# MULTIPLE TRAIT SELECTION IN A POPULATION

# OF EASTERN COTTONWOOD

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# CHAPTER I

## INTRODUCTION

The application of techniques to genetically improve biological populations is relatively new in forestry. Programs for the genetic improvement of southern forest tree species were begun within the last forty years. During this period, emphasis was placed primarily upon improving the southern pines. Consequently, the genetic improvement of southern hardwoods is even newer than for other forest tree species.

The genetic improvement of eastern cottonwood, (*Populus deltoides*, Bartr.), has gained impetus during the past ten years. Fast growth, desirable fiber characteristics, and the ease with which it can be vegetatively propagated make this species a prime candidate for genetic improvement. A great deal of the basic information on inheritance in eastern cottonwood has been derived in the Mississippi delta region where this species is of prime commercial importance. Breeding progress in the Mississippi Valley was reported by Farmer (5) in 1966. Farmer and Mohn (8) reviewed work done from that time until 1970.

Breeding programs for eastern cottonwood have also been instituted by several states and major universities. Such a program was begun at Oklahoma State University in 1967. Progress was summarized by Posey (22) in 1969. The study presented here is one part of this program. Objectives stated at the outset of this study were:

(1) Evaluation of clonal variation in economically important

traits of Oklahoma cottonwood.

(2) Estimation of broad sense heritabilities for each of these traits.

(3) Estimation of genetic correlations between each pair of traits.

These objectives were designed to provide basic genetic information about a population. This information is necessary in planning a program of genetic improvement. It influences the manner in which selections are made and provides a measure of the ease with which each trait considered can be improved.

Since the total value of an individual is often affected by several traits, some form of multiple-trait selection scheme seems appropriate to maximize gains. The method of index selection is usually more efficient than other commonly used multiple-trait selection schemes (28). To date indexes have not been published for selecting in eastern cottonwood populations. The fourth objective of this study is:

(4) The construction of multiple-trait indexes to maximize gains from selecting in an experimentally controlled population of eastern cottonwood.

Clonal selection in experimentally controlled populations is based on estimates of parameters which are dependent on the experimental design used. For example, estimates of variation among clones presented on a clone-mean basis are dependent on the number of blocks and the number of ramets per plot. Thus, indexes developed for clonal selection in experimental plantings are not directly applicable when selecting in the natural population.

The genetic variance in large forest tree populations may be partitioned into a component associated with differences among trees within a geographic location and a component associated with differences among groups of trees from different geographic locations. In most forest tree populations a large proportion of the genetic variance occurs among individuals within geographic locations. Predictions of gains are usually based on this portion of the genetic variance and are expressed on an individual basis. The fifth objective of this study is to:

(5) Construct multiple-trait selection indexes suitable for individual tree selection.

## CHAPTER II

## METHODS AND MATERIALS

### Description of the Natural Population

Selection of the population to be examined in this study was influenced by two basic considerations. First, it seemed desirable to make improved clonal material available as soon as possible. Making selections in Oklahoma and the surrounding area insures that materials will be adapted to local conditions. The second consideration was perhaps more important to the long term success of the program of improvement. One would suspect a considerable amount of differentiation in a wild population occupying a large area characterized by extremes in environmental conditions. If differentiation has occurred in economically important traits within the study area this knowledge will indicate potentially valuable crosses.

The population considered in this study occupies the area depicted in Figure I. Genetic differentiation has most certainly occurred in the study area, This area is occupied by two varieties of eastern cottonwood, (Populus deltoides, Bartr.). P, deltoides var. deltoides occupies the eastern portion of the study area and P. deltoides var. occidentalis Rydb. (P. sargentii, Dode) occupies the western portion. Approximately the western half of Oklahoma is occupied by the intermediate zone of both varieties and intergrades (10,18).

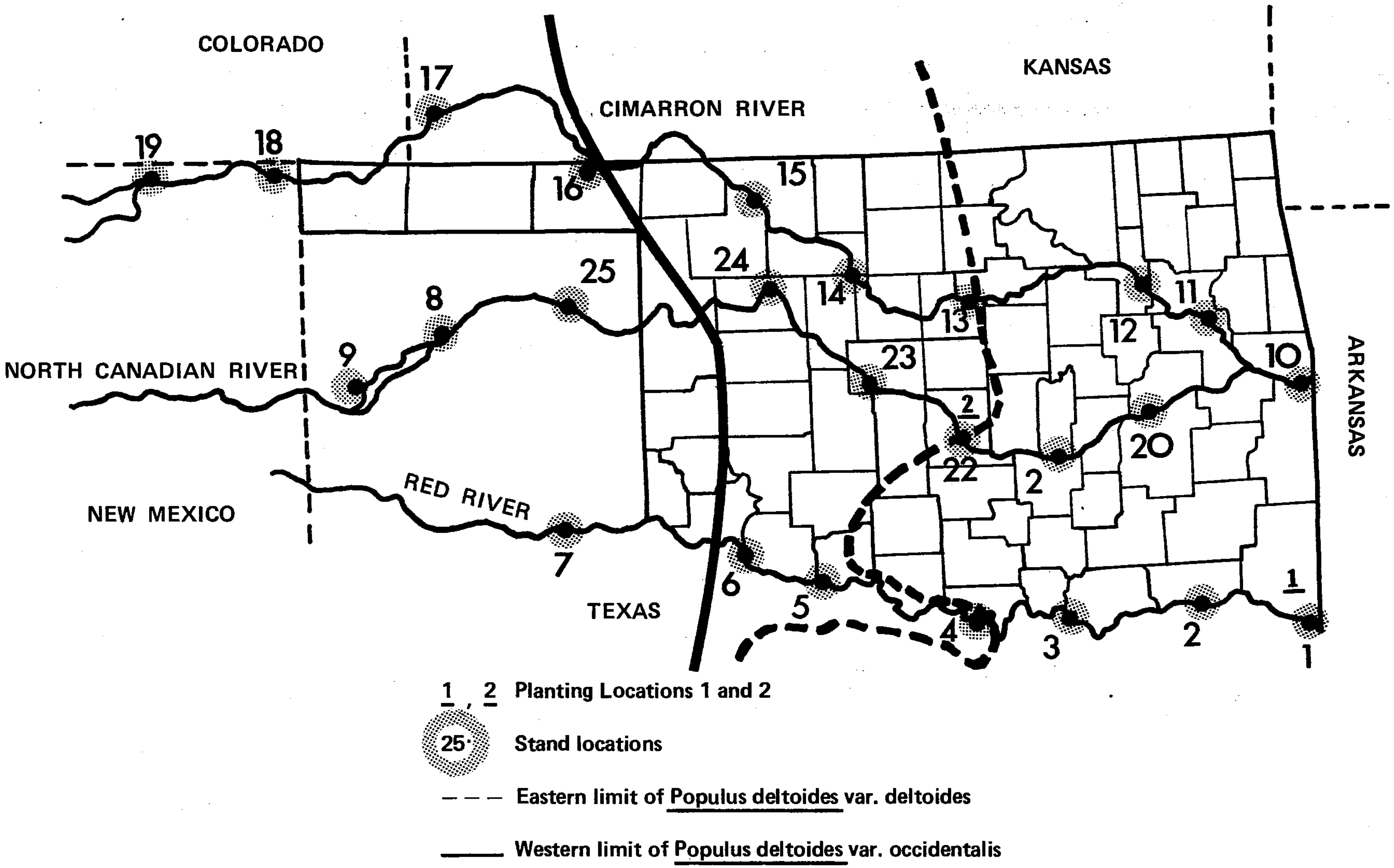


FIGURE 1. LOCATIONS OF THE TWENTY-FIVE SAMPLE STANDS AND TWO PLANTING LOCATIONS

Phenotypic variation in this natural population has been reported by Buxton (3), Posey (22), and Posey, et al. (23), and genotypic variation among vegetatively reproduced one-year-old cuttings from the natural population has been reported by Lynch (19), and Posey (22).

## Sampling in the Natural Population

Twenty-five plots were established sixty miles apart along the Red, Canadian, and Cimarron Rivers from Arkansas to the headwaters of each drainage. Cuttings were collected from ten dominant trees in each stand. This sampling procedure was used to insure the selection of genotypes adapted to each site. Thus, when grown in a common environment, differences among stand means would represent genetic differences resulting from adaptation of the species to varying environmental conditions. This restriction on sampling may have biased the estimates of total genetic variance for the natural population downward since selection of phenotypically similar individuals in each stand may have resulted in greater genetic similarity between individuals in the same population than would be expected had sampling been entirely random.

## Description of the Experimental Material

Vegetative cuttings representing each of the 250 individual trees sampled were rooted in a nursery bed at a 1.5 x 2 feet spacing. This procedure was necessary to produce sufficient numbers of each genotype for inclusion in the experimental plantings. It was also necessary to ameliorate C effects (31). C effects result when the characteristics of the mature ortet (individual which is cloned) are maintained in the propagule. Wilcox and Farmer (31) recommend using cuttings of uniform age and size to minimize these effects. One hundred fifty-seven clones representing 23 stands produced sufficient material for inclusion in the experimental plantings. Stands 12 and 25 are not represented in the experimental plantings.

## Experimental Plantings

Experimental plantings were made at Location 1 which is southeast of Broken Bow, Oklahoma, and at Location 2 which is at the Oklahoma Forest Tree Nursery south of Norman, Oklahoma. Location 1 is between the Little and Mountain Fork Rivers and is characterized by a Pope alluvial soil (11). Location 2 is on an old alluvium of the South Canadian River which has a Vanoss sandy loam soil (11). Each location was chosen in the belief that it represented the general soil types on which eastern cottonwood might be grown in Oklahoma. The first planting of 153 clones was made at Location 1 in 1968. The following year 132 clones were planted at Location 2. Thus, the effect of different planting years is confounded with the effect of different planting locations.

Since the average annual rainfall in Oklahoma decreases rapidly as one proceeds from east to west, it will probably be necessary to irrigate commercial plantings in the central and western parts of the state. The planting at Location 2 was irrigated during periods when moisture became extremely limiting. Thus, selections made at this location should be suitable for commercial plantings in the central and perhaps western part of the state. Both plantings were cultivated periodically to control weeds.

## Experimental Design

The experimental design at both locations was a randomized block with four blocks. The genotype of the ortet was the experimental unit, and was assigned to a plot randomly within each block. Five vegetative cuttings from the same ortet (ramets) were planted in a single plot at Location 2 while four ramets were planted per plot at Location 1. Spacing between ramets was 12 x 12 feet at both locations.

## Measurements on the Experimental Material

The following measurements were recorded for each individual ramet in both plantings at the end of the third growing season.

Height: Total height was measured to the nearest 0.1 foot.

Diameter: Diameter outside bark was measured to the nearest 0.1 inch at one foot above the ground.

Number of Limbs per Foot: The total number of limbs on the mainstem was divided by the total height of the tree in feet.

Specific Gravity: Four millimeter increment cores were extracted at one foot above the ground. Specific gravity was determined using the maximum moisture content method (26).

