differential multiplied by the heritability.

In open-pollinated progeny tests the family component is interpreted as being one-quarter of the additive genetic variance. Therefore the heritability can be calculated by:

$$h^2_a = \frac{4\sigma^2_a}{\sigma^2_a + \sigma^2_e + \sigma^2_w},$$

where

h^2_a = narrow sense heritability (additive genetic variance only),

σ^2_a = additive genetic variance,

σ^2_e = environmental variance among plots in replications, and

σ^2_w = environmental variance among trees in plots.

A heritability estimate is not an exact figure. It is a relative estimate based on many varying factors, such as location, site conditions, cultural practices employed during the experiment, competitive effects of neighboring progeny and age of the test material. As the experimental conditions become more similar to the production conditions, the heritability estimates become more accurate. A more detailed discussion of heritability estimates in forest tree breeding was presented by Rink (1974).

The following progeny test results should be viewed with the above condition in mind. The results should vary as the test conditions vary.

Heritabilities of Growth Characteristics

In a test of 13 stands of Virginia pine planted on four sites in Tennessee, one in Kentucky and one in Alabama, Evans and Thor (1971) reported heritability estimates for second-year heights varied from location to location from 0.16 to 0.48 and for diameters from 0.08 to 0.41. Using a diallel analysis, Kundt (1972) reported height heritability estimates of juvenile Virginia pine to be 0.09, 0.14 and 0.11 for age 2, 7 and 10 months respectively. Meier and Goggins (1977), using one of the planting locations established by Evans, reported heritabilities of 0.50 for first-year heights, 0.49 for second-year heights, 0.29 for fifth-year heights, and 0.59 for eighth-year heights. Meier and Goggins also reported a heritability estimate of 0.33 for diameter after the eighth year.

In another analysis of the progeny tests established in Tennessee, Kentucky and Alabama, Rink (1974) reported that fifth-year heritability estimates of height growth varied from 0.13 to 0.34 with as mean of 0.26. For diameter, the estimates varied from 0.09 to 0.27 with a mean of 0.16. The fifth-year estimates appear to be increasing in uniformity over time. Rink also reported that neither of the two levels of genotype by environment interactions (location x stand and location x family within-stand) accounted for substantial amounts of phenotypic variance although the main effects were statistically significant. In all six locations, the single largest variance component was the within-plot component, which accounted for from 50 to 90 percent of the total variation.

The only study of the genetics of Virginia pine for Christmas tree production was conducted by Warlick, Duba and Goggans (1985). A half-sib progeny test of 167 families from 15 seed sources was evaluated after three years for height, internodal distance, number of branches per node, ground line diameter, crown width, needle length, limb diameter, limb angle and taper. Seed source and family means were found to be significantly different for all characteristics except limb diameter. Heritability estimates for height and diameter were 0.16 and 0.13, respectively. The single largest source of variation observed by Warlick was also the within-plot component. As demonstrated in the above cited studies, initial improvement in Virginia pine can be made by the selection of appropriate seed sources. The variation among half-sib families also suggests that further improvement can be made by family and individual tree selection.

Heritabilities of Crown Characteristics

Silen and Wilson (1977) discovered while rating Douglas-fir Christmas trees that the fastest growing families may not be the best for Christmas tree production if they possess undesirable crown characteristics. Virginia pine is known for its branchiness and poor natural pruning ability which causes excessively knotty wood rendering it unsuitable for lumber (Slocum and Miller, 1953) and undesirable for pulpwood (Curran, 1938). The same characteristics that make Virginia pine an undesirable lumber or pulpwood species make it a desirable Christmas tree species.

Most branching characteristics have been found to be moderately to strongly controlled by genetics in most species (Barber, 1964; Strickland and Goddard, 1965; and Trousdell et al., 1963). Evans (1971) and Rink (1974) have reported heritabilities for branch diameter and branch length to be highly variable based on differences from site to site and year to year from a minimum of 0.05 to a maximum of 0.47. In a comparison of progeny from well pruned and poorly pruned Virginia pine trees, the following heritabilities were reported: branch angle h^2 = 0.75, branch diameter h^2 = 0.29, branch length h_2 = 0.42, total number of branches h^2 = 0.21, and number of nodes h^2 = 0.32 (Bailey et al., 1974). Kundt (1972) obtained a heritability of 0.21 for the number of branch whorls on 10-month-old Virginia pine seedlings.

The most relevant research to date on crown characteristics of Virginia pine Christmas trees was conducted by Warlick, Duba and Goggans (1985). Their heritability estimates were as follows: crown width h^2 = 0.18, taper h^2 = 0.27, internodal distance h^2 = 0.14, limb angle h^2 = 0.25, number of branches per node h^2 = 0.17, and limb diameter h^2 = 0.16. They also reported high correlations among several of the measured characteristics. For example, height was positively correlated with internodal distance (r^2 = 0.52), number of branches per node (r^2 = 0.23) and crown width (r^2 = 0.83). A taller tree tended to have a thinner crown due to larger internodal distances. However, this was partially offset by more branches per node. Their conclusion was that genetic improvement of Virginia pine Christmas trees could be realized by family and individual tree selection.

Because of the high amount of variation exhibited by Virginia pine and the moderate heritability estimates presented above, reasonable genetic gains can be expected from a "typical" tree improvement program in which half-sib seed are collected from numerous parent trees, seedlings are grown under uniform conditions and then outplanted in a replicated progeny test. The results from such a test can then be used to calculate heritabilities and predict potential genetic gains.

Early Selection

The first level of selection could be on the seed prior to planting. Korstian (1927) and McComb (1934) have demonstrated that acorn weight is positively correlated with germination, survival and seedling growth of the oaks. Hough (1952) demonstrated that heavier seed produced significantly heavier 2-0 red pine seedlings. Langdon (1958) and Shoulders (1961) have reported similar results with slash pine. In loblolly pine, seedlings from large and medium seeds were about the same size while seedlings from small seed were smaller (Brown and Goddard, 1959). Wycoff (1962) reported that although there was no difference in the germination of large and small white pine seed, seedlings from small seeds did not start to grow as rapidly as seedlings from large seeds which resulted in smaller seedlings. Burgar (1964) found that seed size did not affect total germination or first year's survival rate in white spruce. However, the seed size did have a highly significant effect on the first and second-years' seedling height and weight. Lavender (1958) reported opposite results for Douglas-fir; seed size did not affect seedling size but did affect survival of two-year-old seedlings.

Using 271 open-pollinated families of ponderosa pine, Wang and Patee (1974) reported highly significant correlations of seed length, seed width, seed weight and germination capacity with the heights of one and two-year seedlings. Correlations of 0.55 and 0.38 were obtained for seed weight with first and second-year heights. Germination capacity gave correlations of 0.41 and 0.51 with these two height measurements. A correlation of 0.50 was obtained between first and second-year seedling heights. Seed size and germination capacity were not found to be correlated. Mann (1979) failed to show any benefits from sizing seed of slash, loblolly, shortleaf and Virginia pines. From eight seed lots (two for each species), four significant correlations were found between seed weight and number of cotyledons. However, cotyledon number and height growth were not significantly related except for one of the seed lots of Virginia pine in which the correlation between the number of cotyledons and 120-day height was -0.34. No explanation for this was offered. Seed weight did not appear to be strongly related to seedling growth. In a comparison of large and medium seeds, and average and select seedlings of loblolly pine, Sluder (1979) demonstrated that both the larger seed and select seedlings were tallest at age 3. However, by age 15 the trees from the two large seed treatments were significantly shorter. Seed size had no effect on survival while the select seedlings had higher survival and growth through age 15.

The above studies were performed on batches of seed, not by family or by individual seeds. Hellum (1976) weighed individual seeds from 9 half-sib families of white spruce and found that the seed weight within a family is distinct and does not span the full range for all 9 families tested. In fact, if the heaviest 5 percent of the seed was selected, only 22 percent of the families would be represented. It can be argued that sampling for seed weight is more of a genotype sampling than an indicator of seed quality. Hellum also reported that seed weight varies greatly from year to year for the same parent tree. A more complete discussion on the relationship of seed and seedling size has been presented by Righter (1945). He came to the conclusion that seed and seedling size are controlled more by the environment than by heredity and cannot therefore be used as indicators of inherent vigor. Several arguments in support of this conclusion were presented. One argument pertains to the seed coat. The seed coat contributes a relatively large percentage of the total seed weight, it varies proportionately to the weight of the seed and it does not contribute anything to inherent vigor of the seedling. However, the seed coats of Virginia pine contribute a smaller percentage to the total seed weight than many other pines (Mann, 1979).

Righter (1945) also presents much evidence to support the idea that seed weight is primarily controlled by the environment and not genetics. For example, seeds from large cones are heavier than those from small cones, even when both cones are from the same tree. Also, seedlings produced from small seed of a superior cross are more vigorous than seedlings from large seeds of a poor cross. He also demonstrated a positive correlation between seed weight and seedling size, but for the above reasons it was justifiably concluded that selection based on seed weight is not a sound nursery practice. Selection within progenies according to either seed size or seedling size would have no adverse genetic consequences. Therefore, it is clearly justifiable to obtain cultural benefits by culling the smaller seeds.

If the first level of selection is on seed, then the second potential level would be at the seedling stage prior to planting. In addition to Sluder's work (1979), Zobel, Goodard and Cech (1957) and Zarger (1965) have shown that "super" seedlings selected in the nursery bed maintained some of their superiority up to 10 years in the field. Zobel reported that "super" loblolly pine seedlings maintained their height superiority in 90 percent of the comparisons made after four years in the field. Zarger reported similar but lower results working with loblolly, shortleaf, and Eastern white pines. Working with either slash or loblolly pine, Foulger (1960), Barber and von Haverbeke (1961), Bengtson (1963), Hunt (1967), and Hatchell et al. (1972) have reported that selected seedlings were between 14 and 45 percent taller than their controls from 4 to 10 years after planting. The above studies were completed to determine if nursery selection was a feasible means of selecting superior genotypes. They were not designed nor did they report any actual relationship between seedling characteristics and similar characteristics at a later age.

One of the strongest arguments against nursery selection is that much of the variation in seedling size is due to nongenetic factors, such as seed quality (as previously discussed) and environmental factors. Another concern is the reliability of the relationship between juvenile and mature characteristics. As the tree grows there may be a shift in the degree to which a set of genes affects a characteristic. A more in-depth discussion of juvenile-mature relationships has been presented by Webb (1963).

The characteristic which has received the most attention has been height growth. Webb (1963) presented a summary of correlations ranging from .48 to .85 between different heights at 2 to 30 years on several different species. These correlations were not strong enough by themselves to warrant their exclusive use in the selection of superior genotypes. Webb concluded that the "true value" of juvenile performance evaluation may be for the elimination of progenies or races showing undesirable traits that are known to be genetically controlled and can be recognized at an early age.

Height growth is only one of several characteristics that affect seedling quality for Christmas trees. Commercial nurseries commonly screen seedlings by root collar diameter. The diameter of the seedling has been accepted as an important factor, especially when used together with seedling height.

