

GENOTYPIC VARIATION AMONG SHORTLEAF PINE
SEEDLINGS WITHIN OKLAHOMA

By

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CHAPTER I

INTRODUCTION

There are approximately five million acres of commercial forest land in Oklahoma. The predominant softwood species on these acres is one of the southern pines, shortleaf pine (Pinus echinata Mill.). This species, along with another southern pine, loblolly pine, (Pinus taeda L.), occupies approximately 1.1 million acres of Oklahoma's forest area. The remaining acreage is covered by broadleaf types such as oak-hickory, elm-ash-cottonwood, and oak-cypress-gum.

Indiscriminate cutting practices have resulted in the removal of the average or better phenotypes. Most trees which are presently producing seed for natural and artificial regeneration are trees which were left in the forest because of low vigor, or poor wood quality. Offspring from poor quality trees form poor natural stands and are low value seeds for forest tree plantings.

Tree improvement research, necessary to improve the productive potential of Oklahoma's forested lands, has already begun. Two breeding orchards for the production of certified shortleaf pine seed are currently being established.

Information sought in this study is necessary for the efficient operation of an applied program of forest tree selection and breeding.

CHAPTER II

LITERATURE REVIEW

Need for Seed Source Testing

Forest tree seed should not be planted on a site different from that to which it is adapted. In pointing out the importance of extremes in climatic conditions in natural selection of genotypes, Bates (2) surmised that variation in climatic conditions can alter the genotypic structure in local populations. Using several forest tree species, Frankhauser (7) gave examples of survival as related to altitude and climate of origin of seed. He concluded that forest tree seed which has been collected as nearly as possible to the planting site should be used. This is not always true. In a study by Posey et al. (15) on wood properties of shortleaf pine, Arkansas races survived as well and produced more cellulose than trees from local Oklahoma sources. Realizing the importance of determining patterns of geographic variation in forest tree species, Squillace (21) stated that "the nature of geographic variation is important to land managers because if differences are largely genetic, they must use care in selecting sources of seed for forest plantings."

A knowledge of variation patterns becomes extremely important when considered in conjunction with tree improvement programs. Rudolf (16) stated that "the primary objective of forest tree improvement usually is to develop trees which combine large size, relatively rapid growth, desirable form and branching habit, and good quality wood. Unless these trees are hardy in the locality in which they are to be grown, possession of these valuable characters will be of little value."

Rangewide Seed Source Tests

Racial variation has been reported in virtually every commercially important tree species. Critchfield (6) found a correlation for the geographic origin of lodgepole pine (Pinus contorta Dougl.) with germination time and germination amount. Three ecotypes for winter hardiness, branching habit, and rooting habit were described by Wright (29) in nursery tests with white ash (Fraxinus americana L.) seedlings from the eastern United States and Canada. A similar nursery test of red ash (Fraxinus pennsylvanica Marsh.) showed that this species was also composed of three ecotypes for one-year height growth and winter hardiness (30). Variation in cotyledon number of Douglas-fir (Pseudotsuga menziesii Mirb.) demonstrated a significant correlation with source of seed in a study by Owen (14). Sitka spruce (Picea sitchensis Bong.) seedlings from forty-seven provenances showed a developmental variation pattern in shoot apex

development which was related to the natural species distribution (4). Significant differences were observed by Genys (8) among one and two-year-old white pine (Pinus strobus L.) seedlings from different sources. He observed that some traits which showed differences were related to geographic factors. By examining differences in foliage characters, Weidman (25) delineated geographic sources in ponderosa pine (Pinus ponderosa Laws.). Squillace (20) stated that thirty-six percent of the variation in height growth of ponderosa pine is due to geographic seed source. An ecotypic pattern of variation was described by Wells (26) both between and within two varieties of ponderosa pine for several characters of one and two-year old seedlings. Needle characteristics of slash pine (Pinus ellioti Engelm.) were correlated with the geographic distribution of that species in studies by Mergen (10) and Sorensen (17). Squillace (21) found highly significant differences for needle length, one-year height, and stomatal distribution in slash pine seedlings from stands throughout the species range. Differences in volume production among geographic seed sources of loblolly pine were reported by Wakeley (23) and Maple (9). Wells (28) reported differences among sources for the same species in height growth and rust infection as did Thor (22) for number of stomatal lines. Differences in height of two-year-old shortleaf pine were reported in southern Illinois by Minckler (12). He attributed the differences to the fact that seed were collected from widely separated parts of the

species range. Wakeley (24) reported significant differences in survival and height growth of shortleaf pine seedlings three and five years of age from different geographic sources. There were differences among sources ranging from north to south, but little or no variation among sources ranging from east to west. This means that, in general, one can go farther east or west to collect seed for plantings than north or south.

Seed Source Studies Involving Smaller Areas

Studies of variation in forest trees, for the most part, have involved samples taken from the entire species range. These studies generally revealed large amounts of both phenotypic and genotypic variation. In carrying out these studies researchers began to realize that with more refined techniques, both experimentally and statistically, a broad region represented by a few sources might be found to be made up of many provenances (11). Rudolf stated that seed source studies should be localized to cover the range of growing conditions in which the species may be planted (16).

In seed source studies representing small portions of a species range, researchers found that differences among seed sources were present but generally smaller than those reported in studies of larger areas.

In a test of thirteen Douglas-fir seed sources, Morris (13) found significant differences in rate of growth. Wright (31) reported differences in winter kill and

branchiness for silver maple (Acer saccharinum L.) seedlings from four sources in Indiana. Barber (1) found significant differences in survival among one-year-old and three-year-old offspring of three loblolly pine stands in Georgia. Many studies have been made over areas involving one or two states. These studies are necessary prerequisites to selection and breeding programs within these states. Squillace (19) showed distinct site-moisture ecotypes as little as one-half mile apart in continuous stands in a study of western white pine (Pinus monticola Dougl.).