Volume: Since this study will be continued until rotation age, it was necessary to develop a prediction equation to nondestructively estimate volume. Volumes were determined for 125 small trees from a nursery bed by determining the volume of each one foot section inside the bark. Measurements for larger trees were obtained by destructively sampling 95 trees at Location 1. Inside bark diameter was recorded for each three foot section. Volumes for individual segments were calculated using the formula for volume of a truncated right cone. Sample trees ranged from 0.8 - 7.0 inches in diameter at one foot above the ground and from 8.8 - 32.1 feet in height. An equation for predicting volumes of standing trees was developed from these data using standard multiple regression techniques. The equation developed was:

$$\hat{Y} = 0.01568 + 0.00142\ D^2H \qquad (1)$$

where $\hat{Y}$ is the estimate of the cubic foot volume inside bark for a single standing tree, D is the diameter in inches outside bark at one foot above the ground, and H is the total height of the tree in feet. The mean ($\bar{Y}$ = 0.327 cubic feet) and the standard error of the estimate (0.098) provide an estimate of the precision of the equation. The square of the multiple correlation coefficient ($R^2$ = 0.968) indicates that about 97 percent of the variation in volume is accounted for by this regression equation.

<u>Dry Weight</u>: Dry weight was calculated using the euation:

$$\hat{Y} = 62.4\ V \cdot S \qquad (2)$$

Where $\hat{Y}$ is the estimated dry weight for an individual tree in pounds, 62.4 is the weight of one cubic foot of water at $15^{o}$ C, V is the volume of the standing tree estimated from equation (1), and S is the estimate of the specific gravity of the whole tree.

The 125 small trees used in developing the volume equation were used to determine the specific gravity of the whole tree. A one inch section from the bottom of each one foot section was used to estimate the specific gravity of that section. Whole-tree specific gravity was then estimated by weighting the specific gravity of each one foot section by its volume. The specific gravity of a four millimeter increment core taken one foot above the ground was used to predict whole-tree specific gravity ($\hat{Y}$) from the equation:

$$\hat{Y} = 0.09901 + 0.76770 \cdot \text{(Specific gravity of the core)}$$

The mean ($\bar{Y}$) is 0.354, the standard error of the estimate is 0.015, and $R^2 = 0.76$.

Disease Score: Damage from disease proved to be a serious problem at Location 1. Early in the third growing season many of the trees in this planting developed large cankers near the ground. These symptoms were the result of infection by *Cytospora* spp.[1/] There appeared to be differences among clones both in occurrence and severity of infection. The following scoring system was devised to classify clones for damage from the disease:

(1) Mainstem missing. Disease evidently the cause.

(2) Seriously affected. Stem weakened, or badly deformed, or an open canker on the mainstem.

(3) Slightly affected. Evidently infected but canker healed over and not deformed.

(4) Apparently uninfected.

Cause could not be determined for the absence of a few trees. Since some of these trees may have been killed by disease the scores for some clones may be high. No damage due to disease was apparent at Location 2.

Insect Damage: The presence of significant numbers of larvae of *Aegeria* spp., a member of the clear-wing moth group, was noted in stems

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[1/] Identified by Dr. E. B. Cowling, North Carolina State University.

being examined to determine the cause of the cankers.[2/] These insects may have been the primary invader which weakened the trees and provided an avenue of attack for the Cytospora fungus.

Although insects caused very little damage at Location 2, there was some evidence of attack by the cottonwood borer, Plectrodera scalator. Damage caused by this insect was scored as follows:

(1) Several entrance holes visible on the mainstem. Tops were broken out of a few trees which had been severely damaged.

(2) One or two entrance holes visible on the mainstem.

(3) Apparently not attacked.

Survival: Location 1 was inundated by water following heavy rains for approximately one week shortly after planting. As a result, survival was reduced to nearly 50 percent. Subsequent insect and disease attacks on the weakened plants reduced survival to 37 percent. Survival at Location 2 was 76 percent.

## Statistical Analysis

Estimated responses to selection in the experimental population were based on estimates of parameters derived from analyses of variance of the form in Table I for each location and Table II for pooled locations. Predicted responses to selection in the natural population were based on estimates of parameters derived from analyses of variance of the form in Table III.

Analyses of variance were performed using plot means as individual observations. Within plot sums of squares were calculated for each

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[2/] Personal communication with Dr. N. W. Flora, Extension Entomologist, Oklahoma State University.

TABLE I

FORM OF THE ANALYSIS OF VARIANCE FOR EACH LOCATION

| Source of Variation | d.f. | Expected Mean Squares |
|---|---|---|
| Blocks | (b-1) | $\frac{\sigma_W^2}{k} + \sigma_{BC}^2 + c\ \sigma_B^2$ |
| Clones | (c-1) | $\frac{\sigma_W^2}{k} + \sigma_{BC}^2 + b\ \sigma_C^2$ |
| Blocks x Clones | (b-1)(c-1) | $\frac{\sigma_W^2}{k} + \sigma_{BC}^2$ |
| Within Plot | $\sum_i (n_i-1)$ | $\frac{\sigma_W^2}{k}$ |

$\sigma_B^2$ = Variance among blocks

$\sigma_C^2$ = Variance among clones

$\sigma_{BC}^2$ = Variance due to interaction of blocks and clones

$\sigma_W^2$ = Within plot variance

b = Number of blocks

c = Number of clones

k = Harmonic mean of plants per plot

$n_i$ = Number of plants in the ith plot

TABLE II

FORM OF THE ANALYSIS OF VARIANCE FOR POOLED LOCATIONS

| Source of Variation | d.f. | Expected Mean Squares |
|---|---|---|
| Locations | (a-1) | $\sigma^2_{BC/L} + c\,\sigma^2_{B/L} + rc\,\sigma^2_{L}$ |
| Blocks/Locations | a(b-1) | $\sigma^2_{BC/L} + c\,\sigma^2_{B/L}$ |
| Clones | (c-1) | $\sigma^2_{BC/L} + b\,\sigma^2_{LC} + ab\,\sigma^2_{C}$ |
| Locations x Clones | (a-1)(c-1) | $\sigma^2_{BC/L} + b\,\sigma^2_{LC}$ |
| Blocks x Clones/ Locations | a(b-1)(c-1) | $\sigma^2_{BC/L}$ |

$\sigma^2_{L}$ = Variance between locations

$\sigma^2_{B/L}$ = Variance among blocks pooled over locations

$\sigma^2_{C}$ = Variance among clones

$\sigma^2_{LC}$ = Variance due to interaction of locations and clones

$\sigma^2_{BC/L}$ = Variance due to interaction of blocks and clones pooled over locations

a = Number of locations

b = Number of blocks in each location

c = Number of clones

TABLE III

FORM OF ANALYSIS OF VARIANCE FOR EACH LOCATION PARTITIONING CLONAL VARIANCE TO ESTIMATE VARIATION AMONG GEOGRAPHIC LOCATIONS AND VARIATION WITHIN GEOGRAPHIC LOCATIONS

| Source of Variation | d.f. | Expected Mean Squares |
|---|---|---|
| Blocks | (b-1) | $\frac{\sigma_W^2}{k} + \sigma_{BC/S}^2 + c\ \sigma_{BS}^2 + sc\ \sigma_B^2$ |
| Stands | (s-1) | $\frac{\sigma_W^2}{k} + \sigma_{BC/S}^2 + b\ \sigma_{C/S}^2 + c\ \sigma_{BS}^2 + bc\ \sigma_S^2$ |
| Blocks x Stands | (b-1)(s-1) | $\frac{\sigma_W^2}{k} + \sigma_{BC/S}^2 + c\ \sigma_{BS}^2$ |
| Clones/Stands | s(c-1) | $\frac{\sigma_W^2}{k} + \sigma_{BC/S}^2 + b\ \sigma_{C/S}^2$ |
| Blocks x Clones/Stands | s(b-1)(c-1) | $\frac{\sigma_W^2}{k} + \sigma_{BC/S}^2$ |
| Within Plot | $\sum_i (n_i - 1)$ | $\frac{\sigma_W^2}{k}$ |

TABLE III (Continued)

$\sigma_B^2$ = Variance among blocks

$\sigma_S^2$ = Variance among stands

$\sigma_{BS}^2$ = Variance due to interaction of blocks and stands

$\sigma_{C/S}^2$ = Variance among clones pooled over stands

$\sigma_{BC/S}^2$ = Variance due to interaction of blocks and clones pooled over stands

$\sigma_W^2$ = Within plot variance

$b$ = Number of blocks

$s$ = Number of stands

$c$ = Adjusted number of clones per stand

$k$ = Harmonic mean of plants per plot

$n_i$ = Number of plants in the ith plot

plot. These sums of squares were pooled over all plots and divided by the harmonic mean of the number of plants per plot. This approximate method is useful when class numbers do not vary greatly (32). Use of this method also dictates that there be no missing plots. Therefore, only clones which had at least one ramet in each block were included in the analysis. Stands 18 and 19 could not be included in the analysis because of their extremely poor survival at both locations. The analysis for Location 1 was performed on 18 clones representing 11 stands. These 11 stands represent a good cross section of the geographic locations sampled. The analysis for Location 2 was performed using 110 clones from 21 stands. Because of the poor survival at Location 1 and the fact that not every clone was planted at both locations, the analysis for both locations was based on 16 clones from 11 stands. Analyses of the arcsin transformation of the survival percentages were performed using all clones at both locations since missing trees were meaningful observations. It was not possible to calculate within plot sums of squares for survival.

Covariance analyses were performed in the same manner as the analyses of variance using sums of products between pairs of variables rather than sums of squares. Components of variance and covariance were estimated by equating mean squares and mean products with their expectations and solving for the desired component.

"F" tests were made in the standard manner for all levels except stands. Satterthwaite's approximate "F" test was used to test this level (4).

# CHAPTER III

## SELECTION IN THE EXPERIMENTAL POPULATION

### Analysis for Pooled Locations

It is important to determine the magnitude of genotype X environment interactions early in any breeding program. The magnitude and type of genotype X environment interaction determines whether selections should be made in one environment or in different environments. It is desirable to repeat a planting in as many locations and as many years as is practical to examine genotype X environment interactions. Most of the genotypes in this study were planted at both locations. As was pointed out previously, planting was done in successive years, thus the genotype X years and genotype X locations components are confounded.

Mean squares for the analysis of clonal variation in the experimental population from the analysis of pooled locations are presented in Table IV. Even though this analysis of variance was done using relatively few clones, statistically significant differences are present for locations X clones for several traits, notably those associated with yield. Comparison of estimates of components of variance for clones and locations X clones in Table V indicates that consideration of the genotype X environment interaction is important when selecting among clones for increased diameter, volume, dry weight, or

## TABLE IV

### MEAN SQUARES POOLED OVER LOCATIONS FOR THE ANALYSIS OF CLONAL VARIATION IN THE EXPERIMENTAL POPULATION

| | | Mean Squares | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Source of Variation | DF | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight | DF | Arcsin of $\sqrt{\text{Survival \%}}$ |
| Locations | 1 | 1087** | 69.87** | .039200** | 6.2658* | 4.0080** | 2281** | 1 | 206959** |
| Blocks/Locations | 6 | 27** | 0.65* | .001373** | 0.7233** | 0.0702** | 37** | 6 | 5538** |
| Clones | 15 | 27** | 1.36 | .003585** | 4.7252** | 0.00874 | 51 | 114 | 1452 |
| Locations x Clones | 15 | 7 | 0.60** | .000390 | 0.4071 | 0.0550** | 30** | 114 | 1202** |
| Blocks x Clones/ Locations | 90 | 4 | 0.23 | .000246 | 0.1995 | 0.0145 | 8 | 684 | 449 |

* $\alpha \leq .05$, ** $\alpha \leq .01$

TABLE V

COMPARISON OF GENOTYPE AND GENOTYPE X ENVIRONMENT INTERACTION COMPONENTS OF VARIANCE

| | Components of Variance | | | | | | |
|---|---|---|---|---|---|---|---|
| Source of Variation | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight | Arcsin of $\sqrt{\text{Survival \%}}$ |
| Clones | 2.5111 | 0.0947 | .000399 | .5397 | 0.004044 | 2.6262 | 31.14 |
| Locations X Clones | 0.6586 | 0.0921 | .000036 | .0519 | 0.010144 | 5.4323 | 188.35 |

survival. Variation due to the interaction of clones X environments is as large or larger than the estimates of genetic variation for these four traits. Thus, if clones were planted in environments different from that at the location where selections were made, predicted gains for these four traits might not materialize. This complication would not be expected with height, specific gravity, or the number of limbs per foot.