The final selection of a superior tree is never based on a single characteristic, such as height or diameter. Superior trees are generally those that exhibit the best combination of a group of desired characteristics. As opposed to the methodologies used in the studies presented above, it would seem logical that the evaluation of juvenile material should also be performed on multiple characteristics. It is unlikely that any one juvenile characteristic will be so strongly correlated with future performance of the several characteristics that it can be used exclusively for selection or screening purposes. There may be several characteristics of the seeds and seedlings that can be related to characteristics of importance in Christmas tree production. These relationships need to be identified in order to select from desirable or eliminate undesirable seedlings. The correlation of multiple characteristics with another set of characteristics is called canonical correlation analysis.

Canonical Correlation Analysis

Canonical correlation analysis, developed by Hotelling (1936), can most easily be explained by first looking at two other correlation techniques that are more familiar to most researchers. The simplest correlation is the product-moment correlation which measures the relationship between two variables. If a linear combination of a set of variables is formed and its relationship to one variable measured, then it is called a multiple regression analysis (Clark, 1975). Multiple regression analysis generally takes the form of a "y" dependent variable with several "x" independent variables. The beta or "b" coefficients determine the linear relationship of the x's to y in the equation $y = b_0 + b_1x_1 + b_2x_2 + \ldots + b_nx_n$. If there are multiple y variables and the relationships between the two sets of variables is measured, then a canonical correlation analysis has been performed. In canonical correlation analysis, the relationship of a linear combination of one set of variables (x's) with another set of variables (y's) is determined. The canonical correlation analysis produces two sets of coefficients that maximize the correlation between the two sets of variables. It does not maximize the amount of variance of one data set accounted for by the other.

Because canonical correlation analysis determines how one set of variables is related to another, a few of its uses could be to relate a set of variables at one time to the same variables at another time, symptom states with disease states, environmental measures with biological measures or easy to obtain data with hard to obtain data. The usage and popularity of this tool has recently been steadily increasing in the biological sciences.

Smith (1980) has proposed that canonical correlation analysis holds "some promise for wildlife habitat studies, and its use should increase as researchers become more familiar with it." She presented a complete review of the use of canonical correlation analysis for wildlife habitat studies that is pertinent to other fields of biology. According to Smith, there are 4 statistical assumptions which apply to canonical correlation analysis. First, "the covariance matrix must be of full rank, i.e., there must be more samples than number of variables in both data sets combined." In reality, the sample size should be at least 3 to 4 times larger than the total number of variables. The second assumption is "no singularities can exist within the data matrices, i.e., all rows (or columns) must be independent." A matrix becomes singular if one of the rows (or columns) is a linear combination of one or more of the other rows (or columns). For example, if volume is a linear function of diameter and height, the use of all three variables would cause a matrix to become singular. The third assumption is that a multivariate normal distribution exists. The final assumption is that there are linear relationships among variables.

A major problem with the interpretation of results from a canonical correlation analysis is that the R^2 value measures the variance shared by the canonical variates and not the original data sets. In order to determine the amount of variance in one set of original variables that is explained by the variate of the other data set, Stewart and Love (1968) developed a measure called redundancy. According to Young (1981), the most useful redundancy measure is that of the response set given the predictor set; that is the proportion of the variance of the response set variables that is explained by the canonical correlation of the predictor set (Rdy). The sum of the Rdy value for each canonical correlation gives the total variance of the response set explained by the successive canonical correlations of the predictor set. A more complete discussion of canonical correlations is presented by Clark (1975), Smith (1980) and Young (1981).

Canonical correlation has been found to be more sensitive and realistic than more conventional methods of analysis such as regression (White and Sinha, 1980; and Young, 1981). White and Sinha were able to relate wheat quality variables (fat acidity values, CO_2%, O_2%, dust weight, moisture %, germ and endosperm damage, and seed germination) with the level of activity of 6 different insects and one fungus. Young combined two sets of data, and obtained similar relationships between 6 plant growth responses and 8 environmental factors to those reported by the original researchers "using more laborious methods of conventional analysis." Not only did the use of canonical correlations allow Young to more efficiently detect known relationships, it "also proved to be sufficiently sensitive to detect hitherto undetected patterns of variation."

CHAPTER III

HERITABILITY AND EXPECTED GAINS OF VIRGINIA PINE CHRISTMAS TREE CHARACTERISTICS

Introduction

In the 1960s and 1970s, Christmas tree growers from several southern states organized growers' associations, signifying the establishment of the industry in the South. The primary species being utilized was Virginia pine (*Pinus virginiana*) (Davis et al., 1981; Hu and Main, 1980). Over 10 million Virginia pines were planted across the South in the 1982-83 planting season (Murray, 1983). It is evident that the Virginia pine has been accepted by consumers and growers and has become the foundation species for the Christmas tree industry in the South.

The key to a successful Christmas tree operation is the production of high-quality trees. The quality of the trees is largely dependent upon the cultural practices used by the grower and the genetic potential of the tree. While appropriate cultural practices were established early, little has been done to improve the genetic component. Seedlings being used to establish Christmas tree plantations are grown from seed collected from wild stands or from parents in seed orchards originally selected for pulpwood characteristics. To compound the problem, a large portion of the seedlings (possibly between 30 and 50 percent) planted throughout the South have originated from one orchard comprised of eight clones, all selected from one county in Alabama.

Estimates of heritabilities are necessary before an effective breeding program can be initiated. They also are used to predict the amount of genetic gain that can be anticipated from the improvement program. The purpose of this study is to give estimates of heritabilities ("narrow sense") and the potential genetic gains they indicate for several characteristics of importance in Virginia pine Christmas tree production.

Objectives

The specific objectives of this study are:

1. To determine if there is a difference between the Kimberly-Clark Corporation seed source and the Highland Rim Forestry Field Station seed source for several characteristics important for the production of Virginia pine Christmas trees.

2. To determine if there are interactions between locations (north Alabama and central Tennessee) x seed sources and locations x families-within-source. This will influence the degree to which the same genetic material can be used for the establishment of seed orchards at both locations.

3. To estimate heritabilities and potential genetic gains for the characteristics of height, diameter, branches per whorl, limb angle, internodal distance, needle color, stem straightness and an overall quality rating.

4. To determine which of the above characteristics should be emphasized in future improvement efforts to produce higher quality Virginia pine Christmas trees.

Materials and Methods

One of the primary sources of Virginia pine seed used by Christmas tree growers throughout the South is the Kimberly-Clark Corporation orchard located in Coosa Pines, Alabama. From this orchard, open-pollinated seed was collected from 20 different clones during the fall of 1979. Because this source was from Jefferson County, Alabama, it may not be suitable as a source for more northern plantings, such as in Tennessee. To compare the performance of trees from this source with that of trees from other sources, seed was also collected from 36 open pollinated trees located in an experimental Virginia pine plantation located at the Highland Rim Forestry Field Station, Tennessee (previously described by Thor, 1964 and Rink and Thor, 1976). The plantation was established in 1967 from open-pollinated seed collected from nine stands in Tennessee and four in Kentucky. It was assumed that these 36 half-sib families were representative of Virginia pine from the south-central part of its range.

Seedlings were grown as containerized stock using Spencer-Lemire roottrainer books during the spring and summer of 1980 in a greenhouse at the University of Tennessee, Knoxville. In August they were moved to a cold frame on the campus of Alabama A&M University and allowed to harden-off for the winter.

During February and March of 1981, the seedlings were planted on two test locations. The first plantation was established on the campus of Alabama A&M University (A&M) on a Decatur silt loam soil that had been used for row crops the previous growing season. It was not subsoiled or otherwise site prepared. The second plantation was established on a Dickson silt loam soil at the University of Tennessee Highland Rim Forestry Field Station (HRFS) located six miles south of Tullahoma, Tennessee. This site was an open field which had previously been occupied by a hardwood stand up to 1969. From 1969 to the establishment of this test, the site was burned twice and periodically bush hogged. The site was bush hogged and disked prior to planting to control hardwood sprouts. The A&M location was noticeably more compacted and harder to plant than the Highland Rim location.

At each location, seedlings were outplanted in rows spaced seven feet apart with six feet between trees within each row. Each set of four consecutive trees formed an experimental unit comprised of four samples of one of the 56 families. The experimental units were arranged in a randomized complete block design with eight replications. One border row was planted around each plantation. The plantations were maintained for 3 years following standard practices for the production of Christmas trees (Holemo and Brown, 1979). This included the use of herbicides for weed control in the rows and mowing of the weeds between rows and regular sprayings for control of the Nantucket pine tipmoth. The plantations were not fertilized nor were the trees sheared.

Measurements

Measurements of all traits described below were made at the end of the third growing season (during January and February of 1984), on all surviving trees in both plantations. Total height was measured to the nearest centimeter. The diameter of the trunk was measured (nearest millimeter) 15 cm above the ground line using a caliper.

An estimate of branches per whorl was obtained by averaging the number of branches on the second, third and fourth whorls from the top of the tree. The limb angle was measured using a large protractor placed vertically on the stem for one limb on each of the three whorls used to estimate branches per whorl. Internodal distance was measured (nearest centimeter) between the second and third whorls and the third and fourth whorls.

Needle color was evaluated by classifying the needles into seven classes. To establish the seven classes, needles were sampled from several trees and sorted by color. This resulted in the formation of five distinguishable classes. One additional class was added to each end of the scale to account for extremely dark or light foliage. Munsel color standards were then selected to match each color group. The Munsel color standards that resulted were 7.5 GY 4/4, 6.5 GY 4/4, 5.6 GY 5/6, 2.5 GY 5/6, 2.5 GY 6/6, 2.5 GY 7/8 and 2.5 GY 8/8. Mature needles of the current year were selected from the south side of each tree. The dorsal surface of the needles were carefully compared to the seven color chips and classified on a scale from 1 to 7, with 1 being the lightest and 7 being the darkest.

Stem straightness and overall quality were subjectively measured on each tree, both on a 5 point scale with 3 as the mean. These measurements and the 7 point color scale approximated a normal distribution which permits statistical analysis of the data as if they were continuous variables. Each tree was evaluated for straightness, with 5 being a straight stem. A classification of 4 was given to those trees that were straighter than the "average" Virginia pine, but not as straight as a 5. A rating of 3 was given to average trees, 2 to trees less than average, and finally 1 to the trees with the worst crooks in the main stem. An overall "quality rating" was assigned to each tree using the following guidelines established by growers of Virginia pine Christmas trees: 1, cull trees that would normally be removed by most growers; 2, trees requiring major corrective work; 3, average trees; 4, trees better than average but with at least one noticeable defect; 5, trees with no noticeable defects.

Statistical Analysis

To analyze the variances between locations and reduce the data matrix to save computing time and expenses, an analysis was performed on plot means combining both locations. All effects were assumed to be random except location and sources, which were fixed. The linear model for this analysis was:

$$Y_{ijkl} = \mu + L_i + R(L)_{ij} + S_k + SL_{ki} + F(S)_{kl} + F(S)L_{ikl} + E_{ijkl} ,$$

where:

$Y_{(ijkl)}$ = the individual plot mean,

μ = the overall mean,

L_i = the effect of the ith location,

$R(L)_{ij}$ = the effect of the jth replication within each location,

S_k = the effect of the kth source,

SL_{ki} = the effect of the interaction of source with location,

$F(S)_{kl}$ = the effect of the lth family within each source,

$F(S)L_{ikl}$ = the effect of the within source interaction of location with family, and

E_{ijkl} = the error term resulting from the pooling of the interactions of replications, sources and families-within-source.