Justification and Aims of a Seed

Source Study Within Oklahoma

If the localities from which sample plots are chosen are characterized by different environments and some degree of reproductive isolation is present, racial variation will occur. It has been shown that selection pressures may discriminate against gene infiltration from trees which are adapted to radically different sites, even though the sites are adjacent. In studies of smaller areas, the areas should be characterized by varying environmental conditions. Upon observation of a few facts concerning the environmental diversity in eastern Oklahoma, it may be seen that the opportunity for racial differentiation does exist.

The values in Table I represent the maximum and minimum for nine site factors at the sites from which seeds were collected. The differences, in some instances, are as large

as those which have been reported for studies of much larger areas. Since Oklahoma is located on the extreme western edge of the shortleaf pine range, the opportunity for differentiation is present.

TABLE I
EXTREMES IN SHORTLEAF PINE SITE CONDITIONS
IN SOUTHEASTERN OKLAHOMA

Site Factor	Max.	Min.	Diff.
Avg. Number of Frost-free Days	240	200	40
Avg. Annual Precipitation, inches	51	41	10
Avg. July Temperature, degrees F.	83.2	79.8	3.4
Avg. January Temperature, degrees F.	44.7	38.7	6.0
Avg. Summer Precipitation, inches (June-Aug.)	4.9	3.5	1.4
Latitude	36°00'	33°45'	3°45'
Longitude	96°00'	94°30'	1°30'
Elevation	2267	403	1864
Site Index	65	29	36

*Site index is a measure of site quality based on the average height that the dominant and codominant trees attain at 50 years of age.

Objectives of the Study

(1) The first objective is to study inherent variation in shortleaf pine seedlings and the association of this variation with environmental factors in Oklahoma.

The amount and type of variation inherent in a tree species can have an important effect upon the method of tree selection and breeding employed. For example, if little variation is present within stands then individual-tree selection would not be a promising method for obtaining improved types. This same principle applies to inherent variation associated with the geographic position of the stand.

If inherent variation can be related to factors of the environment we may conclude that these factors were instrumental in natural selection which alters the genetic structure of a population.

(2) The second objective is to help delineate practical seed collection zones for shortleaf pine in Oklahoma.

Trees should be planted on sites to which they are adapted. Once seedlings are planted, the forester must manage a crop which cannot be easily or cheaply changed.

(3) The third objective is to determine the heritability of some taxonomic and morphological characteristics of shortleaf pine seedlings.

(4) The final objective is to gather evidence to help determine whether the maintenance of two seed orchards separated on the basis of stand location is justified.

The maintenance of two seed orchards can be justified only if heritable differences in economically important traits can be related to the geographic origin of the seed.

CHAPTER III

METHODS AND MATERIALS

In 1964 a study of morphological characters of mature shortleaf pine in Oklahoma was initiated. Fifty stands were selected to provide representation of geographic variation in Oklahoma by choosing stands closest to the intersection of each 15 degrees of latitude and longitude over the range of shortleaf pine in eastern Oklahoma. Each stand consisted of forty acres of timbered land.

From each stand 10 parent trees were selected with the following stipulations:

- (1) No open grown trees were selected.
- (2) Only dominant or codominant trees were chosen.
- (3) Selected trees were at least two hundred feet apart to reduce the likelihood of having the same parentage.

One hundred six parent trees representing thirteen stands in eastern Oklahoma (Figure 1) yielded sufficient seed for nursery planting. The seeds were kept separate by parent trees.

The seeds were stratified by soaking in distilled water at room temperature for twenty-four hours, drawing the water off, then storing at thirty-five degrees fahrenheit for sixty

- 1 -- Stands located on coastal-plain soils.
 3 -- Stands located on Ouachita-highland soils.
 * -- Location of the nursery planting.