Once the presence of significant amounts of genotype X environment interaction are detected, it becomes important to determine if the interaction is one of direction or simply one of magnitude. If the latter case is true, then selection in more than one environment might not be required. The type of genotype X environment interaction was determined by calculating Spearman's rank correlation coefficients between clones at different locations for each trait. The correlation thus calculated indicates the degree to which the rank of a clone mean at one location agrees with the rank of the same clone at the second location. A high rank correlation coefficient would indicate that the genotype X environment interaction was largely one of magnitude, while a low rank correlation coefficient would indicate a difference in the ranking of clone means for the two locations. Rank correlation coefficients are presented in Table VI for traits which had statistically significant genotype X environment interactions. Only the value of $r_s$ for the number of limbs per foot seems large enough to indicate that selections might be made in one environment. Selections for diameter, volume, dry weight, and survival should be made at each location. The rank correlation coefficient is only a gross measure of the type of genotype X environment interaction. It is indicative of major changes in rankings of clones. There could still be some clones which perform about the same in both locations. This was the case in this study. There were three clones (11-3, 22-7, and 22-9) which performed well in both locations and would be selected under criteria to be discussed.

TABLE VI

SPEARMAN'S RANK CORRELATION COEFFICIENTS BETWEEN CLONE MEANS AT TWO LOCATIONS FOR TRAITS WITH STATISTICALLY SIGNIFICANT LOCATION X CLONE INTERACTION

| Trait | $r_s$ |
|---|---|
| Diameter | .43* |
| Number of Limbs/Foot | .86** |
| Volume | .38 |
| Dry Weight | .44* |
| $\sqrt{\text{Arcsin of Survival \%}}$ | .09 |

*,**Significantly different from zero at $\alpha$ = .05 and $\alpha$ = .01

## Genotype X Environment Interactions in Other Studies

Significant clone X site interactions for height and diameter have been found among 79 clones from a natural population of eastern cottonwood along the Mississippi River near Greenville, Mississippi (24). These interactions were present after one, two, and three years for height and after one, two, three, and four years for diameter. Correlation coefficients between sites were .662 for diameter and .619 for height. Both were statistically significant at the 95% level of confidence. These authors concluded that selection for clones adapted to specific sites rather than for clones adapted to a broad spectrum of sites was advisable.

Farmer (7) found significant differences among 30 eastern cottonwood clones grown under different soil moisture regimes for one year. The genotype X environment (clone X treatment) interaction variance, although usually less than the genetic variance, accounted for a substantial portion of the variation in seven growth parameters. Among these were height, diameter, and total dry weight. Specific gravity had only a small portion of the variation associated with the clone X treatment interaction. Rank correlation coefficients between clones in different treatments were all low ($r_s = 0.20$ to $r_s = 0.33$) for the growth parameters.

Results of these studies support the conclusion of this author. Genotype X environment interaction of a nature and magnitude to merit selecting in more than one environment may be expected for growth traits. This requirement may not be necessary for traits like specific gravity and the number of limbs per foot.

## Analyses for Separate Locations

If selections are to be made at both locations, the variance at each must be partitioned. Mean squares for the analyses of clonal variation in the experimental population from the analyses of Locations 1 and 2 are presented in Tables VII and VIII, respectively. Variation

TABLE VII

MEAN SQUARES FOR LOCATION 1 FOR THE ANALYSIS OF CLONAL VARIATION IN THE EXPERIMENTAL POPULATION

| | | Mean Squares | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Source of Variation | D.F. | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight | Disease Score | D.F. | Arcsin of $\sqrt{\text{Survival \%}}$ |
| Blocks | 3 | 168.39** | .3439 | .002105** | 0.6710 | .007682 | 5.60 | 0.3736 | 3 | 11972** |
| Clones | 17 | 14.99** | .7992** | .002017** | 2.6618** | .022342** | 16.14** | 1.2876** | 138 | 1237** |
| Blocks x Clones | 51 | 4.09** | .3062** | .000342 | 0.2863** | .009230** | 6.87** | 0.3002 | 414 | 536 |
| Within Plot $\left(\frac{\sigma^2 W}{k}\right)$ | 90 | 1.86 | .0923 | .000697 | 0.0739 | .002240 | 1.43 | 0.3377 | | |

* $\alpha \leq .05$, ** $\alpha \leq .01$

TABLE VIII

MEAN SQUARES FOR LOCATION 2 FOR THE ANALYSIS OF CLONAL VARIATION IN THE EXPERIMENTAL POPULATION

| | | Mean Squares | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Source of Variation | D.F. | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight | Insect Score | D.F. | Arcsin of $\sqrt{\text{Survival }\%}$ |
| Blocks | 3 | 168.39** | 4.3742** | .002680** | 0.5966** | .596418** | 316.47** | 0.5051** | 3 | 2397** |
| Clones | 109 | 23.77** | 0.9540** | .001852** | 1.7915** | .091444** | 50.52** | 0.3064** | 129 | 1665** |
| Blocks x Clones | 327 | 5.29** | 0.2258** | .000134** | 0.0971** | .025230** | 14.34** | 0.0832** | 387 | 304 |
| Within Plot $\left(\frac{\sigma^2_W}{k}\right)$ | 1389 | 0.37 | 0.0034 | .000017 | 0.0014 | .000315 | 1.85 | 0.0586 | | |

* $\alpha$ = .05, ** $\alpha$ = .01

among clones was significantly greater than zero for all traits at both locations.

Disease score at Location 1 and insect score at Location 2 are both in ordinal scale and analyses of variance are not strictly applicable. Practically, this means that probability levels for tests of significance are not exact. It should also be pointed out that this study was not designed to detect differences among clones for susceptibility to insects or diseases. Every tree in the plantings may not have been exposed to attack. This is probably more true for insect attack at Location 2 than for disease attack at Location 1. The insect damage was spotted throughout the planting. Considering the severity of the damage due to disease at Location 1, it would be difficult to imagine any tree not being exposed to the disease. These observations are supported by the significant block X clone interaction for insect score at Location 2 and a nonsignificant block X clone interaction for disease score at Location 1. The significant mean squares for clones support empirical observations of clonal differences for both insect and disease scores.

Maximum and minimum clone means, population means, and standard deviations for clone means are presented for both locations in Table IX. Means for all traits except survival % are based on 18 clones at Location 1 and 110 clones at Location 2. Sixteen clones are common to both locations. Since means are based on different populations of clones planted in different years, the differences between the two locations are not absolute. Growth was, however, considerably better at Location 2.

TABLE IX

MEANS, RANGES, AND STANDARD DEVIATIONS FOR CLONES AT TWO LOCATIONS

Location 1

| | Height (Ft.) | Diameter (In.) | Specific Gravity | Number of Limbs/Foot | Volume (Cu.Ft.) | Dry Weight (Lbs.) | Disease Score | Survival (%) |
|---|---|---|---|---|---|---|---|---|
| Maximum Clone Mean | 19.2 | 3.4 | .45 | 4.2 | .37 | 9.9 | 2.9 | 100 |
| Population Mean | 14.8 | 2.4 | .42 | 2.8 | .16 | 4.2 | 2.1 | 37 |
| Minimum Clone Mean | 12.0 | 1.7 | .38 | 1.9 | .06 | 1.7 | 1.4 | 0 |
| Std. Dev. of a Clone Mean | 2.4 | .5 | .02 | .7 | .15 | 3.5 | .3 | 12 |

Location 2

| | Height (Ft.) | Diameter (In.) | Specific Gravity | Number of Limbs/Foot | Volume (Cu.Ft.) | Dry Weight (Lbs.) | Insect Score | Survival (%) |
|---|---|---|---|---|---|---|---|---|
| Maximum Clone Mean | 24.3 | 4.8 | .44 | 4.8 | .82 | 20.0 | 3.0 | 100 |
| Population Mean | 19.8 | 3.8 | .38 | 3.1 | .48 | 11.6 | 2.5 | 76 |
| Minimum Clone Mean | 13.9 | 2.5 | .33 | 1.9 | .14 | 3.5 | 1.4 | 0 |
| Std. Dev. of a Clone Mean | 1.9 | 0.4 | .02 | 0.8 | .07 | 2.0 | 0.5 | 9 |

## Broad Sense "Heritabilities"

In segregating populations, the heritability is the ratio of the additive genetic variance to the total phenotypic variance. Heritability indicates the ease with which gains can be had from selection. In populations which may be vegetatively reproduced, the ratio of the total genetic variance to the total phenotypic variance may be viewed in the same fashion.

Broad sense "heritabilities" were calculated on a clone mean basis using the equation:

$$H^2 = \frac{\hat{\sigma}^2_C}{\hat{\sigma}^2_C + \frac{\hat{\sigma}^2_{BxC}}{b} + \frac{\hat{\sigma}^2_W}{b \cdot k}}$$

Estimates of broad sense "heritabilities" and estimates of the parameters used to calculate them are presented for each location in Table X. Although published estimates of heritabilities are scarce for eastern cottonwood, good general agreement for the ratios calculated in this study with those from other studies is evident from comparisons which may be made in Table XI. Heritabilities are strictly applicable only in the environment in which they are estimated. Furthermore, heritabilities estimated on a clone mean basis are dependent on the number of ramets used to calculate the mean. The relative magnitudes of the heritabilities for each trait were the same in each of the four studies. Heritabilities indicate that gains may be made more easily when selecting for height, diameter, specific gravity, or the number of limbs per foot than for the more complex traits, volume and dry weight.