The expected mean squares for this model are presented in Table 1. These analyses were performed using the General Linear Models (GLM) procedure of the Statistical Analysis System (SAS).

Separate analyses were performed for each location using individual tree data. These analyses were performed to obtain the variance components needed to calculate narrow-sense heritabilities for each location. Because of the large size of the data matrices, the GLM procedure of SAS could not be used. Instead, the data were analyzed using the Variance Component procedure. The linear model for this analysis was:

$$Y_{ijk} = \mu + R_i + S_j + RS_{ij} + F(S_{kj}) + RF(S)_{ikj} + E_{ijk} ,$$

Table 1. Analysis of Variance and Expected Mean Squares for Combined Analysis of Alabama A&M and Highland Rim Forestry Field Station Based on Family Plot Means

Source of variation	df	Expected mean squares
Location	L-1	$\sigma^2_E+FS\sigma^2_{R(L)}+RFSK^2_L$
Replications (Locations)	(R-1)L	$\sigma^2_E+FS\sigma^2_{R(L)}$
Sources	S-1	$\sigma^2_E+RFLK^2_S$
Locations x sources	(L-1)(S-1)	$\sigma^2_E+RFK^2_{SL}$
Families (sources)	(F-1)S	$\sigma^2_E+R\sigma^2_{LxF(S)}+RL\sigma^2_{F(S)}$
Locations x families (sources)	(L-1)[(F-1)S]	$\sigma^2_E+R\sigma^2_{LxF(S)}$
Error	L[(F-1)(R-1)S +(S-1)(R-1)]	σ^2_E

L = number of locations.

R = number of replications.

S = number of sources.

F = number of families within sources.

σ^2_E = pooled component of variance due to interaction of replications within locations with sources and replications within locations with families within sources.

$\sigma^2_{R(L)}$ = component of variance among replications within locations.

K^2_L = component of variance between locations.

K^2_S = component of variance between sources.

$\sigma^2_{LxF(S)}$ = component of variance due to interaction of families within sources with locations.

$\sigma^2_{F(S)}$ = component of variance among families within sources.

where:

Y_{ijk} = the individual tree observation,

μ = the overall mean,

R_i = the effect of the ith replication,

S_j = the effect of the jth source.

RS_{ij} = the effect of the interaction of replication with source,

$F(S)_{kj}$ = the effect of the kth family within each source,

$RF(S)_{ikj}$ = the effect of the interaction of replication with families-within-source, and

E_{ijk} = the effect of the individual tree within each plot.

The expected mean squares for each location are presented in Table 2.

Results

Combined Location Analysis

The sources of variation, degrees of freedom, mean squares, and levels of significance are presented in Table 3. The measured parameters that are growth dependent (height, diameter and internodal distance) were significantly different (.01 level) at the two locations. Highly significant differences for all measured parameters were found among replications within each location. These differences were due to the sensitivity of the Virginia pine to site differences. Studies currently being evaluated are demonstrating that soil compaction greatly reduces the growth of young Virginia pine trees. An increase of up to

Table 2. Analysis of Variance and Expected Mean Squares for Half-Sib Families at Each Location

Source of variation	df	Expected mean squares
Replications	R-1	$\sigma^2_W + W\sigma^2_{RxF(S)} + WF\sigma^2_{RxS} + WSF\sigma^2_R$
Sources	S-1	$\sigma^2_W + WFRK^2_S$
Replications x sources	(R-1)(S-1)	$\sigma^2_W + W\sigma^2_{RxF(S)} + WF\sigma^2_{RxS}$
Families (sources)	(F-1)S	$\sigma^2_W + W\sigma^2_{RxF(S)} + WR\sigma^2_{F(S)}$
Replications x families (sources)	(R-1)[(F-1)S	$\sigma^2_W + W\sigma^2_{RxF(S)}$
Within plot	(W-1)RFS	$\sigma^2 W$

R = number of replications.

S = number of sources.

F = number of families within sources.

W = number of trees per plot.

σ^2_W = within plot variance component.

$\sigma^2_{RxF(S)}$ = component of variance due to interaction of replications with families within sources.

$\sigma^2_{F(S)}$ = component of variance among families within sources.

σ^2_{RXS} = component of variance due to interaction of replications with sources.

K^2_S = component of variance between sources.

σ^2_R = component of variance among replications.

Table 3. Analysis of Variance for Christmas Tree Characteristics for Combined Locations

Source of variation	df	Mean Squares							
		Height	Diameter	Branches/ whorl	Limb angle	Internodal distance	Color	Crook	Rating
Location	1	553,929.961**	44,163.309**	5.467	1,342.272*	1,151.084**	0.024	8.410	29.072*
Replications (location)	14	8,717.708**	665.743**	1.659**	256.142**	35.338**	0.603**	7.911**	5.451**
Sources	1	798.633	154.250*	2.302**	145.942*	19.397	2.903**	0.095	0.156
Locations x sources	1	2,895.719*	33.002	0.939*	10.153	51.652*	0.897*	0.063	0.005
Families (sources)	55	1,083.738	81.361**	0.390**	51.741**	18.649**	0.615**	1.058**	0.893**
Locations x Families (sources)	51	617.044	41.254	0.198	34.278	8.892	0.200	0.656	0.408
Error	731	482.018	36.133	0.185	27.092	9.457	0.149	0.517	0.387

*Significant at $\alpha = .05$.

**Significant at $\alpha = .01$.

30 percent in height growth has been obtained by mold-board plowing a heavy clay soil very similar to the soil of the A&M test location. The Highland Rim soil is less compacted, allowing greater root growth. The shortest family at the Highland Rim location was taller than the tallest family at the A&M location.

The means for all characteristics for each location are presented in Table 4. The highly significant differences for all characteristics due to the replications within each location is also a reflection of the sensitivity of this particular test within the experimental design.

There was a significant difference between the two seed sources for diameter, branches per whorl, needle color and limb angle, but not for height, crook, rating or internodal distance. Trees originating from the Kimberly-Clark Corporation orchard tended to be slightly larger, had a slightly higher average number of branches per whorl, less acute limb angle and were slightly darker than the trees originating from the Highland Rim Forestry Field Station plantation. These differences were all relatively small in magnitude (Table 4).

There appears to be a relatively small interaction between locations and sources for the characteristics of height, branches per whorl, needle color, and internodal distance. Although this interaction is significant for the above characteristics, it does not account for more than 0.5 percent of the total variation for any of the characteristics. It appears that the Kimberly-Clark source may have slightly greater height growth, branches per whorl and internodal distance on the Highland Rim location, whereas the differences between the sources were much

Table 4. Location by Source Means for All Characteristics

Characteristic	Source	Location: A&M	Location: H.R.F.S.	Source average[1]
Height (cm)	Highland Rim	129.005	176.966	153.773a
	Kimberly-Clark	127.076	183.345	155.485a
	Location average[1]	128.302b	179.224a	
Diameter (mm)	Highland Rim	30.156	44.182	37.399b
	Kimberly-Clark	30.626	45.662	38.217a
	Location average[1]	30.327b	44.705a	
Branches/ whorl (number)	Highland Rim	3.552	3.662	3.609b
	Kimberly-Clark	3.586	3.837	3.713a
	Location average[1]	3.564a	3.724a	
Limb angle (degrees from stem)	Highland Rim	63.643	60.936	62.245b
	Kimberly-Clark	64.227	62.104	63.155a
	Location average[1]	63.856a	61.350b	
Internodal distance (cm)	Highland Rim	15.798	17.743	16.803a
	Kimberly-Clark	15.581	18.584	17.097a
	Location average[1]	15.719b	18.041a	

Table 4 (continued)

Characteristic	Source	Location: A&M	Location: H.R.F.S.	Source average[1]
Color	Highland Rim	1.723	1.782	1.753b
(7-point	Kimberly-Clark	1.912	1.841	1.876a
Munsell scale)	Location average[1]	1.792a	1.803a	
Crook[2]	Highland Rim	3.297	3.105	3.197a
(5-point	Kimberly-Clark	3.331	3.122	3.225
scale)	Location average[1]	3.309a	3.111a	
	Highland Rim	3.080	2.703	2.885
Rating[3]	Kimberly-Clark	3.099	2.746	2.921a
(5-point	Location average[1]	3.087a	2.718b	
scale)				

[1]Means for each location or each source followed by the same letter do not differ at the 0.05 level of significance according to the Duncan's Multiple Range Test.

[2]The relative amount of crook in the main stem was evaluated on a 5-point scale with 5 being the straight stem.

[3]The overall quality "rating" was evaluated on a 5-point scale with 5 being the best "rating" assigned.

less at the A&M location. Needle color, in contrast, had greater differences observed at the A&M location.

The effect of families-within-source was highly significant for all characteristics. Of greater importance in this analysis is that there were no significant interactions between families and locations.

Individual Location Analysis

The sources of variation, degrees of freedom, mean squares, and levels of significance for each location are presented in Tables 5 and 6. There are two results that were the same for most characteristics. First, the differences among replications and the sources of variation involving the interactions with replications tend to be significant, particularly at the Highland Rim location. This is a reflection of the sensitivity of Virginia pine to site differences and because the first replication at the Highland Rim location was located in a corner bordered on two sides by paved roads. Competition in this replication was largely from various grasses whereas in the other replications competition was from a mixture of woody sprouts, broadleaf weeds and a few grasses. The second general result was that variation among families-within-source was significant for all characteristics except limb angle at the A&M location. The results for each characteristic are as follows:

Height: Height growth differences were not significant between the two seed sources at either location. The height differences among families-within-source was highly significant at the A&M location and significant at the Highland Rim location. The interaction between

Table 5. Analysis of Variance for Christmas Tree Characteristics at Alabama A&M University

Source of variation	df	Mean Squares							
		Height	Diameter	Branches/ whorl	Limb angle	Internodal Distance	Color	Crook	Rating
Replications	7	2,293.498	186.261	4.889*	307.580*	27.365	1.100	14.516**	10.427**
Sources	1	15.876	210.560	0.568	78.050	0.552	10.436**	0.143	0.172
Replications x sources	7	966.933*	78.054	0.990*	51.742	8.736	0.499	0.726	0.948
Families (sources)	52	2,169.918**	133.480**	0.857**	68.362**	34.953**	1.224**	2.641*	2.125**
Replications x families (sources)	349	916.856**	75.293**	0.467	58.075	17.663	0.425**	1.661**	1.204*
Within plot	778	637.124	50.557	0.376	50.672	13.699	0.285	1.165	0.919

*Significant at $\alpha = .05$.

**Significant at $\alpha = .01$.

Table 6. Analysis of Variance for Christmas Tree Characteristics at Highland Rim Forestry Field Station

Source of variation	df	Mean Squares							
		Height	Diameter	Branches/ whorl	Limb angle	Internodal Distance	Color	Crook	Rating
Replications	7	49,149.588**	3,734.800**	4.882**	1,197.472*	127.826	2.827*	34.296**	24.297**
Sources	1	9,939.481	513.334	11.067**	426.878	236.283	0.999	0.015	0.135
Replications x sources	7	2,363.951	130.856	0.249	248.985**	65.322	0.526	2.868*	2.760*
Families (sources)	54	2,709.667*	198.717**	0.852*	179.293**	44.607*	1.317**	2.506**	1.756**
Replications x families (sources)	368	1,695.770**	116.038**	0.528	82.320	33.532	0.427**	1.131	0.929
Within plot	1,020	812.394	58.608	0.381	71.749	24.907	0.278	0.993	0.748

*Significant at $\alpha = .05$.