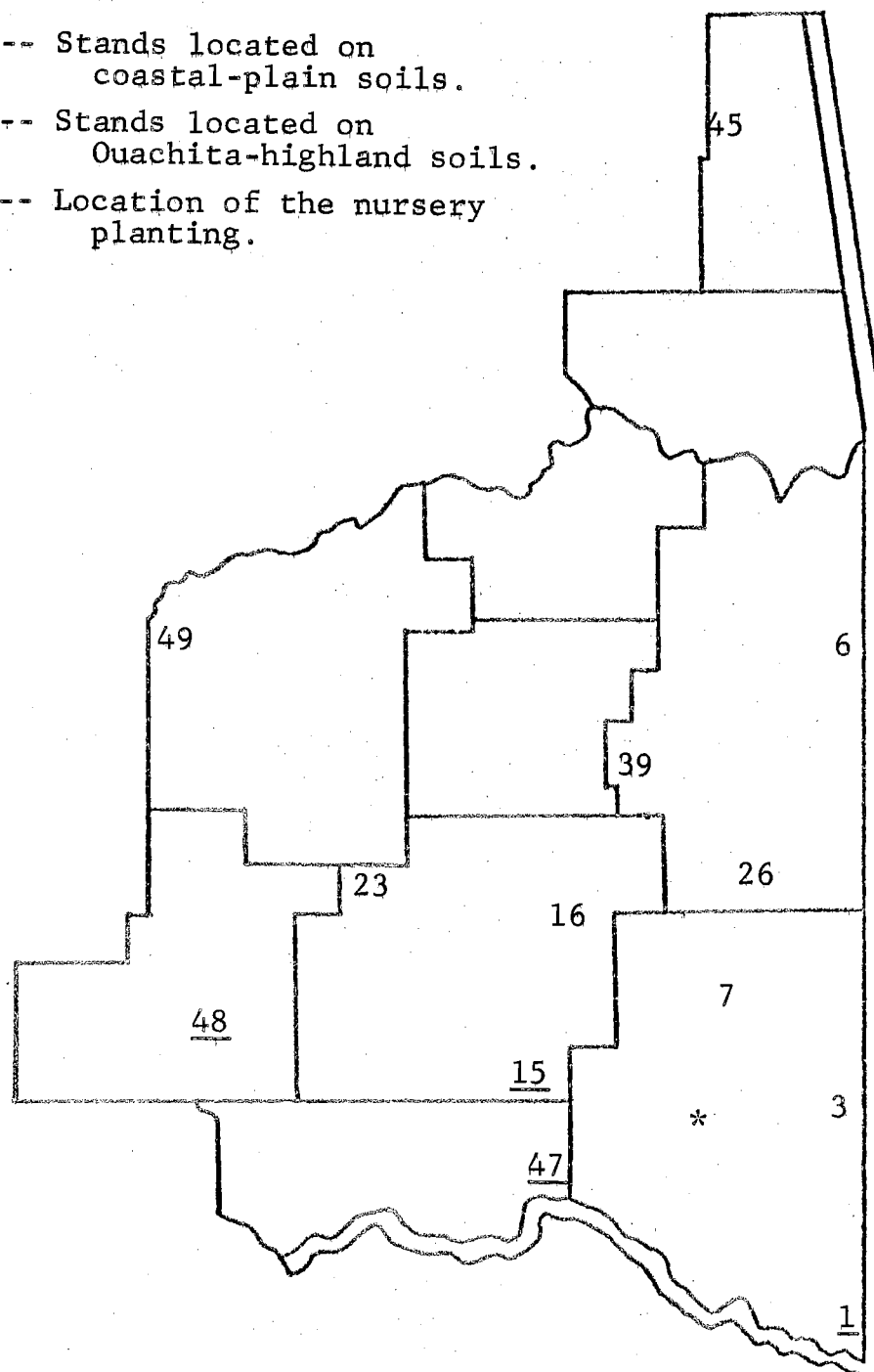


Figure 1. Location of the Thirteen Study Stands in Southeastern Oklahoma

days. After stratification the seeds were treated with latex as a binder, arasan as a bird repellent, and aluminum powder to keep the seeds from sticking together. The seeds were sown in the Oklahoma Forest Tree Nursery at Broken Bow, Oklahoma.

Nursery Layout

The nursery design used was a split-plot. Each of the thirteen stands were randomized within each of eight replications. Each parent tree was then randomized within each stand-plot. All seedlings from a given stand were adjacent in every replication. This was done to facilitate the detection of differences among stands and among parent trees within stands. This design has one undesirable feature in that it will cause an increase in the precision of testing individual-tree progenies and an overestimation of within-stand variance as compared with between-stand variance.

Seeds were planted in a single nursery bed forty inches wide and approximately five hundred feet long. Twenty seeds were sown in each row. Rows were planted six inches apart and seeds two inches apart within each row. Each row of seedlings thus represented a half-sib progeny group.

Sampling

A total of nine seedling characters were sampled. The number of cotyledons was counted on the first five seedlings in each parent-tree row. The length of two cotyledons, one

from the north and one from the south side of the seedling, was measured to the nearest millimeter. The number of growth flushes and the number of limbs were counted immediately before the seedlings were lifted for outplanting. Survival was recorded as the number of surviving seedlings in each parent-tree row. The number of surviving seedlings with winter buds set was counted on December 20, 1967. Seedling height was measured to the nearest half inch as the seedlings were lifted. Seedlings were measured from the root collar to the top of the terminal bud.

Before lifting the seedlings, two needle fascicles were collected for later examination in the laboratory. These needle fascicles were removed just beneath the first whorl of limbs. Only mature needles were chosen. The following measurements were taken from the needles. One needle from each fascicle was measured to the nearest millimeter to determine its length. The number of stomatal lines on the curved face of the same needle was counted.

Trees on the edge of the seedbed were used only when determining survival and the percent survivors with winter buds set.

Statistical Methods

No parent tree which had less than three seedlings surviving in each replication was used in the analysis of the experiment. This reduced the number of parent trees to five per stand, and the total number of individual-tree

progeny to fifteen hundred sixty. This was deemed necessary because of poor survival in the nursery which caused imbalance in all levels of sampling. This imbalance would have made the analysis of data with prepared programs for the I.B.M. 7040 computer extremely difficult. It would also have made the estimation of variance components less reliable.

Analyses of variance were performed for each of the nine study variables in the form shown in Table II. The expected mean squares shown and subsequently the estimates of the components of variance, were derived from a random effects model for a partially heirarchical situation presented by Brownlee (3). To test for significant differences among stands (i.e., $H_0: \sigma_s^2 = 0$) the F' test described by Cochran (5) was used. Confidence levels below the .050 level of confidence will be referred to as nonsignificant.

Simple correlations were computed for all possible combinations of the nine study variables and selected site factors in an attempt to determine which environmental factors might have been involved in natural selection upon the study variables.

Variance components were estimated by solving the equations for the expected mean squares shown in Table II. These estimates were then used to determine heritabilities for the nine study variables.