TABLE X

ESTIMATES OF BROAD SENSE "HERITABILITIES" ON A CLONE MEAN BASIS, COMPONENTS OF VARIANCE, AND THEIR STANDARD ERRORS

Location 1

| Trait | $\sigma^2 C$ | S.E. $\sigma^2 C$ | $\sigma^2 BXC$ | S.E. $\sigma^2 BXC$ | $\frac{\sigma^2 W}{k}$ | S.E. $\frac{\sigma^2 W}{k}$ | Broad Sense "Heritability" |
|---|---|---|---|---|---|---|---|
| Height | 2.72509 | 1.23266 | 1.33813 | 0.93558 | 2.75943 | 0.29597 | .73 |
| Diameter | 0.12324 | 0.06650 | 0.16959 | 0.06427 | 0.13661 | 0.06585 | .62 |
| Specific Gravity | 0.00041 | 0.00016 | -0.00069 | 0.00019 | 0.00103 | 0.00572 | .83 |
| Limbs/Foot | 0.59386 | 0.21635 | 0.17696 | 0.05894 | 0.10942 | 0.05893 | .89 |
| Volume | 0.00327 | 0.00186 | 0.00591 | 0.00188 | 0.00331 | 0.01025 | .59 |
| Dry Weight | 2.31894 | 1.35176 | 4.74573 | 1.38805 | 2.12799 | 0.25991 | .57 |

Location 2

| Trait | $\sigma^2 C$ | S.E. $\sigma^2 C$ | $\sigma^2 BXC$ | S.E. $\sigma^2 BXC$ | $\frac{\sigma^2 W}{k}$ | S.E. $\frac{\sigma^2 W}{k}$ | Broad Sense "Heritability" |
|---|---|---|---|---|---|---|---|
| Height | 4.62019 | 0.80460 | 3.95010 | 0.41620 | 1.34763 | 0.04401 | .78 |
| Diameter | 0.18203 | 0.03231 | 0.08969 | 0.01835 | 0.13620 | 0.01399 | .76 |
| Specific Gravity | 0.00042 | 0.00006 | 0.00007 | 0.00001 | 0.00006 | 0.00029 | .93 |
| Limbs/Foot | 0.42359 | 0.06015 | 0.04658 | 0.00781 | 0.05059 | 0.00852 | .95 |
| Volume | 0.01655 | 0.00310 | 0.01390 | 0.00201 | 0.01132 | 0.00403 | .72 |
| Dry Weight | 9.04566 | 1.71857 | 7.69526 | 1.14670 | 6.65190 | 0.09779 | .72 |

TABLE XI

BROAD SENSE "HERITABILITIES" ON A CLONE MEAN BASIS FROM OTHER POPULATIONS OF EASTERN COTTONWOOD

| Trait | Broad Sense "Heritabilities" | | | | | | |
|---|---|---|---|---|---|---|---|
| | This Study | | Study 1* | Study 2** | | Study 3*** | |
| | Location 1 | Location 2 | | Favorable | Stressful | | |
| Height | .73 | .78 | .66 | .57 | .40 | .66 | .72 |
| Diameter | .62 | .76 | .60 | .41 | .29 | .58 | .61 |
| Specific Gravity | .83 | .93 | | .64 | .76 | | |
| Limbs/Foot | .89 | .95 | .85 | | | .82 | |
| Volume | .59 | .72 | | | | | |
| Dry Weight | .57 | .72 | | .29 | .43 | | |
| | 3 years | 3 years | 1 year | 1 year | 1 year | 1 year | 2 years |
| | Age of Material when "Heritability" was Determined | | | | | | |

* Study 1 - Unpublished data from 43 clones collected along the Red River (Stands 1 through 7, figure 1). Clones were in randomized block at one location. Data were taken after one growing season.

** Study 2 - Farmer (12). Thirty randomly selected clones from Mississippi River flood plain. Clones were in a split-plot at one location. Main effects were favorable and stressful soil moisture regimes. Data were taken after one season's growth in metal pots.

***Study 3 - Wilcox and Farmer (13). Forty-nine clones selected from one stand in Bolivar County, Mississippi. Clones were in a randomized block at one location. Data were collected after one and two growing seasons. Limbiness was measured by counting the total number of limbs.

Phenotypic and Genotypic Correlations

When more than one trait must be considered in the definition of the worth of an individual, the forest tree breeder must concern himself with relationships among traits. He must anticipate changes in genetic structure of the population for all traits that affect the worth of an individual even though selection may not be based on all these traits. Phenotypic correlations measure the observable relationships among traits while genotypic correlations estimate the strength of their genetic associations. Genotypic correlations serve to indicate the manner in which a trait will respond to selection applied to another trait.

Genotypic correlations presented in Tables XII and XIII for Populations (Locations) 1 and 2, respectively, were calculated using the following equation:

$$r_{g(X,Y)} = \frac{\hat{\sigma}^2_{C(X,Y)}}{\sqrt{\hat{\sigma}^2_{C(X)} \cdot \hat{\sigma}^2_{C(Y)}}}$$

where: $r_{g(X,Y)}$ = estimate of the genotypic correlation between traits X and Y, $\hat{\sigma}^2_{C(X,Y)}$ = the estimate of the total genetic covariance between traits X and Y, and $\hat{\sigma}^2_{C(X)}$, $\hat{\sigma}^2_{C(Y)}$ = estimates of the total genetic variance for traits X and Y, respectively. Phenotypic correlations were calculated in the same fashion using estimates of phenotypic variance and covariances on a clone mean basis. Tests of significance were based on phenotypic correlations calculated from mean squares and mean products. The phenotypic correlations calculated using variance and covariance components changed very little from those based on mean squares and mean products. The author knows of no test of significance

TABLE XII

PHENOTYPIC (ABOVE THE DIAGONAL) AND GENOTYPIC (BELOW THE DIAGONAL) CORRELATIONS BETWEEN PAIRS OF TRAITS IN THE EXPERIMENTAL POPULATION FOR LOCATION 1

| | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight |
|---|---|---|---|---|---|---|
| Height | | .851** | .166 | .085 | .905** | .901** |
| Diameter | .900 | | .092 | .160 | .970** | .963** |
| Specific Gravity | .259 | .120 | | .141 | .139 | .209 |
| Number of Limbs/Foot | .040 | .109 | .180 | | .095 | .096 |
| Volume | 1.017 | .971 | .204 | .033 | | .997** |
| Dry Weight | 1.028 | .960 | .286 | .037 | .997 | |

*, ** Correlations statistically significant at $\alpha$ =.05 and $\alpha$ =.01, respectively.

TABLE XIII

PHENOTYPIC (ABOVE THE DIAGONAL) AND GENOTYPIC (BELOW THE DIAGONAL) CORRELATIONS BETWEEN PAIRS OF TRAITS IN THE EXPERIMENTAL POPULATION FOR LOCATION 2

| | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight |
|---|---|---|---|---|---|---|
| Height | | .589** | -.275** | -.314** | .801** | .796** |
| Diameter | .510 | | -.320** | .210* | .933** | .923** |
| Specific Gravity | -.300 | -.374 | | .144 | -.321** | -.204* |
| Number of Limbs/Foot | -.392 | .208 | .169 | | .023 | .040 |
| Volume | .767 | .930 | -.301 | -.012 | | .992** |
| Dry Weight | .762 | .915 | -.245 | .011 | .990 | |

*, ** Correlations statistically significant at $\alpha$ =.05 and $\alpha$ =.01, respectively.

which is strictly applicable to correlations calculated using components of variance and covariance.

Phenotypic and genotypic correlations are strong and show good agreement between the two populations for traits associated with growth and yield. Differences in direction as well as in magnitude are evident between the two populations for phenotypic and genotypic correlations between specific gravity and growth and yield traits and between the number of limbs per foot and growth and yield traits. Consideration of these differences must take into account that correlations for Population 1 were based on 18 clones from a limited number of stands while those for Population 2 were based on 110 clones from a greater geographic area.

Small, positive, phenotypic and genotypic correlations between specific gravity and growth and yield traits were estimated for Population 1. None of these phenotypic correlations were statistically significant at the 95% level of confidence. The very small genotypic correlation between diameter and specific gravity ($r_g$ = 120) is in good agreement with Farmer and Wilcox (9), and Farmer (6) who reported genotypic correlations of $r_A = -.07$ and $r_A = .22$, respectively for two populations of eastern cottonwood from along the Mississippi River. It should be noted that both these correlations are based on the covariance of additive gene effects while correlations based on covariances among clones depend on the total genetic covariance.

Specific gravity was negatively correlated with all the growth traits in Population 2. The phenotypic correlations were all statistically significant at levels of significance at least as great as 95%. The phenotypic correlation between specific gravity and the number of limbs per foot is small and nonsignificant. The negative correlations between specific gravity and all the growth and yield traits in Population 2 were not unexpected. Posey (22), in another study of one year old clones from this same population reported that clones from the western part of the study area were inherently slower growing and higher in specific gravity than clones from the eastern part of Oklahoma. He also pointed out that clones from western Oklahoma were inherently limbier than those from the eastern part of the state. This agrees with the negative correlations between the number of limbs per foot and height at Location 2. The correlations between the number of limbs per foot and volume and the number of limbs per foot and dry weight were small enough to be of no practical importance in either population.

Wilcox and Farmer (31) reported a genotypic correlation of $r_g$ = .26 between the total number of branches and diameter of one year old clones from 49 eastern cottonwood trees selected along the Mississippi River. They reported no relationship ($r_g$ = 0.0) between height and the total number of limbs. In the same study, height and diameter were positively genetically correlated after one year ($r_g$ = .47), and after two years ($r_g$ = .50). These correlations compare favorably with that for Population 2.

## Selection Indexes

The total value of an individual tree is affected by several characters. Thus, forest tree breeders will be forced to utilize multiple-trait selection schemes in the effort to maximize yields. There are three basic multiple trait selection schemes. Both tandem selection and independent culling levels have uses in forest tree breeding (28), but Hazel and Lush (14) have shown that the method of total score or index selection is more efficient than either of these.

Fisher (27) developed the concept of a discriminant function whereby a single component can be maximized relative to other components. Smith (27) applied this concept to plant breeding. Hazel (13) has presented the genetic basis for constructing selection indexes.

Selection indexes have been developed for many plant and animal populations. Notable examples of indexes developed for selecting in animal populations may be found in the works of Harvey and Lush (12) on dairy cattle and in that of Lerner (16) on poultry. A list of indexes developed for the selection of plants should include works by Brim, et al (1) in soybeans, Manning (20) in cotton, and Robinson, et al (25) in corn. Van Buijtenen (29), Burrows (2), and Illy (15) have published indexes for selecting in forest tree populations. Namkoong (21) has suggested the use of a combined index, using information from progeny tests, for culling seed orchards.

A concise outline of methods for constructing indexes and predicting gains used in this study is given by Brim, et al (1).

The development of a selection index is predicated on maximizing the correlation between the aggregate genetic value of an individual and the selection index. The solution of the normal equations for the weights to be given each trait require estimates of the relative economic values for each trait, the phenotypic and genotypic variances for each trait, and the phenotypic and genotypic covariances between each pair of traits. Estimates of phenotypic and genotypic components of variance and covariance are presented in Tables XIV and XV for Populations 1 and 2, respectively.