**Significant at $\alpha = .01$.

families-within-source and replications was highly significant at both locations. This suggests that families that do best on one micro-site may not be the best performer on other micro-sites. However, individual trees cannot be bred for each and every micro-site, nor can fields of trees be managed according to each micro-site within the field. Had the replications been identical, which is improbable, then this source of variation would represent a true error term for the families-within-source in that it is a measure of the amount of variation on repeated measures of the same family. Since Virginia pine is characterized by a large amount of tree to tree variation, it is not unreasonable to assume that a large portion of the interaction term between families-within-source and replications is due to the inherent variation observed among Virginia pine trees. For these reasons, it was assumed that this interaction term when significant, is the most appropriate error term for families-within-source. In those statistical tests where this interaction was not significant, it was pooled with the within-plot term prior to testing the families-within-source.

Diameter: The analysis of variance for diameter was very similar to that of height. Both are growth factors that are controlled by the interaction of site and the genetic makeup of the different families-within-source.

Branches per whorl: The trees from the Kimberly-Clark seed orchard had significantly more branches per whorl at the Highland Rim location but not at the A&M location. There were more branches per whorl for both sources at the Highland Rim location than the A&M location (Table 4), although this difference was not significant. It appears that a better site quality may increase the number of branches per whorl and a poor site may inhibit the expression of any seed source differences. This is supported by the fact that although there was not a significant difference between seed sources at the A&M location, there was a significant interaction between seed sources and replications. There were significant differences among families-within-source at both locations.

Limb angle: Other than for replications, there were no significant differences in limb angle due to any of the sources of variation at the A&M location. There were highly significant differences due to the interaction of replications with sources and due to the families-within-source at the Highland Rim location. However, the significant interaction term only accounted for 1.4 percent of the total variation and may be significant partially because of the sensitivity of the test. Families-within-source accounted for 7.8 percent of the total variation at the Highland Rim location and 5.4 percent at the A&M location. Differences among families, between sources or between locations, although statistically significant, accounted for only a very small percentage of the total variation. These small differences will not likely affect the overall quality of a Christmas tree when compared to the magnitude of the differences of some of the other measured characteristics.

Another factor affecting limb angle became apparent while taking field measurements, but was not analyzed. It appears that there are differences in limb angle due to the location of the limb on the tree. The limb angle generally increases (becomes less acute) from the top of the tree to the bottom.

Internodal distance: Families-within-source was the only significant source of variation in internodal distance at either location.

Color: The effect of seed source on needle color was highly significant at the A&M location, but not significant at the Highland Rim location. The Kimberly-Clark families were darker than the Highland Rim families at the A&M location (Table 4, p. 33). At the Highland Rim location, the Kimberly-Clark families were not as dark as they were at the A&M location, while the Highland Rim families were slightly darker than at the A&M location. These two slight changes resulted in no significant differences between the two sources at the Highland Rim location. The interaction between location and sources may be due to the planting of an extreme southern source (Kimberly-Clark) in a more northern climatic zone. Variation among families-within-source was highly significant at both locations.

Crook: There was a significant interaction between replications and sources at the Highland Rim location but this is not considered to be important because it only accounted for 1.1 percent of the total variation. The families-within-source was significant at the A&M location and highly significant at the Highland Rim location.

Rating: The analysis of the rating scale gave results very similar to those for crook. The only difference was that families-within-source was highly significant at the A&M location for rating while it was only significant for crook. The relationship between crook and rating will be discussed later.

Heritabilities

The variance components obtained in the above analyses can be used to calculate heritabilities (narrow sense) which in turn enable the calculation of expected genetic gains. The estimates of variance components are presented in Tables 7 and 8. The within-plot component was by far the largest source of variation and accounted for between 42 and 61 percent of the total phenotypic variance (Tables 9 and 10). The second largest source of variation in all cases was the component due to the interaction of replications and families-within-source. These two components accounted for between 73 and 90 percent of the total variance for all characteristics. This is another indication of the high amount of inherent variation in Virginia pine.

The estimates of variance components presented in Tables 7 and 8 were used to calculate narrow-sense heritabilities according to the formula:

Table 7. Estimates of Variance Components for Christmas Tree Characteristics at Alabama A&M University

	Estimate of Variance Component							
Variance component	Height	Diameter	Branches/ whorl	Limb angle	Internodal distance	Color	Crook	Rating
Replications	8.911	0.725	0.025	1.723	0.137	0.004	0.094	0.064
Sources	-3.971	0.142	-0.001	0.031	-0.045	0.017	-0.003	-0.003
Replications x sources	-0.009	-0.010	0.007	-0.106	-0.141	0.001	-0.015	-0.004
Families (sources)	55.851	2.534	0.017	0.434	0.767	0.036	0.042	0.041
Replications x families (sources)	99.680	8.780	0.032	2.625	1.406	0.050	0.176	0.101
Within plot	637.123	50.557	0.376	50.672	13.699	0.285	1.165	0.919

Table 8. Estimates of Variance Components for Christmas Tree Characteristics at Highland Rim Forestry Field Station

	Estimate of Variance Component							
Variance component	Height	Diameter	Branches/ whorl	Limb angle	Internodal distance	Color	Crook	Rating
Replications	257.935	19.783	0.026	5.028	0.312	0.013	0.170	0.116
Sources	9.929	0.452	0.016	0.115	0.237	-0.001	-0.006	-0.005
Replications x sources	7.133	0.117	-0.003	1.963	0.370	0.001	0.020	0.022
Families (sources)	36.573	3.012	0.012	3.683	0.399	0.034	0.052	0.031
Replications x families (sources)	269.755	17.424	0.044	3.193	2.606	0.045	0.041	0.054
Within plot	812.394	58.608	0.381	71.749	24.907	0.278	0.993	0.748

Table 9. Percent of Estimated Phenotypic Variance for Christmas Tree Characteristics at Alabama A&M University

Source of variation	Percent of Estimated Phenotypic Variance							
	Height	Diameter	Branches/ whorl	Limb angle	Internodal distance	Color	Crook	Rating
Replications	1.69	1.75	6.32	3.27	1.01	1.70	5.87	5.51
Sources	0.00	0.28	0.10	0.12	0.00	2.30	0.01	0.01
Replications x sources	0.71	0.73	1.28	0.55	0.32	0.77	0.29	0.50
Families (sources)	11.90	9.31	8.22	5.40	9.62	14.03	7.94	8.34
Replications x families (sources)	33.75	35.24	30.12	30.78	32.63	32.74	33.49	31.72
Within plot	51.94	52.68	53.96	59.88	56.41	48.46	52.40	53.91

Table 10. Percent of Estimated Phenotypic Variance for Christmas Tree Characteristics at Highland Rim Forestry Field

Source of variation	Percent of Estimated Phenotypic Variance							
	Height	Diameter	Branches/ whorl	Limb angle	Internodal distance	Color	Crook	Rating
Replications	17.51	18.55	5.03	6.74	2.13	3.67	13.10	12.18
Sources	0.51	0.36	1.63	0.34	0.56	0.19	0.00	0.01
Replications x sources	0.84	0.65	0.26	1.40	1.09	0.68	1.10	1.38
Families (sources)	7.45	7.61	6.77	7.79	5.74	13.19	7.38	6.79
Replications x families (sources)	31.76	30.29	28.59	24.36	29.40	29.12	22.70	24.49
Within plot	41.93	42.53	57.72	59.37	61.07	53.14	55.73	55.14

$$h^2 = \frac{4s^2_{F(S)}}{s^2_{F(S)} + s^2_{RxF(S)} + s^2_{W}} ,$$

These estimates of heritabilities for each characteristic are presented by location in Table 11. The heritabilities for height, branches per whorl and internodal distance were considerably higher at the A&M location than at the Highland Rim location. A higher heritability can be the result of either or both of the following: (1) the denominator of the equation, primarily the component due to the environmental variance, may be smaller, and/or (2) the additive genetic component, families-within-source, is larger.

In this study the relative amount of environmental variance, primarily the within-plot variance component, was less at the Highland Rim location than at the A&M location. This suggests that the better site benefits the poorer trees relatively more than the better trees, resulting in less tree to tree variation within a plot.

The relative amount of variation due to families-within-source was larger for all three characteristics (height, branches per whorl and internodal distance) at the A&M location. Virginia pine is well known for its ability to survive on poor sites. It appears that a poorer site favors the expression of the additive genetic component. The expression of desirable genetic qualities at the family level was greater on a poor site than on a better site, resulting in higher heritability estimates for these characteristics.

Table 11. Estimates of Heritabilities of Three-Year-Old Virginia Pine by Location

Variables	Location		
	A&M	H.R.F.S.	Average
Height	0.282	0.131	0.206
Diameter	0.164	0.152	0.158
Branches/whorl	0.163	0.110	0.136
Limb angle	0.032	0.187	0.110
Internodal distance	0.193	0.057	0.125
Color	0.387	0.377	0.382
Crook	0.122	0.193	0.158
Rating	0.153	0.149	0.151

Application of Results

The first objective was to determine if there was a significant difference between the two seed sources at either of the locations. Because there are no significant differences between the two sources for most of the characteristics, superior families and individuals from either source should be equally successful in a breeding program for north Alabama or central Tennessee. Also, because there were no major interactions between sources and locations, both sources are equally appropriate for both areas.

The next level was selection of the best families within each source. There were significant differences among families for all measured characteristics. There were no significant interactions between families and locations. The best families can be used in a breeding program for both areas negating the need to make separate selections and establish different seed orchards for each area.

The next selection level was the selection of individuals within families. However, this brings up an important question: What characteristics should be emphasized in a breeding program? A quality Christmas tree is a combination of several characteristics, such as good growth, dense crown, straight stem, and dark needle color. To maximize one characteristic would likely be at the expense of other characteristics. This could result in an overall decrease in tree quality or performance.

One purpose in calculating heritabilities is to determine which characteristics can be improved through a breeding program. If a characteristic has a low heritability, then genetic improvement would be slow. A review of the estimated heritabilities in Table 11 reveals that the two lowest estimates are for the characteristics of limb angle and internodal distance. As previously stated, limb angle appears to be a function of the position on the main stem on young trees. An optimum limb angle for Virginia pine Christmas trees has not been established. The minor differences among families was not sufficient to cause any noticeable differences in tree quality.

Internodal distance is closely related to height with a significant correlation of 0.54 at the A&M location and 0.42 at the Highland Rim location. Therefore, selecting individual trees within a family to minimize internodal distance would also have an undesirable effect of the reduction of total height. Trees with excessive internodal distance were down-graded in the "rating" evaluation. For the above reasons, the characteristics of limb angle and internodal distance were eliminated as potential selection characteristics.

Stem diameter was also eliminated as a selection characteristic for similar reasons. The best Christmas tree would be the tallest with the smallest stem diameter. However, there is a positive correlation between height and diameter of 0.83 at the A&M location and 0.80 at the Highland Rim location. Selection for a smaller stem diameter may result in a negative effect on height.