TABLE II
FORM OF ANALYSES OF VARIANCE

Source of Variation	d.f.	Expected Mean Squares
Replications	(r-1)	$\frac{2}{V_P} + p \frac{2}{V_{RXM(S)}} + mp \frac{2}{V_{RXS}} + smp \frac{2}{V_R}$
Stands	(s-1)	$\frac{2}{V_P} + p \frac{2}{V_{RXM(S)}} + mp \frac{2}{V_{RXS}} + rp \frac{2}{V_{M(S)}} + rmp \frac{2}{V_S}$
Reps X Stands	(r-1)(s-1)	$\frac{2}{V_P} + p \frac{2}{V_{RXM(S)}} + mp \frac{2}{V_{RXS}}$
Parent-trees in Stands	s(m-1)	$\frac{2}{V_P} + p \frac{2}{V_{RXM(S)}} + rp \frac{2}{V_{M(S)}}$
Parent-trees X Reps in S	s(r-1)(m-1)	$\frac{2}{V_P} + p \frac{2}{V_{RXM(S)}}$
Progeny in Pt in Reps in S	rsm(p-1)	$\frac{2}{V_P}$

$\frac{2}{V_S}$ = variance due to difference in geographic location of the stands.

$\frac{2}{V_{RXS}}$ = variance due to the failure of progeny from a stand to perform the same in each rep.

$\frac{2}{V_{M(S)}}$ = variance due to differences among families pooled across stands.

$\frac{2}{V_{RXM(S)}}$ = variance due to the failure of progeny of a parent-tree to perform the same in each rep pooled across stands.

$\frac{2}{V_P}$ = variance due to differences within a family.

Form of Heritabilities

Heritability is a measure of the relative degree of influence of heredity compared to environment. The narrow sense heritability of a character is the fraction of the total variation that is contributed by additive genetic differences and is thus important to plant breeders.

Narrow sense heritabilities were computed in the following form for each of the nine study characters except survival and winter bud set.

$$h^2 = \frac{4 \overline{V_M}^2}{\overline{V_P}^2 + \overline{V_{RXM(S)}}^2 + \overline{V_M}^2}$$

Narrow sense heritabilities were computed for survival and winter bud set on a progeny-mean basis.

$$h^2 = \frac{\overline{V_M}^2}{\frac{\overline{V_{RXM(S)}}^2}{R} + \overline{V_M}^2}$$

This was necessary because of the lack of an estimate of variance within a parent-tree row for these two study characters.

A high heritability indicates that the character is under a high degree of genetic control and is affected little by the environment.

CHAPTER IV

RESULTS AND DISCUSSION

Physiological traits are related to the life processes and functions of organs and tissues. The plant breeder's interest in improving traits which enable the plant to survive or perform better in its environment should be obvious. Interest in studying other traits may be somewhat less evident.

There are three reasons for studying these traits. The first is that if genetic differences in these traits exist between populations these traits provide a means for identifying the populations. This is particularly important in young plants. The identification of individuals not adapted to a site before planting saves the expense of planting and maintaining that individual which would perform less well than an adapted plant. Secondly, these characters provide a means of studying inheritance in trees at an early age. Lastly, these seemingly unimportant traits in young plants can provide meaningful information about variation in a population. If natural selection can modify the genetic structure of a population for these traits, modification of the genetic structure of the same population for more immediately important traits would seem likely.

Numerical Results

Means, maximum, and minimum values for the nine study characters on the basis of stand means and parent-tree means are presented in Table V for comparison.

Simple linear correlation coefficients for the nine study characters with selected site factors are presented in Table VI. Correlation coefficients were computed on the basis of stand means.

In Tables VII through XV mean squares and estimates of variance components for each of the nine study characters are presented for comparison. Levels of significance are also shown in these same tables for each test performed.

For each comparison, the components of variance for stands and for parent-trees within stands are presented in Table XVI as a ratio. This ratio was computed by dividing both components of variance by the component of variance associated with stands.

Cotyledon Number

Cotyledon number is a useful trait in distinguishing between intra-specific hybrids in forest trees. Hybridity was confirmed in Douglas-fir seedlings by observing average cotyledon numbers, even though the cotyledon numbers on individual seedlings varied from 5 to 9, and the average cotyledon number of the crosses varied from 6.6 to 7.6 (18). Differences in cotyledon number have been demonstrated in

other forest tree species both among and within geographic locations (21, 8).

In this study cotyledon numbers ranged from 3 to 10 among individual seedlings, from 5.7 to 6.5 on a stand mean basis, and from 4.7 to 6.8 when considering parent-tree averages. Differences among stand means are significant at the .025 level of confidence, and differences among parent-tree means are significant at the .005 level (Table VII).

By examining the ratio of variance associated with stands to that associated with parent trees, 1:3.0, it may be seen that most of the genetic variation associated with this trait is due to differences among parent-trees within stands. A meaningful portion is also related to the location of the stand. The 1:3.0 ratio means that 25% of the total genetic variation is associated with differences among stands and 75% with differences among trees within stands.

Stands with a high average number of cotyledons are from low elevations while stands with low averages are found at high elevations. The correlation coefficient between elevation and number of cotyledons is -0.642 .

Elevation in itself could not cause natural selection. Changes in environmental factors, such as temperature, moisture availability, and soil characteristics, which are associated with changes in elevation are likely responsible for genetic differentiation.

The average number of cotyledons varies positively with the average number of frost-free days and negatively with

the average precipitation during June, July, and August. The correlation coefficients are +0.607 and -0.587, respectively.

Elevation of the stand and the average precipitation during the summer are very strongly correlated. The correlation coefficient is +0.898. Thus, when there is a correlation between elevation and a study character, there is a corresponding correlation of the same sign with summer precipitation.