TABLE XIV

ESTIMATES OF PHENOTYIC AND GENOTYPIC (IN PARENTHESIS) COMPONENTS OF VARIANCE AND COVARIANCE ON A CLONE MEAN BASIS FOR POPULATION 1

| | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight |
|---|---|---|---|---|---|---|
| Height | 3.7494<br>(2.7250) | .7368<br>(.5215) | .0072<br>(.0087) | .1347<br>(.0511) | .1310<br>(.0961) | 3.5044<br>(2.5830) |
| Diameter | | .1998<br>(.1232) | .0009<br>(.0008) | .0582<br>(.0295) | .0324<br>(.0195) | .8646<br>(.5131) |
| Specific Gravity | | | .0005<br>(.0004) | .0025<br>(.0028) | .0002<br>(.0002) | .0094<br>(.0089) |
| Number of Limbs/Foot | | | | .6654<br>(.5938) | .0057<br>(.0014) | .1581<br>(.0436) |
| Volume | | | | | .0055<br>(.0032) | .1497<br>(.0869) |
| Dry Weight | | | | | | 4.0373<br>(2.3189) |

TABLE XV

ESTIMATES OF PHENOTYPIC AND GENOTYPIC (IN PARENTHESIS) COMPONENTS OF VARIANCE AND COVARIANCE ON A CLONE MEAN BASIS FOR POPULATION 2

| | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight |
|---|---|---|---|---|---|---|
| Height | 5.9446<br>(4.6201) | .7010<br>(.4677) | -.0144<br>(-.0133) | -.5115<br>(-.5486) | .2951<br>(.2119) | 6.8957<br>(4.9241) |
| Diameter | | .2385<br>(.1820) | -.0033<br>(-.0033) | .0685<br>(.0576) | .0688<br>(.0510) | 1.6017<br>(1.1735) |
| Specific Gravity | | | .0004<br>(.0004) | .0020<br>(.0022) | -.0010<br>(-.0008) | -.0156<br>(-.0152) |
| Number of Limbs/Foot | | | | .4478<br>(.4235) | .0023<br>(-.0010) | .0962<br>(.0209) |
| Volume | | | | | .0228<br>(.0165) | .5329<br>(.3830) |
| Dry Weight | | | | | | 12.6324<br>(9.0456) |

Stonecypher (28) has pointed out the difficulties associated with obtaining accurate estimates of relative economic values for forest trees. When economic values are not known, one approach to index selection is to define the goal of selection in terms of one trait, e.g., yield (25,28).

Indexes with Increased Volume as the Goal of Selection. Indexes constructed for both populations using increased volume as the goal of selection are presented in Table XVI. Relative efficiencies in Table XVI are the ratios of gains in each case expressed as a percentage of the gain that can be had by performing clonal selection using volume itself as the criterion for selection. Examination of these values indicates that clonal selection, already an efficient method of selection (17), can be made more so by selecting on an index.

It is interesting to note that selection for increased height results in a greater increase in volume than selecting on volume itself in Population 1. The same relationship has been found by Stonecypher[1/] in a population of loblolly pine, (Pinus taeda). Illy (15) has also emphasized the importance of height in selection indexes for maritime pine, (P. pinaster). An analogous situation has been reported by Robinson, et al. (25) in corn.

Another apparent anomaly appears upon examining the partial regression coefficients for Population 1. Although the goal of selection is increased volume, volume itself is given a negative weight in indexes 2 and 4. Further examination reveals that both these indexes also contain height. Since height is a better criterion for selecting

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[1/] Personal communication with Dr. R. W. Stonecypher, Oklahoma State University.

TABLE XVI

COMPARISON OF INDEXES WITH INCREASED VOLUME AS THE GOAL
OF SELECTION FOR POPULATIONS 1 AND 2

| Population | Criterion for Selection | Partial Regression Coefficients: Height | Partial Regression Coefficients: Diameter | Partial Regression Coefficients: Volume | $G_I$ (Cu.Ft.) 1/ | $G_I$ As % of Population Mean (%) | Relative Efficiency (%) |
|---|---|---|---|---|---|---|---|
| 1 | Volume | | | | .035 | 22 | 100 |
| | Height | | | | .040 | 25 | 114 |
| | Diameter | | | | .035 | 22 | 100 |
| | Index 1 | .0234 | .0113 | | .040 | 25 | 114 |
| | Index 2 | .0285 | | -.0814 | .040 | 25 | 114 |
| | Index 3 | | .0420 | .3429 | .035 | 22 | 100 |
| | Index 4 | .0323 | .1080 | -.7974 | .041 | 25 | 117 |
| 2 | Volume | | | | .191 | 40 | 100 |
| | Index 1 | .0160 | .1670 | | .191 | 40 | 100 |
| | Index 2 | -.0008 | | .7343 | .191 | 40 | 100 |
| | Index 3 | | .0371 | .6124 | .193 | 40 | 101 |
| | Index 4 | .0053 | .0695 | .4458 | .193 | 40 | 101 |

1/ $\Delta G_I$ is the gain in cubic foot volume from selection. Proportion selected for Population 1 is 50 percent (selection intensity = i = 0.7979) and 10 percent for Population 2 ( i = 1.7550).

for increased volume than is volume itself, volume is relegated to the role of a correction factor in indexes 2 and 4. This is supported by the positive weight given volume in index 3 in which height does not appear.

The situation in Population 2 is very different. Only indexes 3 and 4 are very slightly superior to clonal selection for increased volume. This may be attributed to the fact that in this population the estimates of broad sense "heritabilities" for volume, height, and diameter are essentially the same.

It appears that while selection for increased volume in Population 1 should be based on index 4, clonal selection on volume itself will provide essentially the same gain as selection on an index in Population 2.

It should be pointed out that expected gains from selecting on indexes 3 and 4 are greater than that from clonal selection for increased volume. However, the increase in gain seems too small to justify the added expense of calculating indexes.

Neither situation should be construed to be a general result. The expected gains apply only for the population under consideration and where volume is the single goal of selection.

Indexes with Increased Dry Weight as the Goal of Selection. Because of its fast growth, desirable fiber characteristics, and the ease with which it may be vegetatively propagated, eastern cottonwood is especially desirable as a pulping species. If improvement in one trait were to be singled out as the goal of selection, it should more properly be dry weight than volume. Dry weight takes into consideration not only the volume of wood substance but its density as well.

Selection indexes considering increased dry weight as the goal of selection are presented in Tables XVII and XVIII for Populations 1 and 2, respectively. The importance of height when selecting for increased dry weight manifests itself in Population 1 as it did when the goal of selection was increased volume. Clonal selection for increased height will result in a greater increase than clonal selection on dry weight itself.

Selection based on indexes using different combinations of height, diameter, and specific gravity do not give appreciably greater response than selection on height. However, if these traits are used to calculate volume and dry weight and these are included in an index, an appreciable increase in gain is predicted. In contrast, index selection for increased dry weight in Population 2 promises very little advantage over clonal selection for dry weight alone. This may be attributed to the high broad sense "heritability" of clone means for dry weight. Clonal selection to increase dry weight promises to be so effective that using an index can increase precision of selection only a small amount.

Responses of Several Traits When Selection is for Increased Dry Weight. Defining the goal of selection in terms of a single trait avoids rather than solves the problem of unknown relative economic values. This approach is simply a method of increasing the accuracy of selection for a single trait. Although this method can increase the accuracy of selection, it retains the disadvantages of any other form of single trait selection.

Expected responses in six traits to selection based on index 26 of Population 1 and index 15 of Population 2 are shown in Table XIX.

TABLE XVII

COMPARISON OF INDEXES WITH INCREASED DRY WEIGHT AS THE GOAL OF SELECTION FOR POPULATION 1

| Criterion for Selection | Partial Regression Coefficients: Height | Diameter | Specific Gravity | Volume | Dry Weight | $\Delta G_I$ (Lbs.) 1/ | $\Delta G_I$ as % of Population Mean | Relative Efficiency (%) |
|---|---|---|---|---|---|---|---|---|
| Dry Weight | | | | | | .92 | 22 | 100 |
| Height | | | | | | 1.06 | 25 | 116 |
| Volume | | | | | | .92 | 22 | 101 |
| Index 1 | .6689 | .1015 | | | | 1.06 | 25 | 116 |
| Index 2 | .6734 | | 8.0072 | | | 1.07 | 25 | 117 |
| Index 3 | .8038 | | | -3.2886 | | 1.06 | 25 | 116 |
| Index 4 | .8058 | | | | -.1250 | 1.06 | 25 | 116 |
| Index 5 | | 2.5081 | 13.0954 | | | .94 | 22 | 103 |
| Index 6 | | .7238 | | 11.3692 | | .93 | 22 | 101 |
| Index 7 | | 1.1307 | | | .3322 | .92 | 22 | 101 |
| Index 8 | | | 10.6568 | 15.1238 | | .94 | 22 | 103 |
| Index 9 | | | 7.2700 | | .5574 | .92 | 22 | 101 |
| Index 10 | | | | 30.2995 | -.5494 | .93 | 22 | 101 |
| Index 11 | .6385 | .1762 | 8.1874 | | | 1.07 | 25 | 117 |
| Index 12 | .8935 | 2.5492 | | -20.1894 | | 1.07 | 25 | 117 |
| Index 13 | .8430 | 1.9218 | | | -.5689 | 1.08 | 26 | 118 |

TABLE XVII (Continued)

| Criterion for Selection | Partial Regression Coefficients Height | Diameter | Specific Gravity | Volume | Dry Weight | $\Delta G_I$ [1/] (Lbs.) | $\Delta G_I$ as % of Population Mean | Relative Efficiency (%) |
|---|---|---|---|---|---|---|---|---|
| Index 14 | .7834 | | 7.8858 | -3.1401 | | 1.07 | 26 | 117 |
| Index 15 | .8174 | | 8.8483 | | -.1558 | 1.07 | 26 | 117 |
| Index 16 | .8007 | | | 3.4034 | -.2468 | 1.06 | 25 | 116 |
| Index 17 | | 1.1631 | 11.6859 | 8.3295 | | .95 | 23 | 103 |
| Index 18 | | 2.0185 | 11.8528 | | .1145 | .94 | 22 | 103 |
| Index 19 | | .5536 | | 24.1577 | -.4402 | .93 | 22 | 101 |
| Index 20 | | | 112.2436 | 439.9007 | -16.0023 | 1.16 | 28 | 127 |
| Index 21 | .8797 | 2.9011 | 10.1119 | -22.3326 | | 1.10 | 26 | 120 |
| Index 22 | .3912 | | 93.8185 | 359.5241 | -13.3179 | 1.19 | 28 | 129 |
| Index 23 | .9027 | 2.6927 | | -29.8955 | .3229 | 1.08 | 26 | 118 |
| Index 24 | .8886 | 3.1770 | 16.1990 | | -.9151 | 1.11 | 26 | 121 |
| Index 25 | | -1.4143 | 116.3696 | 470.6476 | -16.8494 | 1.17 | 28 | 128 |
| Index 26 | .3821 | -.1416 | 94.6564 | 364.4551 | -13.4645 | 1.19 | 28 | 129 |

1/ $\Delta G_I$ is the expected gain in pounds of dry wood fiber from selection. Proportion selected is 50 percent (i = .7979).

TABLE XVIII

COMPARISON OF INDEXES WITH INCREASED DRY WEIGHT AS THE GOAL OF SELECTION FOR POPULATION 2

| Criterion for Selection | Partial Regression Coefficients: Height | Diameter | Specific Gravity | Volume | Dry Weight | $\Delta G_I$ [1] (Lbs.) | $\Delta G_I$ as % of Population Mean | Relative Efficiency (%) |
|---|---|---|---|---|---|---|---|---|
| Dry Weight | | | | | | 4.46 | 38 | 100 |
| Index 1 | -.0063 | | | | .7195 | 4.46 | 38 | 100 |
| Index 2 | | .7519 | | | .6207 | 4.47 | 38 | 100 |
| Index 3 | | | -9.2211 | | .7047 | 4.47 | 38 | 100 |
| Index 4 | | | | 3.9484 | .5495 | 4.46 | 38 | 100 |
| Index 5 | .0875 | 1.1801 | | | .5187 | 4.47 | 38 | 100 |
| Index 6 | -.0324 | | -9.6523 | | .7218 | 4.48 | 38 | 100 |
| Index 7 | -.0142 | | | 4.1065 | .5506 | 4.46 | 38 | 100 |
| Index 8 | | .6945 | | 1.5449 | .5628 | 4.47 | 38 | 100 |
| Index 9 | | .4475 | -7.8324 | | .6496 | 4.48 | 38 | 100 |
| Index 10 | | | -47.5931 | -44.2320 | 2.5231 | 4.51 | 39 | 101 |
| Index 11 | -.0518 | | -49.1551 | -45.2386 | 2.5919 | 4.51 | 39 | 101 |
| Index 12 | .1012 | 1.3105 | | -1.7097 | .5668 | 4.47 | 38 | 100 |
| Index 13 | .0191 | .5648 | -7.2144 | | .6251 | 4.48 | 38 | 100 |
| Index 14 | | .6260 | -47.0721 | -45.8708 | 2.5136 | 4.51 | 39 | 101 |
| Index 15 | .0114 | .6961 | -46.6693 | -45.8324 | 2.4973 | 4.51 | 39 | 101 |

[1] $\Delta G_I$ is the expected gain in pounds of dry wood fiber from selection. Proportion selected is ten percent (i = 1.7550).