In an attempt to determine which characteristics have the greatest influence on overall tree quality, a multiple regression analysis was performed using the rating as the dependent variable being predicted by the other characteristics. The most significant characteristic accounting for more than 37 times the amount of variation of the second factor, was the crook value. The magnitude of importance of this characteristic was somewhat surprising. To verify this, three Christmas tree growers and two experienced field workers remeasured and evaluated one replication at the A&M location. The result of the regression analysis of the data was similar, in that crook was the predominant predictor of overall tree quality. A shorter or "open" tree can still be a merchantable product, whereas a crooked tree, regardless of its height or density is commonly not salable. It is obvious that growers would rather have shorter salable trees than tall culls. Therefore, one of the most important characteristics for a breeding program is stem straightness.

Next in importance in accounting for variation in the rating index was height. This was followed by needle color and branches per whorl, although neither of these two characteristics accounted for more than two tenths of 1 percent of the total variation in rating. Needle color had the highest heritability estimate, indicating the greatest potential for improvement. However, the darkest color recorded was still too light to be merchantable without the application of a colorant spray.

Needle color, because of its high heritability, could be considered as a characteristic that should be improved separately from the other characteristics. For example, trees would be selected only for their darker color, bred for maximum color gain and then selected for the straightest, tallest, best trees to be eventually crossed with trees selected for stem straightness and height.

Based on the above findings, it appears that the selection of superior trees should be most heavily weighted by the "quality rating" characteristic and stem straightness, followed by height growth with the least emphasis being placed on branches per whorl and needle color.

A commonly used method of selecting families for more than one trait is to remove all families not significantly better than the family with the worst performance. As previously stated, there was a large amount of variation in the error term for families-within-source. This results in a relatively large value as the least significant difference (L.S.D.). For example, the tallest family at the A&M site averaged 148 cm tall compared to 110 cm for the shortest family. Although there is a 38 cm difference between the tallest and shortest, the L.S.D. value was 18 cm. When adjusted by a Duncan's Multiple Range means separation, this would result in 33 families being removed because of being not significantly better than the worst. Repeating this procedure would result in the removal of 38 families for crookedness and 30 families for rating. The final result would be that only 8 families at the A&M location and 16 families at the Highland Rim location would survive this culling procedure. Only two families would be suitable for use at both locations. This culling is too drastic to maintain the genetic diversity needed for a breeding program.

The method utilized in this study was based on the calculation of the standard error of the means for each characteristic. Those families which were more than one standard error below the overall mean for two or more characteristics were culled. All families more than two standard errors less than the overall mean for any one characteristic were also culled. This procedure resulted in the culling of 14 families at the A&M location and 9 families at the Highland Rim location. This resulted in the removal of the worst families at both locations, while leaving a broad genetic base for future improvement efforts.

From the remaining families, the 20 best individuals were selected for each location according to the following criteria:

a. A score of 4 or 5 for both the crook rating and overall rating.

b. Maximum height growth.

c. When two or more trees had approximately the same height, then the tree with the higher number of branches per whorl or darker needle color was favored.

Only one tree from each family was selected.

The difference between the means of the 20 select trees and the overall mean for each characteristic was computed, resulting in the selection differential. Expected genetic gains were then computed according to the formula:

Gain = heritability x selection differential.

These results are presented in Table 12. For comparison the maximum expected gains were also computed for each characteristic. Between 80 and 90 percent of the gain can be realized for the combined selection of crook, rating and height. Needle color should show some improvement with a very modest increase in the number of branches per whorl.

Table 12. Expected Gains for Selection for Each Characteristic Individually and in Combination with Other Characteristics

	Plantation			
	A&M		H.R.F.S.	
Variables	Maximum gain	Select trees	Maximum gain	Select trees
Height	19.15 cm	15.93 cm	11.24 cm	9.20 cm
Branches/whorl	0.248	0.066	0.165	0.044
Color	0.545	0.216	0.569	0.263
Crook	0.206	0.176	0.364	0.328
Rating	0.293	0.247	0.341	0.276

The expected gain for most characteristics, such as height, has a definite, clear meaning. For example, the expected gain for height was calculated to be between 9.20 cm and 15.93 cm at age three. This simply means that the progeny from the selected trees should exhibit a 9 to 16 cm increase in height. However, the expected gains in "quality rating" of 0.247 at the A&M location and 0.276 at the Highland Rim location do not have a clear meaning. One method for obtaining a better understanding of the meaning and impact of these gains is to study the rating frequencies which produced the observed means and the changes which are anticipated to realize the expected gains.

The actual rating frequencies (adjusted to a per 1000 tree basis) observed at each location are presented in Table 13. These frequencies produced the observed means of 3.112 and 2.752 for the quality rating. If the expected gains are realized, then the progeny will have means of 3.359 and 3.028 at the A&M and Highland Rim locations, respectively. A straight percentage increase from each rating to the next, would result in a 26.1 and 28.0 percent increase from each rating class to the next to achieve the new means at the A&M and Highland Rim locations, respectively. This would result in the expected frequencies presented in Table 13. These increases may be slightly inflated because of the top limit of 5 on the ratings. Each lower rating had to be adjusted slightly more to compensate for no increase from 5 to 6.

Assuming that a 27 percent average increase from one rating class to the next is realistic, then there would be 27 percent reduction in 1 rated trees which are all culls. There would also be approximately a

Table 13. Actual and Expected Rating Frequencies per 1000 Trees

	A&M		H.R.F.S.	
Rating	Actual	Expected	Actual	Expected
1	91	66	119	86
2	165	145	254	215
3	353	305	402	361
4	323	332	206	261
5	68	152	19	77
Average rating	3.112	3.359	2.752	3.028

14 percent reduction in 2 rated trees--those which require major corrective procedures. It is impossible to correct all trees rated 2 to make them all salable. In fact, it would be more accurate to assume that only 50 percent of 2 rated trees can be made into a salable product. A 27 percent reduction in 1 rated trees and a 14 percent reduction in 2 rated trees, assuming half of these are not salable, represents an average increase of 44 merchantable trees per 1000 or approximately per acre.

A clearer understanding and more meaningful measure of the above gains can be obtained by assigning a dollar value to them. Assuming a value of $2.00 per foot, or $12.00 per tree as a wholesale price for a 6-foot Virginia pine Christmas tree, an additional 44 trees marketed per acre represents an increase in income of $528.00. An increase in height of 12.57 cm (the average gain of the two test plots) on 834 trees per acre would represent a gain of $688.00. Of possibly greater importance, but not easily measured, is the percentage of the trees that will be of better quality and will have required less maintenance. Also, more trees will be merchantable at an earlier age, increasing the rate of return on a grower's investment.

It is apparent that the genetic improvement of Virginia pine Christmas trees will provide significant gains to the industry. However, it is also apparent that no amount of genetic improvement will compensate for a poor site.

Gains from mass selection, as was done in this study, are usually lower than gains from two or three-stage selection. However, this test was not designed to test multiple sources and the two sources that were tested were not significantly different. Furthermore, the method utilized for family selection effectively eliminated the poor families, rather than selecting only the best. Therefore, an increase in gains from family selection would be fairly small.

The precision of the estimates of heritabilities and genetic gains is not a critical consideration. The actual gains will be evident within three years. The A&M plantation has already been rogued to 80 select trees. Seed is being collected from all parent trees for further progeny testing prior to the final selection of orchard trees. A similar procedure will be followed at the Highland Rim plantation to convert it to a seed orchard for Tennessee.

A conclusion from this study of Virginia pine is that there is a large amount of inherent variation in young Virginia pine trees. This conclusion became evident from the results presented earlier in the analyses of variance. Two trees from the same family planted six feet apart are often very different. This has two serious consequences.

First, it has a large negative influence on the estimates of heritabilities and consequently on the expected gains. This is attributed to the large replication by families-within-source interaction and the within-plot variance components. Every effort should be made in future research to make test conditions as uniform as possible. However, despite these efforts, a certain amount of this variation is inevitable particularly when evaluating young trees. For example, maternal effects may still be present in some trees more than others. Differences in planting or site preparation may also have a residual effect on a tree even after three years in the field. These effects could result in at least a height reduction of one foot. This reduction of one foot has a greater influence on the relative variation in height of three-year-old trees than it would have on five-year-old trees.

The second consequence of the high amount of variation in young Virginia pine trees is that actual genetic gains may not be readily identified by most growers. An increase of 12 cm in height may be difficult to detect without accurate measurement. Such a gain in height is even less discernible because of inter-tree variation in a production planting. Without an inventory, it is impossible to determine the number of merchantable trees per acre. Most growers do not measure the heights of their trees nor do they know precisely how many trees per acre they are managing. Consequently, the gains may actually be realized but may not be apparent to the growers. Additional genetic gains will be necessary to have a plantation of improved trees that will be visibly superior to most Christmas tree growers. Fortunately, Virginia pine flowers at a very early age (by their fifth year) which permits a breeding program to establish crossings among select trees at an early age for the eventual establishment of a second generation orchard. This work has already been initiated and should result in second generation selections in 1991.

Conclusions

The objective of this study was to estimate heritabilities and predict genetic gains for several characteristics of Virginia pine

Christmas trees. This information can then be used to initiate a breeding program for the genetic improvement of Virginia pine Christmas trees. To accomplish this objective, the genetic and environmental sources of variation were determined by evaluating data collected from open-pollinated progeny tests planted at Alabama A&M University and the Highland Rim Forestry Field Station. The progeny originated from two seed sources, the Kimberly-Clark Corporation seed orchard in Coosa Pines, Alabama and a previously established progeny test at the Highland Rim Forestry Field Station in Tullahoma, Tennessee.

On the basis of the results obtained in this study, the following conclusions were reached:

1. There was not a major difference between the two seed sources and the interactions of sources x locations and families-within-source x locations were relatively minor. This implies that families from either source can be used as breeding material for either location. Separate seed orchards for north Alabama and central Tennessee will not be required.

2. Based on the calculated estimates of heritabilities and potential genetic gains, the genetic improvement of Virginia pine for Christmas trees is possible and practical.

3. The greatest improvement of Virginia pine for Christmas trees can be achieved if the selection of superior trees primarily focuses on the characteristics of overall quality rating and stem straightness, followed by height growth with the least emphasis being placed on branches per whorl and needle color.

4. The selection of the 20 best individuals for each location should result in progeny which average over 12 cm taller at age three. The progeny should also produce approximately five percent fewer cull trees per acre. These two factors alone represent an increase in commercial value of at least $1,200.00 per acre.

5. The Virginia pine is a species which is characterized by a large amount of tree-to-tree variation, which is particularly pronounced in juvenile trees. One objective of future research efforts should be to try to minimize the environmental source of variation within a test location. This variation causes reduced estimates of heritabilities and may mask much of any realized genetic gains without accurate measurements.

CHAPTER IV

CANONICAL CORRELATION OF SEED, SEEDLING AND FIELD CHARACTERISTICS OF VIRGINIA PINE CHRISTMAS TREES

Introduction

The method of selecting superior trees used in the preceding chapter required the planting of almost 2,000 trees at each of the two locations--A&M and H.R.F.S. These trees were managed for three years and then evaluated. This represents a considerable commitment of resources for the eventual selection of twenty to forty select trees. There are two potential ways to expedite the identification of these trees and reduce maintenance costs. First, if there are seed or seedling characteristics which can be utilized as predictors of field performance, then screening for such characteristics would increase the total number of select trees. Secondly, if there are characteristics at the seed, seedlings, or first and second-year growth stage which are indicators of a poor third-year performance, then these characteristics could be used to eliminate individual trees, thereby reducing the total number of trees maintained in order to achieve the same end result. However, in order to accomplish this goal, the relationships among seed, seedling, first, second and third-year field performance must be known.