The average number of cotyledons is correlated positively with seed weight. The correlation coefficient is +0.605.

Cotyledon Length

Cotyledon length varied from 21.1 mm. to 25.6 mm. on the basis of stand means and from 18.1 mm. to 28.6 mm. on the basis of parent-tree means. Stand means are significantly different at the .050 level of confidence and parent-tree means are different at the .005 level (Table VIII).

The average cotyledon length is strongly correlated with the average number of frost-free days at the Parent-tree stand (+0.832). Average cotyledon length is positively correlated with the average January temperature at the stand (+0.576) and with the average July temperature at the stand (+0.645). Cotyledon length is strongly correlated with seed weight (+0.842).

Upon consideration of the ratio of among stand to within stand variation (1:4.2) it may be seen that the proportion

of genetic variation associated with differences among stands is approximately 20% of the total genetic variation and thus would deserve due consideration in a program of selection and breeding.

Number of Stomatal Rows

Stomatal analyses have been shown to be a valid test for identifying putative pine hybrids (10). The number of stomatal lines showed evidence of racial variation among six loblolly pine sources tested in Tennessee (22).

In this study no significant differences were found among stands for the number of stomatal rows at the .050 level of significance (Table IX). The stand means ranged from 7.0 to 7.8. There is considerable variation among parent trees within stands. Parent-tree means range from 6.6 to 9.0. These differences are significant at the .005 level of significance (Table IX).

The number of stomatal rows is negatively correlated with annual precipitation at the parent stand (-0.564). Seedlings with more rows of stomates are from stands which have smaller amounts of precipitation annually. This trend may seem reversed, but the relationship between environment and stomatal frequency is much more complicated than the simple correlation between annual precipitation and the number of stomatal rows suggests.

Upon examination of the ratio of variance among stands to variance within stands, (1:13.1), it is evident that the

importance of selecting among stands is less important than with cotyledon number or cotyledon length.

Needle Length

The stand means for needle length varied from 82.0 mm. to 99.5 mm. and demonstrated a positive correlation with seed weight (+0.622). Parent-tree averages ranged from 80.4 mm. to 109.8 mm.. Differences among these means are significant at the .005 level of confidence (Table X).

The variance component associated with stands is insignificant when compared to the variance component associated with parent trees within stands. The ratio of these two components of variance is 1:81.7.

Number of Limbs

The number of limbs is an important consideration in trees of merchantable age. In conifers compression wood is associated with limbs. Compression wood has an increased amount of lignin and an accompanying decrease in cellulose content. The effect of compression wood is to make the wood less desirable as lumber or for pulping.

If the relationships between trees in this study hold constant in the continuing study of the outplanted seedlings, this will provide an important tool for use in early screening of selections.

Variation on an individual seedling basis for number of limbs is very great in this study. Seedlings had from 0 to

9 limbs. Stand means were not significantly different at the .050 level of significance, ranging from 1.3 to 2.1. However, differences among parent trees within stands are significant at the .005 level of confidence (Table XI). On a parent-tree mean basis the minimum and maximum are 0.5 and 3.3.

The estimate of the component of variance associated with differences among stands is a small negative value. The best estimate for this component is zero, hence the 0:1 ratio between variance components associated with stands and parent trees within stands. This ratio demonstrates that selection for number of limbs should be carried out on an individual-tree basis.

Seedling Height

One-year seedling heights vary from 5.0 inches to 8.5 inches within stands and from 5.2 inches to 7.2 inches among stands. These differences are numerically small. However, they represent increases in height over the poor tree of 70% and the poor stand of 19%, respectively. Differences among stand means are not significantly different at the .050 level of confidence. These differences are significant at the .25 level of confidence (Table XII).

The 1:4.7 ratio between variance components associated with differences among and within stands demonstrates that about 20% of the genetic variation is associated with

location of the stand and thus becomes important in an improvement program.

If these relationships hold as the outplanted seedlings approach merchantable age, differences will be very meaningful.

One-year seedling heights on a stand mean basis are negatively correlated with elevation (-0.883) and positively related to the average number of frost-free days ($+0.555$). Seedling heights are also negatively correlated with the average amount of summer precipitation (-0.807).

It is interesting to note that the four stands with the highest mean seedling heights are not lowest in elevation or highest in the average number of frost-free days. These four stands are the only stands located on coastal-plain soils. Coastal-plain soils are light-colored acid sandy to loamy soils as opposed to heavier and shallower soils developed on sandstone and shales which characterize the Ouachita highlands (Figure 1). This may be indicative of an adaptation to soil-moisture relationships which favor rapid early growth in shortleaf pine seedlings.

Winter Bud Set

Many woody plants protect themselves from the rigors of winter by going dormant. In forest trees this is commonly called "hardening off". Shortleaf pine seedlings exhibit a characteristic purple hue in their needles when they go dormant. Many of the seedlings also set terminal buds.

Differences in winter bud set were significant among stands at only the .10 level of confidence (Table XIII). Stand means varied from 4.9% to 16.7%. Differences among parent trees within stands are significant at the .005 level of confidence (Table XIII). These means range from 1.2% to 25.9%.

Stand means for winter bud set were negatively correlated to average annual precipitation (-0.592). It is tempting to attribute the onset of dormancy to a lack of moisture. There are, in all likelihood, several other factors which contribute to bringing about dormancy in seedlings. This statement is supported by the relationship of longitude with winter bud set. The correlation between winter bud set and longitude of the parent-tree site is very strong (+0.758). Since longitude and average annual rainfall are significantly correlated this suggests that other factors of the environment which are associated with latitude are affecting the apparent natural selection for percentage of winter buds set. The relationship of position of stand to winter bud set may offer more information. The four stands which have the greatest percentage of buds set, stands 23, 45, 48, and 49 (Figure 1), are located on the extreme limits of the short-leaf pine range. This may mean that trees on the extremes of the species range have adapted to extremes in environmental factors by going dormant earlier.