When selection is based on index 26 all six traits are expected to increase. This result was expected since dry weight, the goal of selection, is positively genetically correlated with each of the other five traits. When selection is based on index 15 only the expected change in specific gravity is in the negative direction.

The responses of height, diameter, and volume when selecting for increased dry weight are in the desired direction. Larger trees have economic value above and beyond that associated with increased dry weight. For example, larger trees handled as units may be logged more economically.

The desired direction of change in specific gravity should be given careful consideration. Increased specific gravity is desirable from the standpoint of increasing dry weight. Specific gravity also has economic worth above and beyond that associated with dry weight. Trees with higher density wood produce stronger lumber. Since specific gravity is related to important fiber characteristics, such as cell wall thickness, it is also an important indicator of the strength and quality of paper. High density wood produces stronger, lower quality papers while lower density wood with thinner cell walls is used to produce high grade slick papers. To further confuse matters, lower specific gravity wood, like that of eastern cottonwood, may be mixed with higher density wood, such as southern pine, to produce the desired product. It would seem desirable to increase the specific gravity of eastern cottonwood, at least to a certain point, since selected clones may be used to produce lumber as well as wood pulp.

Selection based on either index in Table XIX may result in increases in the number of limbs per foot. This is undesirable since

TABLE XIX

RESPONSES FOR SIX TRAITS WHEN THE GOAL OF INDEX SELECTION IS INCREASED DRY WEIGHT

| Criterion for Selection | Height (ft.) | Diameter (in.) | Specific Gravity | Number of Limbs/Foot | Volume (cu.ft.) | Weight (lbs.) | Proportion Selected (%) | Selection Intensity (i) |
|---|---|---|---|---|---|---|---|---|
| Index 26 (Pop. 1) | 1.098 | .249 | .005 | .119 | .043 | 1.190 | 50 | .7979 |
| Index 15 (Pop. 2) | 2.444 | .598 | -.015 | .018 | .186 | 4.515 | 10 | 1.7550 |

limbs decrease the quality of sawn lumber as well as the quality of pulp produced.

Indexes With Complex Goals of Selection. Information necessary to determine relative economic values for specific gravity, the number of limbs per foot, and dry weight is not available. The effect of varying the relative economic values for these traits in both populations may be examined in Tables XX and XXI.

Height, diameter, specific gravity, number of limbs per foot, and dry weight were all used to construct indexes to select for increased specific gravity and dry weight and for decreased limbiness. The goal of selection was defined in terms of these traits. Height, diameter, and volume were assigned relative economic weights of zero in every index for both populations. Increased yield was considered to be the most critical goal of selection and was given the relative economic weight of +1 in every index. Specific gravity was assigned relative economic values of 0.0, 0.1, 0.5, and 1.0. Number of limbs per foot was assigned relative weights of 0.0, -0.1, -0.5, and -1.0 at each of the four relative weights for specific gravity. Phenotypic values for all six traits were used to construct an index for each of the sixteen combinations of relative economic weights.

Expected responses for each of the six traits considered in this study are given for each index. $\Delta G_I$ is the expected response in the aggregate value. $\Delta G_I$ is the sum of the products of the economic weights and the gains in their respective traits and is in units of pounds of dry weight equivalent since specific gravity and number of limbs per foot were assigned economic weights on the basis of their worth relative to dry weight. A relative economic value of 0.1 for specific

TABLE XX

COMPARISON OF GAINS FROM SELECTING ON AN INDEX WITH DIFFERENT GOALS OF SELECTION FOR POPULATION 1

| Relative Economic Weights | | | Responses of the Traits Used to Construct the Index | | | | | | | Efficiency of Index Relative to | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Specific Gravity | Number of Limbs/Ft. | Dry Weight | Height (Ft.) | Diameter (In.) | Specific Gravity | Number of Limbs/Ft. | Volume (Cu.Ft.) | Dry Weight (Lbs.) | $\Delta G_I$ | Assumed Goal | Clonal Selection |
| 0 | -1 | 1 | .99 | .22 | .003 | -.24 | .039 | 1.09 | 1.33 | 98% | 148% |
| .1 | -1 | 1 | .99 | .22 | .003 | -.24 | .039 | 1.09 | 1.33 | 98 | 148 |
| .5 | -1 | 1 | .99 | .22 | .003 | -.24 | .039 | 1.09 | 1.33 | 98 | 148 |
| 1 | -1 | 1 | .99 | .22 | .003 | -.24 | .039 | 1.09 | 1.34 | 98 | 148 |
| 0 | -.5 | 1 | 1.06 | .24 | .003 | -.13 | .042 | 1.18 | 1.24 | 100 | 136 |
| .1 | -.5 | 1 | 1.06 | .24 | .003 | -.13 | .042 | 1.18 | 1.24 | 100 | 136 |
| .5 | -.5 | 1 | 1.07 | .24 | .003 | -.12 | .042 | 1.18 | 1.24 | 100 | 136 |
| 1 | -.5 | 1 | 1.07 | .24 | .003 | -.12 | .042 | 1.18 | 1.24 | 100 | 136 |
| 0 | -.1 | 1 | 1.09 | .26 | .004 | -.02 | .043 | 1.21 | 1.21 | 98 | 132 |
| .1 | -.1 | 1 | 1.09 | .26 | .004 | -.02 | .043 | 1.21 | 1.21 | 98 | 132 |
| .5 | -.1 | 1 | 1.09 | .22 | .004 | -.02 | .043 | 1.21 | 1.21 | 98 | 132 |
| 1 | -.1 | 1 | 1.09 | .26 | .004 | -.02 | .043 | 1.21 | 1.22 | 98 | 132 |
| 0 | 0 | 1 | 1.09 | .26 | .004 | .02 | .043 | 1.21 | 1.21 | 97 | 132 |
| .1 | 0 | 1 | 1.09 | .26 | .004 | .02 | .043 | 1.21 | 1.21 | 97 | 132 |
| .5 | 0 | 1 | 1.09 | .26 | .004 | .02 | .043 | 1.21 | 1.21 | 97 | 132 |
| 1 | 0 | 1 | 1.09 | .26 | .005 | .02 | .043 | 1.21 | 1.22 | 97 | 132 |

1/ Selection intensity = i = 0.7979

TABLE XXI

COMPARISON OF GAINS FROM SELECTING ON AN INDEX WITH DIFFERENT GOALS OF SELECTION FOR POPULATION 2

| Relative Economic Weights | | | Responses of the Traits Used to Construct the Index | | | | | | | Efficiency of Index Relative to | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Specific Gravity | Number of Limbs/Ft. | Dry Weight | Height (Ft.) | Diameter (In.) | Specific Gravity | Number of Limbs/Ft. | Volume (Cu.Ft.) | Dry Weight (Lbs.) | $\Delta G_I$ | Assumed Goal | Clonal Selection |
| 0 | -1 | 1 | 2.75 | .55 | -.017 | -.28 | .182 | 4.39 | 4.67 | 99% | 105% |
| .1 | -1 | 1 | 2.75 | .54 | -.017 | -.28 | .182 | 4.39 | 4.67 | 99 | 105 |
| .5 | -1 | 1 | 2.74 | .54 | -.017 | -.28 | .182 | 4.39 | 4.66 | 99 | 105 |
| 1 | -1 | 1 | 2.74 | .54 | -.015 | -.28 | .184 | 4.39 | 4.65 | 99 | 105 |
| 0 | -.5 | 1 | 2.62 | .58 | -.017 | -.15 | .186 | 4.48 | 4.56 | 100 | 102 |
| .1 | -.5 | 1 | 2.62 | .58 | -.017 | -.15 | .186 | 4.48 | 4.56 | 100 | 102 |
| .5 | -.5 | 1 | 2.62 | .58 | -.015 | -.15 | .186 | 4.48 | 4.55 | 100 | 102 |
| 1 | -.5 | 1 | 2.62 | .58 | -.015 | -.15 | .186 | 4.48 | 4.54 | 100 | 102 |
| 0 | -.1 | 1 | 2.49 | .59 | -.015 | -.04 | .187 | 4.52 | 4.52 | 100 | 101 |
| .1 | -.1 | 1 | 2.49 | .59 | -.015 | -.04 | .187 | 4.52 | 4.52 | 100 | 101 |
| .5 | -.1 | 1 | 2.49 | .59 | -.015 | -.04 | .187 | 4.52 | 4.51 | 100 | 101 |
| 1 | -.1 | 1 | 2.48 | .59 | -.015 | -.04 | .187 | 4.52 | 4.50 | 100 | 101 |
| 0 | 0 | 1 | 2.45 | .60 | -.015 | -.02 | .187 | 4.52 | 4.52 | 99 | 101 |
| .1 | 0 | 1 | 2.45 | .60 | -.015 | -.02 | .187 | 4.52 | 4.52 | 99 | 101 |
| .5 | 0 | 1 | 2.45 | .60 | -.015 | -.02 | .187 | 4.52 | 4.51 | 99 | 101 |
| 1 | 0 | 1 | 2.45 | .60 | -.015 | -.02 | .187 | 4.52 | 4.50 | 99 | 101 |

1/ Selection intensity = i = 1.7550

gravity indicates that an increase of one unit in specific gravity is worth the same as a 0.1 pound increase in dry weight. Assigning a relative economic weight of -0.5 to the number of limbs per foot assumes that a decrease of one limb per foot is worth as much as a one half pound increase in dry weight.

Varying the economic weights changes the goal of selection. This made comparisons of indexes on the basis of the $\Delta G_I$ values unwise. Comparisons were made among indexes for each location on the basis of the efficiencies relative to an assumed goal in Tables XX and XXI. These efficiencies were calculated under the assumption that the true relative economic weights for specific gravity, the number of limbs per foot, and dry weight are 0.1, -0.5, and 1.0, respectively. All other sets of economic weights would then represent incorrect descriptions of the goal of selection. $\Delta G_I$ values were calculated for each index using an assigned set of economic weights. Each $\Delta G_I$ calculated in this fashion was expressed as a percentage of $\Delta G_I$ for the index constructed using the set of economic weights assumed correct.

Efficiencies relative to clonal selection are also presented in both tables. These values were determined by expressing the $\Delta G_I$ from selecting on each index as a percentage of the gain in the aggregate genetic value from clonal selection for increased dry weight. The gain in the aggregate genetic value from clonal selection was determined in the following manner. Gain in dry weight and the correlated responses for specific gravity and the number of limbs per foot were predicted. These responses were multiplied by the same relative economic value assigned to that trait when constructing the index. The sum of these products is the gain in the aggregate genetic value from clonal selection and is directly comparable to the gain in the aggregate genetic value from selecting on the index.