Objectives

The specific objectives of this study are:

1. To determine if seed or seedling characteristics can be used to predict third-year field performance of Virginia pine Christmas trees, thereby permitting the screening of seed and/or seedlings to increase the relative number of select trees.

2. To determine if first or second-year field performance can be used to predict third-year field performance of Virginia pine Christmas trees thereby permitting the culling of test trees at an earlier period.

3. To determine the specific tree characteristics from reliable predictor sets which can be used for screening purposes.

4. To evaluate the use of canonical correlations as a statistical tool for measuring the above relationships and for developing a selection strategy.

Materials and Methods

To determine the relationships among seeds, seedlings and field performance, eight full seeds were selected from each of 57 half-sib families of Virginia pine. The 57 families were originally selected from eight different seed sources located in Alabama, Mississippi and Tennessee. The 57 families from eight sources were utilized to assure genetic diversity and to assure that the material tested is representative of Virginia pine in these three states.

Each seed was weighed to the tenth of a milligram and the length and width were measured to the tenth of a millimeter. Each seed was then placed in an individual cell of a Spencer-Lemire roottrainer book filled with a growing medium (Jiffy-Mix) with one seed of each family in each of eight replications. They were then moved to a greenhouse on the campus of Alabama A&M University, watered and allowed to germinate and grow for one year. Initially, they were checked daily in order to record the number of days to germination for each seed. Each new seedling was remeasured within four weeks for the height to the cotyledons, number of cotyledons and length of the cotyledons. The seedlings were allowed to continue to grow and then harden-off in a cold frame during the onset of autumn. They were measured for height, stem diameter, number of branches and total number of buds immediately prior to field planting.

Due to seed which did not germinate and seedling mortality, the field arrangement was modified to eliminate missing cells. The seedlings were planted in one-tree-plots of 52 families, replicated six times and arranged in a randomized complete block design, hereafter referred to as the canonical correlation experiment. Spare seedlings were used to fill in blanks within the field layout and in an extra row on one side of the entire plot. One border row was planted around the experiment. The use of a randomized complete block design was not necessary for the determination of the relationships among the various characteristics at different ages. However, if a set of relationships was found to be useful for screening purposes, then the results of the screening could be compared directly with the results of the analysis of the randomized complete block design.

The trees were measured at the end of the first year in the field for total height, diameter at 15 cm above ground and total number of branches. All trees were remeasured after two and three years for total height, diameter at 15 cm, number of branches per whorl (average of the 2nd, 3rd and 4th whorls from the top), stem straightness and an overall quality rating (both on a 5-point scale as previously described).

To obtain a more reliable estimate of the relationships among first, second and third-year field performances, two half-sib progeny tests located at Alabama A&M University and the Highland Rim Forestry Field Station were measured at the end of the first and second growing seasons for the same characteristics as above. The first and second-years' data were combined with the third-year data obtained for the experiments described in Chapter III.

Statistical Analysis

The data from the canonical correlation experiment were divided into the following data subsets: seed, seedling, first-year field results, second-year field results and third-year field results. The data obtained from the two progeny tests were each divided into three subsets, one for each year's data. This resulted in the analysis of three different experiments, two each with 3 data subsets and one with 5.

Each data subset within an experiment was compared to each other subset by use of the canonical correlation procedure of the S.A.S. (Statistical Analysis System) program. These analyses yielded the linear relationship of one subset of data to the next which had the maximum correlation between the two subsets. For example, the analysis of the first experiment yielded the correlations of seed characteristics with seedling characteristics, first, second and third-year field results. An analysis was then conducted to determine the correlation of seedling characteristics with the data obtained from each year's measurements. Each year's measurements were then used as a predictor set for the following year's measurements. The same procedure was used with the data from both of the progeny tests, resulting in the linear relationships between the first and second, first and third and second and third-year's field measurements.

Simple product-moment correlations were also obtained between all variables within an experiment (Appendix A). An analysis of redundancy was performed, which gave the proportion of the variance of the response set of variables which is accounted for by the canonical variables of the predictor set.

Results

The canonical correlations between each data set and those that follow it are shown in Table 14. Seed measurements were significantly correlated with seedling measurements, but not with first and second-year field performance. The were significantly correlated with the third-year field performance, however the correlation was low (r = 0.2936). The seedling characteristics were significantly correlated (.01 level) with the first and second-years' field performance, although these correlations were also low. First-year field performance was significantly correlated (.01 level) with both the second and third-year results at all three locations. There was a 0.10 to 0.12 reduction in

Table 14. Canonical Correlations of Seed Through Year 3 Measurements

Response Set		Predictor Set: Seed	Seedling	Year 1	Year 2
Seedling (Can. Corr. Exp.)		0.3289**			
Year 1 (Can. Corr. Exp.)		0.2725	0.2995**		
Year 2	Can. Corr. Exp.	0.2985	0.2835**	0.8118**	
	A & M test			0.5818**	
	Highland Rim test			0.7678**	
Year 3	Can. Corr. Exp.	0.2936*	0.1994	0.6955**	0.8516**
	A & M test			0.4750**	0.8864**
	Highland Rim test			0.6603**	0.8969**

*Significant at $\alpha = .05$.

**Significant at $\alpha = .01$.

the correlations between first and third-year field response compared to that between first and second-year field response, indicating a general reduction in correlation as the time period between measurements increased. Second and third-year field performance was significantly correlated (.01 level) (correlations were between 0.85 and 0.90) at all three locations.

To be an effective predictor of future responses, a set of canonical variables needs to not only be significantly correlated with the response variables, but also explain a relatively high proportion of the variance of the response set. Table 15 shows the proportion of the variance of the response sets which is explained by the canonical variables of the predictor sets for all three experiments. The seed or seedling data sets when used as predictors account for less than 4 percent of the variances of all response sets. First-year field performance accounts for between 26 and 56 percent of the variation in second-year measurements, but drops to accounting for between 18 and 36 percent of the variance of the third-year measurements. Between 58 and 71 percent of the variation in third-year measurements is explained by the canonical variates of the second-year measurements.

It appears that because of the highly significant correlation between second and third-year field performance and the relatively high percentage of the third-year variance explained by the canonical variates of the second year, the second-year measurements can be used to predict third-year performance. Up to this point the results are somewhat abstract in that they do not present a clear understanding of the

Table 15. Proportion of Variance of Response Sets Explained by Canonical Variables of Predictors (Redundancy Analysis)

Response Set		Predictor Set: Seed	Seedling	Year 1	Year 2
Seedling (Can. Corr. Exp.)		0.0248			
Year 1 (Can. Corr. Exp.)		0.0220	0.0048		
Year 2	Can. Corr. Exp.	0.0316	0.0340	0.5619	
	A & M test			0.2620	
	Highland Rim test			0.5059	
Year 3	Can. Corr. Exp.	0.0170	0.0213	0.3478	0.5792
	A & M test			0.1806	0.7138
	Highland Rim test			0.3558	0.6682

linear relationship between the sets of measurements. However, there are several possible linear combinations of two sets of original variables. Canonical correlation analysis determines the linear combination with the maximum correlation, and then determines each new linear combination that maximizes a new correlation, subject to the condition that each linear combination is independent or uncorrelated with the others. Each pair of linear combinations is referred to as a canonical variate. Tables 16, 17 and 18 present a more in-depth analysis of the first three canonical variates for the second and third-year relationships for each of the three experiments.

The first set of numbers in these tables shows the raw canonical coefficients, which can be used with the original variables in a similar manner as multiple regression coefficients. For example, using the first canonical variate of Table 16, if X_i represents the second-year variables and Y_i represents the third-year variables, then the two linear combinations are:

$$V_1=0.0290X_1+0.0517X_2-0.0320X_3-0.0734X_4+0.1282X_5$$

$$W_1=0.0119Y_1+0.0525Y_2-0.0850Y_3-0.0969Y_4+0.0537Y_5$$

The canonical variables, V_1 and W_1, have a highly significant correlation of 0.8516.

Because each variable was measured in different units, the size of the raw coefficients cannot be used to indicate the relative importance or size of the contribution of each original variable to the final

Table 16. Canonical Correlation Analysis of Second and Third-Year Measurements of Canonical Correlation Experiment

Canonical Coefficients:

Canonical variate:	1		2		3	
	Raw	Standardized	Raw	Standardized	Raw	Standardized
Year 2:						
Height	0.0290	0.5790	-0.0374	-0.9473	-0.0447	-1.1312
Diameter	0.0517	0.4379	0.0354	0.2999	0.1748	1.4794
Branches/whorl	-0.0320	-0.0282	0.4662	0.4110	0.3136	0.2765
Crook	-0.0734	-0.0689	0.6055	0.5691	-0.0009	-0.0009
Rating	0.1282	0.1093	0.5449	0.4648	-0.6740	-0.5749
Year 3:						
Height	0.0119	0.4879	-0.0172	-0.7058	-0.0253	-1.0349
Diameter	0.0525	0.5994	0.0281	0.3216	0.0982	1.1222
Branches/whorl	-0.0850	-0.0688	0.3914	0.3171	0.4534	0.3673
Crook	-0.0969	-0.0928	0.0976	0.0935	-0.1936	-0.1854
Rating	0.0537	0.0523	0.8770	0.8547	-0.3237	-0.3154
Canonical correlation:	0.8516		0.4038		0.2868	
Canonical R-square:	0.7252		0.1630		0.0822	
F-statistic:	21.3308		5.1617		3.4748	
Prob > F	0.0000		0.0000		0.0003	
Year 3 variance explained by:						
Own canonical variables:	0.7987		0.0058		0.1395	
Year 2 canonical variables:	0.5792		0.0009		0.0115	

Table 17. Canonical Correlation Analysis of Second and Third-Year Measurements of Alabama A&M Half-Sib Progeny Test

Canonical Coefficients:

Canonical variate:	1		2		3	
	Raw	Standard-ized	Raw	Standard-ized	Raw	Standard-ized
Year 2:						
Height	0.0340	0.5989	-0.0948	-1.6715	0.0170	0.2090
Diameter	0.0865	0.3627	0.3052	1.2798	-0.2056	-0.8618
Branches/whorl	0.0279	0.0198	0.2427	0.1717	0.1066	0.0754
Crook	-0.0282	-0.0324	0.0624	0.0756	0.5100	0.6184
Rating	0.1262	0.1268	0.5006	0.5027	0.4401	0.4419
Year 3:						
Height	0.0207	0.5551	-0.0521	-1.3978	0.0282	0.7579
Diameter	0.0673	0.5055	0.1459	1.0962	-0.1386	-1.0415
Branches/whorl	0.0119	0.0076	-0.0093	-0.0060	0.0911	0.0586
Crook	0.0182	0.0212	0.0972	0.1131	0.5147	0.5991
Rating	-0.0279	-0.0282	0.6329	0.6389	0.2297	0.2318
Color	-0.0163	-0.0101	-0 0850	-0.0525	0.1399	0.0863
Canonical correlation:	0.8864		0.4764		0.3923	
Canonical R-square:	0.7857		0.2270		0.1539	
F-statistic:	93.7629		25.7295		17.0984	
Prob > F	0.0000		0.0000		0.0000	
Year 3 variance explained by:						
Own canonical variables:	0.9085		0.0492		0.0360	
Year 2 canonical variables:	0.7138		0.0112		0.0055	