The percent winter buds set showed a meaningful portion of genetic variation associated with stands. The ratio of

1:3.1 between components of variance associated with stands and trees in stands suggests that the location of the stand from which trees are selected is very important in improvement for this trait. This means that about 25% of the total genetic variation is associated with the geographic position of the stand.

Survival

Survival for the experiment as a whole was poor. The average number of survivors per parent-tree row for the whole experiment was 11.8. This represents a survival percentage of 59 based on a possible twenty survivors per parent-tree row.

This low survival can be attributed in great part to heavy rains during the week following planting. These rains washed seeds in some areas of the seed bed completely away and moved others so that identification was impossible. These unidentifiable seedlings were pulled shortly after they emerged and thus were not included in survival counts. For this reason the results of the analysis on survival cannot be extended to apply to natural populations of shortleaf pine seedlings.

Number of survivors per parent-tree row averaged 10.8, (54%), to 13.4, (67%). These differences are not statistically significant. Differences within stands are significant at the .005 level of confidence (Table XIV). They range from 8.2, (41%), to 16.0, (80%). Survival is strongly

correlated with seed weight (+0.776). This indicates that selection for heavier seed for plantings is advantageous from the standpoint of survival.

The best estimate of the component of variance associated with differences among stands is again zero. The ratio of variances associated with stands and trees in stands, (0:1), points to the fact that selection among stands for survival would not be as profitable as selection on an individual-tree basis.

Number of Growth Flushes

The average number of growth flushes showed essentially no differences among stands. The mean of parent trees varied only from 1.2 to 2.2 even though they were statistically significant at the .005 level of confidence (Table XV).

The ratio 0:1 between variance components associated with stands and trees in stands again demonstrates that genetic differences among stands are small as compared to differences among trees within stands.

The average number of growth flushes exhibited a correlation coefficient of +0.585 with seed weight.

General

The basic premise underlying a seed source study is a simple one. Forest trees growing in different localities are phenotypically different. They differ due to differences in genotype and environment. Seeds from different trees

grown in a common environment exhibit only genotypic differences. The difficulty in studies of this type, especially when examining very young trees, is providing a common environment.

The difficulties become evident when one considers that each genotype has carried a little of its environment with it to the study site in the form of the seed. Thus, it may be seen that if a character is strongly related to seed characteristics, differences may not be entirely genetic in nature.

Cotyledon number, cotyledon length, survival, needle length, and the number of flushes are correlated with seed weight on a stand mean basis.

If there is an effect of seed weight upon the genotypic expression of a character it would tend to make maternal half-sibs more alike due to a common environment during seed formation than progenies less closely related. Thus, another indication of non-genetic maternal effects might be an unusually large component of variance associated with parent-trees in relation to the component of variance associated with its error term (21). Table III shows ratios of the variance component associated with differences due to parent-tree X replication interaction for each study variable.

The correlation between seed weight and cotyledon length equals +0.842 and the correlation between seed weight and cotyledon number equals +0.605. The ratios between the components of variance associated with parent-trees to its

TABLE III

RATIO OF COMPONENT OF VARIANCE ASSOCIATED WITH PARENT-TREES IN STANDS TO THE COMPONENT ASSOCIATED WITH PARENT-TREES X REPLICATIONS IN STANDS FOR NINE SEEDLING CHARACTERS OF SHORLEAF PINE

Study Character	Ratio
Cotyledon Number	6.8
Cotyledon Length	48.6
Number of Stomatal Lines	1.2
Needle Length	1.2
Number of Limbs	1.6
Seedling Height	1.0
Winter Bud Set	0.2
Survival	0.3
Number of Growth Flushes	2.2

error term for cotyledon length and cotyledon number are 48.6 and 6.8, respectively. Based on this apparent association with seed weight and on these large ratios it may be seen that maternal effects probably play an important role in determinations of genetic variation in cotyledon length, and possibly to a lesser degree in cotyledon number.

The other variables associated with seed weight (survival, needle length, and the number of growth flushes) may not be related directly to seed weight, but to some factor of the environment which also affects seed weight.

Cotyledon length and cotyledon number show significant statistical differences among stands at the .050 and .025 levels of confidence, respectively. All nine study variables demonstrate differences among parent-trees within stands significant at the .005 level of confidence.

Significance of differences among stands for the remaining seven study variables may be masked by three factors. First, the replication X stand interaction is very large for most of the study variables. Secondly, the nursery planting utilized does not allow separation of the effects of differences among stands from the effects due to differences among the plots in which all trees from the stand were planted. Finally, the F' test may not be precise for the case of four variances (5).

Differences among and within stands are numerically small for all study variables. This is not surprising in one-year-old material collected from stands located in a

relatively small area. If these relationships hold as the outplanted seedlings approach maturity, these differences will take on new meaning. The ability to select for economically important characters based on seedling performance would be very advantageous.

The maintenance of two seed orchards may be justified. This study has revealed that differences between one-year seedling heights and the number of cotyledons are related to the elevation of the stand. This fact in itself is not sufficient justification, but lends credence to empiric observations on the natural population which seem to justify this dual maintenance. Further justification may be found in the study of differences in the outplanted seedlings as they mature.

Heritabilities

Heritabilities for all nine study characters are presented in Table IV. These values are not to be interpreted as exact values because estimates of heritability based on a relatively small number of families grown in only one location tend to be unreliable. The heritabilities computed in this study may be examined relative to one another.