Examination of the efficiencies relative to the assumed goal in both populations reveals that choosing any of the sets of relative economic values will result in very little change in the expected gain. The magnitude of these differences would be greater if extreme sets of relative economic weights were used as the basis for comparison. The weights assumed correct were the result of subjective judgments on the author's part. They are, however, more reasonable estimates than extreme sets of relative weights.

Comparisons of efficiencies calculated using clonal selection for increased dry weight as a basis indicated that selection on any of the indexes constructed for Population 1 promised greater gains than clonal selection.

The maximum predicted loss of efficiency from choosing a wrong set of relative economic values in Population 1 was 3 percent of the expected gain, or a loss of only 0.04 pounds of dry weight equivalent. The index with the least efficiency relative to clonal selection promised additional gains of 32 percent over those predicted for clonal selection (an additional increase of 0.37 pounds of dry weight equivalent) in this population. It would seem advantageous to make selections based on an index in Population 1 even though exact economic values are not known for the traits considered in the definition of worth.

The situation in Population 2 was somewhat different. There was still little loss of efficiency from choosing a set of relative economic weights different from those assumed to be correct. However, selection on none of the indexes promised the increased efficiency over clonal selection predicted for Population 1. Calculating index values on which to base selections could prove to be a needless expense in this population unless accurate estimates of economic weights can be determined. It should be noted that selection based on any index in Population 2 promised gains at least equal to those predicted for clonal selection.

## CHAPTER IV

## SELECTION IN THE NATURAL POPULATION

The procedure for selecting in natural forest tree populations has been to select the best individuals within stands. Although the size of a stand may vary, it usually is an area no larger than a few acres in which gross environmental features such as soil type are reasonably uniform. Candidate trees are compared with the best trees in the stand and are accepted or rejected on the basis of their relative performance. Information from provenance studies is used to choose geographic areas in which selections will be made.

The concept of provenance studies is a simple one. Phenotypes from the natural population are grown at a common location. Once the effects of the microenvironment at the planting site are statistically accounted for, the remaining variance is genetic.

The total genetic variance among clones from the natural population may be partitioned into two components. Variation among clones from the same stand is the component upon which selection should be based when selection is performed among trees within a stand. Variation among groups of clones from different stands is the result of genetic differentiation within a large population in response to selection pressure by the environment.

## Analyses of Variance and Covariance

The number of clones included in the analysis of variance for Location 1 was so small that it was felt no attempt should be made to infer that estimates of parameters from this location were representative of the natural population. The large number of clones at Location 2 provided relatively precise estimates of parameters for the natural population. Since parameters were estimated at one location, predictions of performance of clones selected from the natural population apply only when environmental circumstances are similar to those described at Location 2.

Total variances and covariances were partitioned in the manner shown in Table III. Variation among stands and among clones within stands was statistically significant for six traits at levels of significance greater than 99 percent (Table XXII). Comparisons of the estimates of components of variance for stands ($\hat{\sigma}^2_S$) and for clones within stands ($\hat{\sigma}^2_{C/S}$) in Table XXIII indicated that care must be taken in choosing the geographic areas in which selections will be made. The stand component of variance was large enough with respect to the clone/stand component that gains from selecting the best trees within stands could be lost if clones were planted on sites to which they are not adapted.

## Components of Variance and Covariance

Estimates of phenotypic and genotypic components of variance and covariance on which predictions of responses to selection in the natural population were based are presented in Table XXIV. The component of

TABLE XXII

ANALYSES OF VARIANCE PARTITIONING VARIATION AMONG CLONES INTO VARIATION AMONG STANDS AND AMONG CLONES WITHIN STANDS

| Source of Variation | D.F. | Mean Squares | | | | | |
|---|---|---|---|---|---|---|---|
| | | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight |
| Blocks | 3 | 168.39** | 4.3742** | .002680** | .5966** | .596418** | 316.47** |
| Stands | 20 | 75.89** | 1.7786** | .003513** | 5.2259** | .199346** | 106.30** |
| Blocks x Stands | 60 | 6.90* | .2847* | .000115 | 1.0197 | .034719 | 19.14 |
| Clones/Stands | 89 | 12.06** | .7687** | .001479** | .1023** | .067196** | 37.99** |
| Blocks x Clones/ Stands | 267 | 4.93** | .2126** | .000138** | .0960** | .023097** | 13.27** |
| Within Plot $\left(\frac{\sigma^2 W}{k}\right)$ | 1389 | .37 | .0037 | .000017 | .0505 | .000315 | 1.85 |

* $\alpha \leq .05$, ** $\alpha \leq .01$

TABLE XXIII

COMPONENTS OF VARIANCE FROM ANALYSES OF VARIANCE PARTITIONING VARIATION AMONG CLONES INTO VARIATION AMONG STANDS AND AMONG CLONES WITHIN STANDS

| Trait | $\hat{\sigma}^2_S$ | S.E. $\hat{\sigma}^2_S$ | $\hat{\sigma}^2_{BXS}$ | $\hat{\sigma}^2_{C/S}$ | S.E. $\hat{\sigma}^2_{C/S}$ | $\hat{\sigma}^2_{BXC/S}$ | $\hat{\sigma}^2_W$ |
|---|---|---|---|---|---|---|---|
| Height | 2.84339 | 1.05678 | .36239 | 1.78253 | .45968 | 3.58844 | 4.83260 |
| Diameter | .04310 | .02532 | .01325 | .13902 | .02885 | .07646 | .48841 |
| Specific Gravity | .00009 | .00005 | .00000 | .00033 | .00005 | .00007 | .00021 |
| Number of Limbs/Foot | .19304 | .07276 | .00115 | .23093 | .03785 | .04543 | .18144 |
| Volume | .00554 | .00281 | .00213 | .01102 | .00254 | .01176 | .04062 |
| Dry Weight | 2.86989 | 1.50506 | 1.07931 | 6.181156 | 1.43699 | 6.61812 | 23.85373 |

TABLE XXIV

ESTIMATES OF PHENOTYPIC COMPONENTS OF VARIANCE AND COVARIANCE ON AN INDIVIDUAL BASIS AND GENOTYPIC COMPONENTS OF VARIANCE AND COVARIANCE (IN PARENTHESIS) BASED ON VARIATION AMONG CLONES WITHIN STANDS

| | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight |
|---|---|---|---|---|---|---|
| Height | 10.2035<br>(1.7825) | 2.0328<br>(.2604) | -.0073<br>(-.0033) | .1201<br>(-.0729) | .6683<br>(.1017) | 15.9808<br>(2.3990) |
| Diameter | | .7039<br>(.1390) | -.0019<br>(-.0019) | .1386<br>(.0663) | .2004<br>(.0371) | 4.8064<br>(.8615) |
| Specific Gravity | | | .0006<br>(.0003) | -.0003<br>(.0006) | -.0006<br>(-.0004) | -.0016<br>-.0039 |
| Number of Limbs/Foot | | | | .4578<br>(.2309) | .0327<br>(.0132) | .7779<br>(.3313) |
| Volume | | | | | .0634<br>(.0110) | 1.5161<br>(.2577) |
| Dry Weight | | | | | | 36.6534<br>(6.1815) |

variance associated with clones/stands was used to estimate genetic variances and covariances. Estimates of phenotypic variances and covariances are dependent upon the nature of the units of selection. Estimates of these parameters used to make selections in the experimental populations were on the basis of clone means (Chapter III). These estimates were dependent on the number of ramets per plot as well as the number of blocks used in the experimental plantings. Estimates of phenotypic variances and covariances used in making selections in the natural population were calculated on an individual basis since individual trees are the units of selection.

Broad Sense "Heritabilities" on an Individual Basis

Broad sense "heritabilities" were calculated on an individual basis in the following manner:

$$H^2 = \frac{\hat{\sigma}^2_{C/S}}{\hat{\sigma}^2_{C/S} + \hat{\sigma}^2_{BxC/S} + \hat{\sigma}^2_{W}}$$

Values for six traits calculated in this fashion are presented in Table XXV. These estimates compare will with those of Wilcox and Farmer (30). These authors calculated broad sense heritabilities on an individual basis for 49 clones grown at one location after one and two growing seasons. Heritabilities were .25 and .31 for height and .20 and .21 for diameter. Heritability for the total number of branches was estimated to be .43 after one growing season.

The "heritabilities" estimated in this study indicated that if individual tree selection were performed on each trait separately, gains could be made with greater ease for specific gravity and the number of limbs per foot than for growth and yield traits.

TABLE XXV

BROAD SENSE "HERITABILITIES" ON AN INDIVIDUAL BASIS
FOR SIX TRAITS MEASURED AT LOCATION 2

| Trait | Broad Sense "Heritability" |
|---|---|
| Height | .17 |
| Diameter | .20 |
| Specific Gravity | .53 |
| Number of Limbs per Foot | .50 |
| Volume | .17 |
| Dry Weight | .17 |

Broad sense "heritabilities" calculated on an individual basis were used to predict the response to individual tree selection for each trait (Table XXVI). Predicted gains were calculated using the equation:

$$\Delta G = \cdot \frac{\hat{\sigma}_G^2}{\hat{\sigma}_P^2} \cdot \hat{\sigma}_P$$

where: $\Delta G$ = the expected gain from individual tree selection in units of the trait being selected on, i = the selection intensity, $\hat{\sigma}_G^2$ = estimate of the total genetic variance among clones within stands, and $\hat{\sigma}_P^2$ = estimate of the phenotypic variation on an individual basis.

TABLE XXVI

PREDICTED RESPONSES TO INDIVIDUAL TREE SELECTION FOR SIX TRAITS AT TWO INTENSITIES OF SELECTION

| Trait | Proportion Selected = 1/1000 (i=3.3671) | | Proportion Selected = 1/10,000 (i=3.9583) | |
|---|---|---|---|---|
| | Expected Gain in Units of Trait | Expected Gain as % of Population Mean | Expected Gain in Units of Trait | Expected Gain as % of Population Mean |
| Height (Ft.) | 1.83 | 12 | 2.15 | 14 |
| Diameter (In.) | .56 | 23 | .66 | 28 |
| Specific Gravity | .04 | 10 | .05 | 12 |
| Limbs/Foot | -1.13 | 41 | -1.34 | 48 |
| Volume (Cu.Ft.) | .14 | 90 | .17 | 105 |
| Dry Weight (Lbs.) | 3.43 | 30 | 4.07 | 35 |

Gains estimated in this fashion are not strictly applicable when selecting in the natural population since phenotypic variance in the natural population is greater than that in the experimental planting. Heritability in the natural population would be smaller since phenotypic variance is larger, thus gains estimated using estimates of phenotypic variance from the experimental plantings represent upper limits for gains that may be realized from selection in the natural population. Predicted responses in Table XXVI are the result of applying selection pressure to one trait at a time. When changes are sought in several traits at once, expected response for each trait will be lower than the values presented. Genetic correlations between traits affect gains when selection is for more than one trait.