Table 18. Canonical Correlation Analysis of Second and Third-Year Measurements of Highland Rim Half-Sib Progeny Test

Canonical Coefficients:

Canonical variate:	1		2		3	
	Raw	Standardized	Raw	Standardized	Raw	Standardized
Year 2:						
Height	0.0192	0.4917	-0.0692	-1.7744	-0.0007	-0.0177
Diameter	0.0862	0.5041	0.2467	1.4424	-0.1030	-0.6024
Branches/whorl	0.0439	0.0304	-0.0268	-0.0186	-0.0561	-0.0389
Crook	-0.0641	-0.0778	0.1323	0.1605	0.6315	0.7658
Rating	0.1159	0.1123	0.3977	0.3854	0.4653	0.4508
Year 3:						
Height	0.0124	0.4430	-0.0406	-1.4465	0.0135	0.4814
Diameter	0.0683	0.6516	0.1176	1.1209	-0.0806	-0.7688
Branches/whorl	0.0146	0.0099	-0.0635	-0.0429	0.1509	0.1019
Crook	-0.0677	-0.0745	0.1433	0.1578	0.6955	0.7661
Rating	-0.0616	-0.0591	0.5807	0.5570	0.1354	0.1299
Color	0.0836	0.0509	-0.1700	-0.1035	0.3688	0.2246
Canonical correlation:	0.8969		0.4498		0.2868	
Canonical R-square:	0.8045		0.2023		0.0823	
F-statistic:	119.5851		25.4859		14.1813	
Prob > F	0.0000		0.0000		0.0000	
Year 3 variance explained by:						
Own canonical variables:	0.8306		0.0696		0.0718	
Year 2 canonical variables:	0.6682		0.0141		0.0059	

canonical correlation. Therefore, the coefficients for the standardized data are also given (Tables 16, 17 and 18).

The probabilities of obtaining a larger F-statistic from the canonical correlations of the first three variates from all three locations indicate that they all are highly significant. However, only the second-year canonical variables within the first canonical variate account for a reasonably large amount of the third-year variance. Therefore, the second and third canonical variates do not possess much value and will not be discussed further.

The standardized canonical coefficients for the first canonical variate for each location are almost identical. It is primarily the growth variables, height and diameter, which are highly correlated from the second to the third year. Over 80 percent of V_1 and W_1 is due solely to these two factors, with less than 20 percent being accounted for by the branches per whorl, stem crookedness, and overall rating.

Because the use of canonical correlation analysis is less conventional, a more familiar approach would be to use multiple regression analysis to predict each variable from the previous years' measurements. For example, how well does the second-years' measurements of height, diameter, branches per whorl, crook rating and overall rating predict third year height? To cross-check the results of the canonical correlation analyses, multiple regression analysis was performed on each individual variable using the previous sets of measurements as the independent variables. This resulted in the generation of 79 multiple regression equations. For the purpose of simplicity, only the squared multiple correlations (R^2) and corresponding F-values are given (Appendix B).

The multiple regression analyses produced results that were in complete agreement with the results generated by the canonical correlation analyses. The only R^2 values over 0.50 for all three experimental locations were those resulting from predicting third-year height or diameter from the second-year measurements. The only other R^2 values over 0.50 were those predicting the second-year heights or diameters from first-year measurements on the canonical correlation experiment and the Highland Rim half-sib progeny test. Trees at these two test locations had superior initial growth. In all three test locations, the third-year variance explained by the second-year canonical variables is within 1 percent of the multiple regression R^2 value for either height or diameter, whichever was lowest for each location. For example, the greatest difference between the amount of variance accounted for by the canonical correlation analyses and the multiple regression analyses occurred in the analysis of the third-year results of the Highland Rim half-sib progeny test. The second-year canonical variables accounted for 67 percent of the total third-year variance. Whereas, the second-year variables in the multiple regression analyses accounted for 68 and 76 percent of the variances of height and diameter, respectively.

Application of Results

The objective of this research was to determine the relationships among seed, seedling, first, second and third-year variables for Virginia pine Christmas trees. It was done in an attempt that these relationships could then be used to develop a more efficient method for conducting tree improvement field experiments, either by prescreening for desirable seed or seedling characteristics, or by early detection and elimination of undesirable trees.

However, seed, seedling and first-year field characteristics cannot be used to accurately predict future characteristics. Most relationships were not significant, or if they were, they did not account for enough of the variance of the response set to be usable. The lowest canonical correlations were obtained between seed or seedling characteristics and field performance measurements. It appears that when the seedlings are planted, they are exposed to a new set of environmental conditions which are not related to the measured seed or seedling characteristics. As indicated by previous research, Virginia pine is a species which exhibits a large amount of tree-to-tree variation and its growth may be affected by various site factors. The micro-site conditions at the planting site appears to contribute more to the initial growth of the tree than any of the seed or seedling characteristics which were evaluated.

Once the trees become established, then a trend toward higher correlations among characteristics from one year to the next was observed.

It is also apparent that the physical condition of the soil affects the initial growth of the trees. This has a direct effect on the length of time required to obtain reliable measurements to predict future responses. The Highland Rim half-sib progeny test was planted on a site with noticeably less compacted soil than the A&M half-sib progeny test. It produced the greatest average of growth per tree for the three years of the study. The canonical correlation between first and third-years' measurements was 0.66 for the Highland Rim test compared to only 0.48 for the A&M test. The canonical correlation experiment was planted two years later on a site next to the A&M test in a soil almost identical to the original site. However, this site was intensively prepared by subsoiling, multiple turnings and diskings in an effort to loosen the soil and create more uniform site conditions. This resulted in a canonical correlation between first and third-years' measurements of 0.70 as compared to 0.48 for the A&M test located next to it.

Regardless of site condition, it appears that the trees are established after two years in the field. All three test sites had canonical correlations between second and third-year measurements of between 0.85 and 0.90. The canonical variates derived from the second-year measurements accounted for from 58 to 71 percent of the variation in third-year measurements. The second-year measurements can be used to predict third-year results allowing the culling of undesirable trees after two years in the field.

The primary characteristics which had the highest correlations from the second to third years were height and diameter. Based on these correlations, the removal of undesirable trees after two years culls those trees which exhibit the slowest growth.

The canonical correlation analysis of the data from the A&M and Highland Rim half-sib progeny tests allows evaluation of actual cases of the application of these results. These two tests were evaluated using a randomized complete block design. Heritabilities, variance components and genetic gains had already been calculated (Chapter III). Based on this information, superior trees were selected for height growth, stem straightness, overall quality rating, branches per whorl and needle color. Comparison of the canonical variables (V_1) calculated for the first and second-years' measurements of the select trees against all trees permits the determination of how many trees could have been rogued after the first and second years without removing any of the select trees. Based on a ranking of canonical variable values, trees in the lowest 24 and 66 percentile for the first and second year respectively, could have been removed without the loss of any of the select trees.

The roguing of the smallest 24 percent of all trees one year after planting should be a conservative thinning because it is based on protecting the select trees in the A&M half-sib progeny test. Trees within this test had the slowest growth and the lowest canonical correlation between first and third-year measurements. The removal of up to 66 percent of the trees after two years appears to be an effective technique for conservation of time and costs regardless of site conditions.

The use of canonical correlation analysis was found to yield more information which was easy to assimilate and interpret than the use of multiple regression analysis. This research required the interpretation of 16 different canonical correlation analyses. The same research would have required the interpretation of 79 multiple regression analyses that would not have yielded any information on the interrelationships among the response set of variables. The canonical correlation analyses produced results which compared very favorably to the multiple regression analyses in being able to account for the variation in the response sets.

Conclusions

The selection of a few superior trees often involves growing and maintaining several thousand trees. If a characteristic or set of characteristics pertaining to the seed or seedlings of a species is related to field performance, then the screening of the seed and/or seedlings for the related characteristics would increase the efficiency of a breeding program. Additionally, if first or second-years' field performance measurements are related to third-year measurements, then they can be utilized to rogue trees after the first and second year to reduce maintenance costs of the experiment. To determine if these goals could be successfully accomplished for the improvement of Virginia pine Christmas trees, the relationships among seed and seedling characteristics and their subsequent years' field performance were evaluated.

On the basis of the results obtained in the study, the following conclusions are warranted:

1. Seed and seedling characteristics of Virginia pine are not highly correlated to third-year field performance and should not be used for screening purposes. The ability of a seedling to adjust to field conditions appears to far outweigh any measured characteristics of the seed or seedling.

2. A minimum of one year after planting is required to detect reliable relationships among each year's characteristics. The physical condition of the soil affects the initial growth of the trees which in turn affects the amount of time required before reliable estimates of year-to-year relationships can be determined. If newly planted trees do not grow well during the first year, then a second year is required before culling more than 24 percent of the trees.

3. Second-year-field characteristics are strongly related to third-year-field characteristics and can be used to cull up to 66 percent of the trees without substantially reducing the number of select trees.

4. The relationships detected were primarily those related to growth factors, namely height and diameter. The screening of trees after one or two years in the field is a culling of the slowest growing trees.

5. The use of canonical correlation analysis was more efficient, yielded more complete information and accounted for similar amounts of variation of the response sets when compared to multiple regression analysis.

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APPENDIXES

APPENDIX A

PEARSON PRODUCT-MOMENT CORRELATIONS

Table A-1. Correlations Between Virginia Pine Characteristics From Canonical Correlation Experiment of Seed Through Third-Year Field Performance

		Seed Characteristics						
		Weight	Length	Width	Germination days	Cotyledon height	Cotyledon Length	Number Cotyledons
SEED	Weight	1.000						
	Length	.625**	1.000					
	Width	.610**	.276**	1.000				
	Germ. days	-.112*	-.051	.020	1.000			
	Cot. hgt.	.261**	.216**	.067	-.165**	1.000		
	Cot. lgth.	.465**	.344**	.203**	-.248**	.492**	1.000	
	Num. cot.	.302**	.160**	.255**	.008	.122*	-.038	1.000
SEEDLING	Height	.056	.039	.000	.021	.091	.088	-.103
	Diameter	.038	.057	-.045	.020	.053	.081	.029
	Branches	.103	.084	.022	.022	.198**	.185**	.112*
	Buds	-.027	-.027	.013	.054	-.014	.042	.061
YEAR 1	Height	.068	.002	-.019	.010	.005	.127*	.002
	Diameter	.112	-.040	-.001	-.023	-.016	.139*	.063
	Branches	.012	.001	-.058	-.024	-.031	.057	.006

Table A-1 (continued)

		Seed Characteristics						
		Weight	Length	Width	Germination days	Cotyledon height	Cotyledon Length	Number Cotyledons
Y	Height	.061	.045	-.075	-.025	-.058	.122*	-.101
E	Diameter	.039	-.003	-.030	-.033	-.061	.058	.004
A	Branch/wh	-.097	-.116	-.023	.080	-.037	.052	-.165**
R	Crook	.008	.060	-.078	-.021	.066	.069	-.124*
2	Rating	-.015	-.002	-.141	-.059	-.011	.058	-.154**
Y	Height	.009	-.021	-.071	.017	-.030	.102	-.083
E	Diameter	.039	.021	.000	-.054	-.081	.037	-.013
A	Branch/wh	-.022	-.002	.065	.131	-.092	-.020	-.081
R	Crook	-.115	-.081	-.053	-.075	.093	-.005	-.037
3	Rating	-.066	-.018	-.104	-.085	-.010	.014	-.048

*Significant at α = .05 under Ho: no association (RHO = 0).