Cotyledon length and cotyledon number both have very high heritabilities. They are 1.00 and 0.82, respectively. The estimate of heritability for cotyledon length exceeded 1.00. This value is not possible on the scale from 0.0 to 1.0 where 1.0 denotes complete control by the genotype and

no environmental modification. The cause of this inflated estimate is probably that the variance among half-sib families is inflated due to maternal effects. These non-genetic effects probably affected the estimate of heritability for cotyledon number in the same way.

It should be pointed out again that the estimates of heritability for survival, 0.70, and the percent winter bud set, 0.62, were computed on a family-mean basis. A great over-estimate of genetic gain will result if family heritabilities are used when the selection is based on the phenotypic performance of individual trees (32).

Needle length, number of limbs, number of stomatal rows, and the number of growth flushes have heritabilities of 0.38, 0.34, 0.32, and 0.30, respectively.

The estimate of heritability for seedling height is 0.48. Traits that have meaningful variation on an individual-tree basis and relatively high heritabilities, offer great prospects for improvement. As an example, 70% difference was noted earlier between the low and high parent-tree means for one-year seedling height. If we use 70% as the selection differential, and apply the heritability of 0.48 for seedling height, we can expect gains of 33.6% in one generation of individual-tree selection.

TABLE IV
NARROW SENSE HERITABILITIES FOR NINE SEEDLING
CHARACTERS OF SHORLEAF PINE

Study Character	Heritability
Cotyledon Number	0.82
Cotyledon Length	1.00*
Number of Stomatal lines	0.32
Needle length	0.38
Number of Limbs	0.34
Seedling Height	0.48
Winter Bud Set	0.62
Survival	0.70
Number of Growth Flushes	0.30

*The value of h^2 for Cotyledon length exceeded 1.00.

CHAPTER V

SUMMARY AND CONCLUSIONS

The findings of this study indicate that there is considerable variation among seedlings of shortleaf pine from natural stands in Oklahoma.

Correlations between environmental factors at the parent-tree site and patterns of variation in seedlings grown in the nursery suggest that these environmental factors caused selection pressure and subsequent clinal variation in several traits of shortleaf pine seedlings.

These relationships further suggest that a separation of seed orchards on the basis of geographic location of the parent-tree stand may prove practical.

Comparison of the components of variance associated with differences among stands and differences among parent-trees within stands indicate that if selections were made for any of the nine study variables, the greatest gains could be made by individual-tree selection. However, for cotyledon length, cotyledon number, seedling height, and percent winter bud set, the location of the stand should be considered when making selections.

Seedlings from lower elevations exhibited greater height growth at the end of one growing season. Among

stands from lower elevations, those on coastal-plain soils produced seedlings with the greatest one-year heights. Seedlings from stands at lower elevations also had the greatest number of cotyledons.

Seedlings from stands with the longest frost-free periods had the longest cotyledons.

The percent seedlings with winter buds set on one date was associated with average annual precipitation and longitude of the parent-tree stand. The four stands with the highest percentage of winter buds are located on the extremes of the range of shortleaf pine in Oklahoma.

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A P P E N D I X

TABLE V

MEANS, MAXIMUM AND MINIMUM VALUES FOR NINE SELECTED
CHARACTERS OF SHORLEAF PINE ON THE BASIS OF
STAND MEANS AND PARENT-TREE MEANS

Seedling Character	Population Mean	Stand Means		Parent-tree Means	
		Min.	Max.	Min.	Max.
Cotyledon Number	6.0	5.7	6.5	4.7	6.8
Cotyledon Length (mm.)	23.7	21.1	25.6	18.1	28.6
Number of Stomatal Lines	7.6	7.0	7.8	6.6	9.0
Needle Length (mm.)	91.5	82.0	99.5	80.4	109.8
Number of Limbs	1.7	1.3	2.1	0.5	3.3
Seedling Height (in.)	6.4	5.2	7.2	5.0	8.5
Winter Bud Set (%)	10.0	4.9	16.7	1.2	25.9
Survival	11.8	10.8	13.4	8.2	16.0
Number of Growth Flushes	1.7	1.5	1.8	1.2	2.2

TABLE VI
SIMPLE CORRELATION COEFFICIENTS AMONG NINE SEEDLING
CHARACTERS OF SHORLEAF PINE AND SELECTED SITE
FACTORS ASSOCIATED WITH THE GEOGRAPHIC
LOCATION OF THE STAND

Character	Corr. Coeff.	Site Factor
Cotyledon Number	-0.642*	Elevation
Cotyledon Number	0.607*	Av. No. of Frost-Free Days
Cotyledon Number	-0.587*	Summer Precipitation
Elevation	0.898**	Summer Precipitation
Cotyledon Number	0.605*	Seed Weight
Cotyledon Length	0.832**	Av. No. of Frost-Free Days
Cotyledon Length	0.576*	Av. January Temperature
Cotyledon Length	0.645*	Average July Temperature
Cotyledon Length	0.842**	Seed Weight
No. of Stomatal Rows	-0.564*	Av. Annual Precipitation
Needle Length	0.622*	Seed Weight
Seedling Height	-0.883**	Elevation
Seedling Height	0.555*	Av. No. of Frost-Free Days
Seedling Height	-0.807**	Summer Precipitation
% Winter Bud Set	-0.592*	Av. Annual Precipitation
% Winter Bud Set	0.758**	Longitude
No. of Survivors	0.776**	Seed Weight
No. of Flushes	0.585*	Seed Weight

* indicates the correlation coefficient is significantly different from zero at the .050 level of confidence.