## Phenotypic and Genotypic Correlations on an Individual Basis

Genotypic correlations were calculated as in equation (3) using the components of variance and covariance associated with variation among clones within stands to estimate genetic variances and covariances. Phenotypic correlations were calculated on an individual basis. Phenotypic and genotypic correlations are presented in Table XXVII. Phenotypic correlations among all the growth traits are statistically significant at levels of significance at least as great as 95%. The phenotypic correlation between diameter and the number of limbs per foot was also significant at the 95% level of confidence. No other phenotypic correlation including specific gravity or the number of limbs per foot was significant at these confidence levels.

Genotypic correlations are smaller than or equal to those

TABLE XXVII

PHENOTYPIC (ABOVE THE DIAGONAL) AND GENOTYPIC (BELOW THE DIAGONAL) CORRELATIONS BETWEEN PAIRS OF TRAITS ON AN INDIVIDUAL TREE BASIS

| | Height | Diameter | Specific Gravity | Number of Limbs/Foot | Volume | Dry Weight |
|---|---|---|---|---|---|---|
| Height | | .759** | -.092 | .056 | .831** | .826** |
| Diameter | .523 | | -.094 | .244* | .949** | .949** |
| Specific Gravity | -.137 | -.284 | | -.020 | -.099 | -.011 |
| Number of Limbs/Foot | -.114 | .370 | .071 | | .192* | .190* |
| Volume | .726 | .950 | -.236 | .263 | | .994** |
| Dry Weight | .723 | .929 | -.086 | .277 | .988 | |

* $\alpha \leq .05$, ** $\alpha \leq .01$

calculated on a clone mean basis in Chapter III. This was expected since the covariance associated with changes between geographic locations was not included in the genetic covariance. Only one correlation exhibited a change in direction when calculated on a within stand basis. Limbs/foot X volume is a very small negative correlation (-.012) on a clone mean basis and is .263 when calculated on a within stand basis. This change reflects a negative covariance between these two traits on a stand mean basis.

If the aggregate genetic value of an individual is defined in terms of specific gravity, the number of limbs per foot, and dry weight as in Chapter III, the genetic relationships between these traits are of concern. Selection to increase dry weight should result in an increase in limbiness and a decrease in specific gravity.

## Indexes for Selection on an Individual Basis

Indexes in Table XXVIII were constructed using different combinations of five traits to select for increases in dry weight. The importance of diameter in selecting trees for increased dry weight becomes evident upon examining these indexes. It is also apparent that using height, diameter, and specific gravity to calculate dry weight and including it in the index resulted in further increases in efficiency of selection.

Efficiencies in Table XXVIII were expressed as a percentage of the expected gain from individual tree selection for increased dry weight. These efficiencies indicated that increases of up to four percent of the gains expected from individual tree selection may be had from selection based on an index. This represents a gain of only 0.14

TABLE XXVIII

COMPARISON OF INDEXES FOR SELECTING ON AN INDIVIDUAL BASIS TO INCREASE DRY WEIGHT

| Criterion for Selection | Partial Regression Coefficients: Height | Diameter | Specific Gravity | Volume | Dry Weight | $\Delta G_I$ 1/ (Lbs.) | $\Delta G_I$ as % of Population Mean | Relative Efficiency (%) |
|---|---|---|---|---|---|---|---|---|
| Dry Weight | | | | | .1686 | 3.43 | 29 | 100 |
| Diameter | | 1.2239 | | | | 3.46 | 30 | 101 |
| Volume | | | | 4.0650 | | 3.43 | 29 | 100 |
| Index 1 | -.0205 | 1.2833 | | | | 3.46 | 30 | 101 |
| Index 2 | -.1006 | | | 5.1255 | | 3.50 | 30 | 102 |
| Index 3 | -.0915 | | | | .2085 | 3.46 | 30 | 101 |
| Index 4 | | 1.2172 | -2.4053 | | | 3.46 | 30 | 101 |
| Index 5 | | .6641 | | 1.9656 | | 3.50 | 30 | 102 |
| Index 6 | | .6918 | | .0779 | | 3.50 | 30 | 102 |
| Index 7 | | | -2.2255 | 4.0431 | | 3.43 | 29 | 100 |
| Index 8 | | | -5.8003 | | .1684 | 3.46 | 30 | 101 |
| Index 9 | | | | 2.9829 | .0453 | 3.43 | 29 | 100 |
| Index 10 | -.0215 | 1.2790 | -2.4615 | | | 3.46 | 30 | 101 |
| Index 11 | -.0863 | .5655 | | 3.1865 | | 3.53 | 30 | 103 |
| Index 12 | -.0794 | .6242 | | | .1214 | 3.53 | 30 | 103 |
| Index 13 | -.1012 | | -2.3510 | 5.1084 | | 3.50 | 30 | 102 |
| Index 14 | -.1057 | | -6.9162 | | .2144 | 3.53 | 30 | 103 |
| Index 15 | -.1007 | | | 4.0306 | .0458 | 3.50 | 30 | 102 |
| Index 16 | | .6639 | -2.2178 | 1.9445 | | 3.50 | 30 | 102 |
| Index 17 | | .6596 | | 1.4186 | .0235 | 3.50 | 30 | 102 |

pounds per tree over gains from individual tree selection. However, these gains were calculated for three year old trees. If the same percentage gains could be expected at rotation age, four percent would represent a considerable gain. Selection based on any of the indexes in Table XXVIII does not apply direct selection pressure on any trait other than dry weight.

## Indexes With Complex Goals of Selection

The procedure used in Chapter III to examine the effect of varying the relative economic weights has been used to examine multiple trait selection indexes constructed on an individual basis. Variances and covariances for height, diameter, specific gravity, number of limbs per foot, volume, and dry weight were used to construct indexes for which the aggregate genetic value was changed. Redefinition of the aggregate genetic value was accomplished by varying the relative economic weights for specific gravity, number of limbs per foot, and dry weight. Height, diameter, and volume were assigned the relative economic weight zero in every index. Indexes constructed in this manner are presented in Table XXIX.

Efficiencies were calculated as described in Chapter III. Efficiencies relative to the assumed goal indicated that fairly small losses in efficiency occurred when incorrect relative weights were assigned to specific gravity, number of limbs per foot and dry weight. Losses up to 2 percent (0.07 pounds) may occur when incorrect weights are chosen. Gains of 2 to 6 percent (0.06 to 0.21 poinds) over individual tree selection may be expected when selection is based on one of the indexes

TABLE XXIX

COMPARISONS OF EXPECTED GAINS FROM INDIVIDUAL SELECTION BASED ON AN INDEX WITH DIFFERENT GOALS OF SELECTION

| Relative Economic Weights | | | Responses of the Traits Used to Construct the Index | | | | | | | Efficiency of Index Relative to | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Specific Gravity | Number of Limbs/Ft. | Dry Weight | Height (Ft.) | Diameter (In.) | Specific Gravity | Number of Limbs/Ft. | Volume (Cu.Ft.) | Dry Weight (Lbs.) | $\Delta G_I$ 1/ (Lbs.) | Assumed Goal | Individual Tree Selection |
| 0 | -1 | 1 | 1.28 | .53 | -.010 | .138 | .152 | 3.47 | 3.34 | 98% | 102% |
| .1 | -1 | 1 | 1.28 | .53 | -.010 | .138 | .152 | 3.47 | 3.33 | 98 | 102 |
| .5 | -1 | 1 | 1.28 | .53 | -.010 | .138 | .152 | 3.47 | 3.33 | 98 | 102 |
| 1 | -1 | 1 | 1.28 | .53 | -.010 | .141 | .152 | 3.47 | 3.32 | 98 | 102 |
| 0 | -.5 | 1 | 1.13 | .57 | -.010 | .333 | .158 | 3.62 | 3.46 | 100 | 103 |
| .1 | -.5 | 1 | 1.13 | .57 | -.010 | .333 | .158 | 3.62 | 3.45 | 100 | 103 |
| .5 | -.5 | 1 | 1.12 | .57 | -.010 | .333 | .158 | 3.62 | 3.45 | 100 | 103 |
| 1 | -.5 | 1 | 1.12 | .57 | -.010 | .333 | .155 | 3.62 | 3.44 | 100 | 103 |
| 0 | -.1 | 1 | .99 | .59 | -.007 | .468 | .158 | 3.66 | 3.61 | 99 | 106 |
| .1 | -.1 | 1 | .99 | .59 | -.007 | .468 | .158 | 3.66 | 3.61 | 99 | 106 |
| .5 | -.1 | 1 | .99 | .59 | -.007 | .471 | .158 | 3.66 | 3.61 | 99 | 106 |
| 1 | -.1 | 1 | .99 | .59 | -.007 | .471 | .158 | 3.66 | 3.61 | 99 | 106 |
| 0 | 0 | 1 | .96 | .59 | -.007 | .502 | .158 | 3.66 | 3.66 | 99 | 106 |
| .1 | 0 | 1 | .96 | .59 | -.007 | .502 | .158 | 3.66 | 3.66 | 99 | 106 |
| .5 | 0 | 1 | .96 | .59 | -.007 | .502 | .158 | 3.66 | 3.66 | 99 | 106 |
| 1 | 0 | 1 | .95 | .59 | -.007 | .502 | .158 | 3.66 | 3.66 | 99 | 106 |

1/ $\Delta G_I$ is the expected gain in pounds of dry wood fiber equivalent. Proportion selected is 1/1000 (i = 3.3671).

in Table XXIX. These comparisons indicated that increases in efficiency over individual tree selection as a result of selecting on an index may be too small to warrant the expense of constructing and using an index.

# CHAPTER V

## SUMMARY AND CONCLUSIONS

The primary purpose of this investigation was to determine how selections were to be made to genetically improve eastern cottonwood in Oklahoma. To accomplish this, genetic information was derived from two experimental plantings of eastern cottonwood. Cottonwood clones studied represented stands from along the Red, Canadian, and Cimarron Rivers from the western border of Arkansas to the headwaters of each drainage.

The magnitude and type of genotype X environment interactions for growth and yield traits examined dictated that selection be performed at each location for clones best suited to that particular environment. Three clones were found that performed well in terms of yield at both locations.

Clonal selection was compared to multiple trait selection indexes in each of the two experimental populations. In Population 1 significant increases in efficiency over clonal selection were predicted for index selection when either increased volume or dry weight was the goal of selection. In Population 2 there was no appreciable increase in predicted gain over clonal selection when selection was based on an index.

The value of an individual is more appropriately expressed in terms of several traits. If maximum gain in economic value is the goal then relative economic values for each trait affecting the worth of an individual must be known. Since information needed to determine relative economic values is not available for forest trees, the effect of varying economic values for specific gravity, number of limbs per foot, and dry weight was examined in both populations. In Population 1 estimated gains in efficiency over clonal selection were large enough that they overshadowed estimated losses from choosing a wrong set of relative economic values for the three traits mentioned. In Population 2, predicted gains in efficiency associated with indexes constructed using different sets of economic values were not large enough to justify choosing index selection over clonal selection unless accurate estimates of relative economic values could be determined.

Parameters estimated from Population 2 on an individual basis were used to determine the selection method to be used in performing selections on an individual basis. Comparisons of predicted gains indicated that added gains of up to four percent could be had by selecting on an index value rather than individual tree selection for increased dry weight. These estimates of gains are strictly applicable only in the environment in which parameters were estimated. However, gains for the two methods of selection may be compared. The procedure of calculating gains for different indexes while varying the relative economic values for specific gravity, number of limbs per foot, and dry weight indicated that estimates of relative economic values for these traits might be used without incurring serious losses in predicted efficiencies for index selection.

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