**Significant at α = .01 under Ho: no association (RHO = 0).

Table A-2. Correlations Between Virginia Pine Characteristics From Canonical Correlation Experiment of Seedling and Year One With Seedling Through Third-Year Field Performance

		Seedling				Year 1		
		Height	Diameter	Branches	Buds	Height	Diameter	Branches
SEEDLING	Height	1.000						
	Diameter	.278**	1.000					
	Branches	-.038	.228**	1.000				
	Buds	.181**	.238**	.186**	1.000			
YEAR 1	Height	.180**	.126*	.143*	.108	1.000		
	Diameter	-.038	.114	.178**	.015	.671**	1.000	
	Branches	-.008	.123*	.254*	.097	.669**	.660**	1.000
YEAR 2	Height	.101	.126*	.149*	.155**	.686**	.675**	.598**
	Diameter	-.009	.131*	.181**	.150*	.643**	.733**	.619**
	Branches/wh	-.005	.006	.113	-.044	.176**	.194**	.218**
	Crook	.033	.140*	.093	.147*	.327**	.234**	.388**
	Rating	.021	.119*	.124*	.077	.479**	.436**	.536**
YEAR 3	Height	.100	.086	.064	.119*	.518**	.542**	.425**
	Diameter	.040	.115	.072	.102	.517**	.618**	.506**
	Branches/wh	.061	-.023	.026	.051	.033	-.047	.090
	Crook	.087	.070	.007	.013	.057	.025	.099
	Rating	.044	.048	-.005	-.024	.198**	.179**	.243**

*Significant at α = .05 under Ho: no association (RHO = 0).

**Significant at α = .01 under Ho: no association (RHO = 0).

Table A-3. Correlations Between Virginia Pine Characteristics From Canonical Correlation Experiment of Seedling and Year Two With Seedling Through Third-Year Field Performance

		Year 2				
		Height	Diameter	Branches/wh	Crook	Rating
Y	Height	.751**	.678**	.204**	.293**	.510**
E	Diameter	.728**	.791**	.248**	.318**	.510**
A	Branches/wh	.004	.041	.192**	.077	.111
R	Crook	.129*	.100	.120*	.314**	.309**
3	Rating	.293**	.273**	.215**	.410**	.443**

*Significant at α = .05 under Ho: no association (RHO = 0).

**Significant at α = .01 under Ho: no association (RHO = 0).

Table A-4. Correlations Between Virginia Pine Characteristics from Alabama A&M Half-Sib Progeny Test

		Year 1			Year 2				
		Height	Diameter	Branches	Height	Diameter	Branch/wh	Crook	Rating
Y	Height	.381**	.471**	.391**	1.000				
E	Diameter	.348**	.542**	.401**	.827**	1.000			
A	Branch/wh	.030	.172**	.158**	.380**	.413**	1.000		
R	Crook	-.074*	.057*	.135**	.302**	.216**	.245**	1.000	
2	Rating	.119**	.261**	.247**	.620**	.595**	.381**	.675	1.000
Y	Height	.281**	.379**	.333**	.853**	.751**	.345**	.304**	.597**
E	Diameter	.268**	.425**	.374**	.782**	.829**	.386**	.226**	.581**
A	Branch/wh	.030	.107**	.087**	.302**	.277**	.175**	.168**	.298**
R	Crook	-.075**	.079**	.114*	.164**	.200**	.196**	.386**	.394**
3	Rating	.029	.173**	.195**	.368**	.428**	.286**	.396**	.531**
	Color	.067*	.085**	.079**	.167**	.149**	.091**	.061*	.161**

*Significant at α = .05 under Ho: no association (RHO = 0).

**Significant at α = .01 under Ho: no association (RHO = 0).

Table A-5. Correlations Between Virginia Pine Characteristics from Highland Rim Half-Sib Progeny Test

		Year 1			Year 2				
		Height	Diameter	Branches	Height	Diameter	Branch/wh	Crook	Rating
Y	Height	.660**	.615**	.473**	1.000				
E	Diameter	.614**	.682**	.510**	.819**	1.000			
A	Branch/wh	.211**	.261**	.292**	.400**	.353**	1.000		
R	Crook	.193**	.193**	.270**	.472**	.355**	.347**	1.000	
2	Rating	.345**	.368**	.350**	.656**	.580**	.417**	.706**	1.000
Y	Height	.550**	.498**	.405**	.822**	.738**	.352**	.392**	.587**
E	Diameter	.525**	.572**	.423**	.783**	.857**	.348**	.362**	.590**
A	Branch/wh	.038	.106**	.108**	.187**	.169**	.159**	.133**	.193**
R	Crook	.069**	.107**	.108*	.184**	.219**	.141**	.327**	.316**
3	Rating	.176**	.234**	.211**	.321**	.388**	.199**	.324**	.430**
	Color	.124**	.116**	.103**	.201**	.173**	.022	.148**	.169**

*Significant at $\alpha = .05$ under Ho: no association (RHO = 0).

**Significant at $\alpha = .01$ under Ho: no association (RHO = 0).

APPENDIX B

MULTIPLE REGRESSION RESULTS

Table B-1. Squared Multiple Correlations of Multiple Regression Analyses of Virginia Pine Characteristics Using Prior Years' Measurements as Predictors from Canonical Correlation Experiment of Seed Through Third-Year Field Performance

Dependent variable	Independent variable set	R^2	F value
Seedling:			
Height	Seed	0.0290	1.256
Diameter	Seed	0.0247	1.062
Branches	Seed	0.0984	4.584**
Buds	Seed	0.0252	1.086
Year 1:			
Height	Seed	0.0429	1.375
	Seedling	0.0507	3.696**
Diameter	Seed	0.0590	1.922*
	Seedling	0.0411	2.965*
Branches	Seed	0.0157	0.489
	Seedling	0.0736	5.506**
Year 2:			
Height	Seed	0.0639	2.680*
	Seedling	0.0503	3.630**
	Year 1	0.5644	119.651**
Diameter	Seed	0.0339	1.377
	Seedling	0.0641	4.690**
	Year 1	0.6218	151.834**
Branches/whorl	Seed	0.0574	2.394*
	Seedling	0.0165	1.152
	Year 1	0.0523	5.093**
Crook	Seed	0.0320	1.300
	Seedling	0.0364	2.589*
	Year 1	0.1623	17.895**
Rating	Seed	0.0534	2.216*
	Seedling	0.0259	1.821
	Year 1	0.3146	42.382**

Table B-1 (continued)

Dependent variable	Independent variable set	R^2	F value
Year 3:			
Height	Seed	0.0454	1.426
	Seedling	0.0220	1.527
	Year 1	0.3470	48.525**
	Year 2	0.5892	78.583**
Diameter	Seed	0.0284	0.878
	Seedling	0.0238	1.654
	Year 1	0.4456	73.413**
	Year 2	0.6494	101.513**
Branches/whorl	Seed	0.0573	1.824
	Seedling	0.0088	0.600
	Year 1	0.0279	2.619
	Year 2	0.0534	3.091**
Crook	Seed	0.0530	1.680
	Seedling	0.0115	0.787
	Year 1	0.0124	1.149
	Year 2	0.1150	7.119**
Rating	Seed	0.0334	1.036
	Seedling	0.0053	0.363
	Year 1	0.0612	5.949**
	Year 2	0.2174	15.222**

*Significant at $\alpha = .05$.

**Significant at $\alpha = .01$.

Table B-2. Squared Multiple Correlations of Multiple Regression Analyses of Virginia Pine Characteristics Using Prior Years' Measurements as Predictors from Alabama A&M Half-Sib Progeny Test

Dependent variable	Independent variable set	R^2	F value
Year 2:			
Height	Year 1	0.2650	137.018**
Diameter	Year 1	0.3188	177.799**
Branches/whorl	Year 1	0.0439	17.465**
Crook	Year 1	0.0347	13.665**
Rating	Year 1	0.0769	31.659**
Year 3:			
Height	Year 1	0.1794	84.696**
	Year 2	0.7336	607.950**
Diameter	Year 1	0.2159	106.658**
	Year 2	0.7215	571.900**
Branches/whorl	Year 1	0.0135	5.302**
	Year 2	0.0927	22.567**
Crook	Year 1	0.0361	14.494**
	Year 2	0.1840	49.794**
Rating	Year 1	0.0537	22.000**
	Year 2	0.2953	92.525**
Color	Year 1	0.0103	4.012**
	Year 2	0.0330	7.536**

**Significant at $\alpha = .01$.

Table B-3. Squared Multiple Correlations of Multiple Regression Analyses of Virginia Pine Characteristics Using Prior Years' Measurements as Predictors from Highland Rim Half-Sib Progeny Test

Dependent variable	Independent variable set	R^2	F value
Year 2:			
Height	Year 1	0.5107	506.511**
Diameter	Year 1	0.5415	573.264**
Branches/whorl	Year 1	0.1021	55.185**
Crook	Year 1	0.0728	38.083**
Rating	Year 1	0.1724	101.089**
Year 3:			
Height	Year 1	0.3569	267.082**
	Year 2	0.6848	611.764**
Diameter	Year 1	0.3933	312.056**
	Year 2	0.7572	877.978**
Branches/whorl	Year 1	0.0181	8.868**
	Year 2	0.0480	14.208**
Crook	Year 1	0.0143	6.965**
	Year 2	0.1308	42.359**
Rating	Year 1	0.0666	34.335**
	Year 2	0.2222	80.479**
Color	Year 1	0.0204	10.024**
	Year 2	0.0529	15.721**

**Significant at $\alpha = .01$.

VITA

George Francis Brown, Jr. was born in Augusta, Georgia, on July 4, 1949. From 1950 to 1967, he moved several times, living in five different states, ending in Connecticut where he graduated from Enfield High School in 1967. The following September he enrolled in the University of Connecticut, and four years later, in June, 1971, he received his Bachelor of Science with High Honors degree with a major in forestry.

In 1971, he enrolled in North Carolina State University where in 1973 he received his Master of Science degree in forestry. From 1973 to 1976 he served as a Security Police Officer for the 341st Security Police Squadron, Malmstrom Air Force Base, Montana.

In 1976 he was employed as an Instructor at Alabama A&M University and began a research project for the development of Christmas trees for commercial production in Alabama. In 1979 he was promoted to Assistant Professor and began a research project on the genetic improvement of Virginia pine for Christmas trees. In addition to this project, he currently is the statistical advisor for the Department of Plant and Soil Science, coordinator of Renewable Resources Extension Act projects, and principal investigator of a U.S.D.A. Forest Service cooperative project on the life cycle of the pine tortoise scale.