* indicates the correlation coefficient is significantly different from zero at the .010 level of confidence

TABLE VII
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR COTYLEDON NUMBER OF SHORLEAF PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Signif- icance
Replications	7	0.72222	0.00066	N.S.
Stands	12	7.77189	0.03740	.025
R X S	84	0.59215	0.00836	N.S.
Parent-trees in stands	65	3.15833	0.11214	.005
Parent-trees X R in stands	364	0.46675	0.01648	.005
Progeny in Pt X R in stands	1040	0.41730	0.41730	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$.

N.S. means level of significance is less than .05.

TABLE VIII
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR COTYLEDON LENGTH OF SHORLEAF PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Signif- icance
Replications	7	45.13605	0.18311	.005
Stands	12	279.56966	1.22631	.050
R X S	84	9.38988	0.20642	.010
Parent-trees in stands	65	129.31506	5.12589	.005
Parent-trees X R in stands	364	6.29348	0.10537	.005
Progeny in Pt X R in stands	1040	5.97737	5.97737	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$.

N.S. means level of significance is less than .05.

TABLE IX
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR NUMBER OF STOMATAL LINES OF
SHORTLEAF PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Significance
Replications	7	2.17635	-0.00044	N.S.
Stands	12	6.42611	0.00960	N.S.
R X S	84	2.26264	0.04198	.050
Parent-trees in stands	65	4.64399	0.12546	.005
Parent-trees X R in stands	364	1.63283	0.10345	.005
Progeny in Pt X R in stands	1040	1.32247	1.32247	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$.

N.S. means level of significance is less than .05.

TABLE X
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR NEEDLE LENGTH OF SHORLEAF PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Signif- icance
Replications	7	126.60750	-8.64401	N.S.
Stands	12	2511.36458	0.32429	N.S.
R X S	84	1812.19040	101.31743	.005
Parent-trees in stands	65	928.36530	26.49735	.005
Parent-trees X R in stands	364	292.42890	21.12720	.005
Progeny in Pt X R in stands	1040	229.04730	229.04730	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$.

N.S. means level of significance is less than .05.

TABLE XI
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR THE NUMBER OF LIMBS OF SHORLEAF
PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Signif- icance
Replications	7	1.55199	-0.02482	N.S.
Stands	12	9.73557	-0.01829	N.S.
R X S	84	6.39268	0.24260	.005
Parent-trees in stands	65	8.29134	0.23073	.005
Parent-trees X R in stands	364	2.75361	0.14116	.005
Progeny in Pt X R in stands	1040	2.33013	2.33013	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$.

N.S. means level of significance is less than .05.

TABLE XII
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR SEEDLING HEIGHT OF SHORLEAF PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Signif- icance
Replications	7	9.08609	-0.06793	N.S.
Stands	12	39.85046	0.07490	N.S.
R X S	84	22.33350	1.27128	.005
Parent-trees in stands	65	11.79246	0.35534	.005
Parent-trees X R in stands	364	3.26429	0.33595	.005
Progeny in Pt X R in stands	1040	2.25643	2.25643	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$.

N.S. means level of significance is less than .05.

TABLE XIII
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR WINTER BUD SET OF SHORLEAF PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Signif- icance
Replications	7	938.32100	12.52940	N.S.
Stands	12	533.23100	6.31517	N.S.
R X S	84	123.91000	5.45180	.005
Parent-trees in stands	65	253.36500	19.58925	.005
Parent-trees X R in stands	364	96.65100	96.65100	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$.

N.S. means level of significance is less than .05.

TABLE XIV
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR SURVIVORS PER PARENT-TREE ROW OF
SHORTLEAF PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Signif- icance
Replications	7	4.17133	-0.36664	N.S.
Stands	12	20.57560	-0.54027	N.S.
R X S	84	28.00324	4.37254	.005
Parent-trees in stands	65	20.32403	1.77293	.005
Parent-trees X R in stands	364	6.14053	6.14053	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$. N.S. means level of significance is less than .05.

TABLE XV
MEAN SQUARES AND ESTIMATES OF VARIANCE COMPONENTS
FOR THE NUMBER OF FLUSHES OF SHORLEAF
PINE SEEDLINGS

Source of Variation	d.f.	Mean Squares	Estimate of Variance Component	Level of Significance
Replications	7	0.24101	-0.00289	N.S.
Stands	12	1.11046	-0.00199	N.S.
R X S	84	0.80600	0.03401	.005
Parent-trees in stands	65	0.84006	0.02268	.005
Parent-trees X R in stands	364	0.29574	0.01033	.005
Progeny in Pt X R in stands	1040	0.26474	0.26474	

The significance level associated with each mean square denotes the probability of obtaining an F (or F' in testing for differences among stands) as large as the calculated value of F (or F') under the null hypothesis, $H_0: \sigma^2 = 0$.

N.S. means level of significance is less than .05.

TABLE XVI
 RATIO OF VARIANCE COMPONENT ASSOCIATED WITH STANDS
 TO VARIANCE COMPONENT ASSOCIATED WITH PARENT-
 TREES IN STANDS FOR NINE SEEDLING CHARACTERS
 OF SHORLEAF PINE

Study Character	Ratio
Cotyledon Number	1 : 3.0
Cotyledon Length	1 : 4.2
Number of Stomatal Lines	1 : 13.1
Needle Length	1 : 81.7
Number of Limbs	0 : 1
Seedling Height	1 : 4.7
Winter Bud Set	1 : 3.1
Survival	0 : 1
Number of Growth Flushes	0 : 1

VITA ~

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