Three of the four families with high frequencies of self-pollination seedlings came from small stands; the fourth from a tree which was contributing very few filled seeds to the regeneration seed pool. For widespread stands, the median appears to provide a better estimate of natural production of self-seedlings for central Oregon lodgepole pine than does the mean. Natural inbreeding appears to occur at relatively low frequency and should have negligible impact on natural or artificial regeneration of *P. contorta* var. *murrayana* in Oregon, except perhaps for a few stands or for a few individuals. The low level of natural self-fertilization is comparable to results reported for *P. contorta* var. *latifolia* in northeastern Washington (EPPERSON and ALLARD 1984) and British Columbia (YEH and LAYTON 1979).

Acknowledgement

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Genetic Variation in Juvenile Characters of Populus deltoides Bartr. from the Southern Great Plains [1])[2])

By C. D. NELSON and C. G. TAUER[3])

Summary

Genetic variation in first and second year characters of eastern cottonwood (*Populus deltoides* BARTR.) from the southern Great Plains was assessed. Open-pollinated seed from four trees in each of 40 natural stands (159 families) was collected in June 1982 and sown in a greenhouse in July 1982. The seedlings were outplanted to two nursery locations in Oklahoma following seven weeks of greenhouse-growth.

The following data were collected during the first two years of growth: greenhouse height (GHT); first year height (HT1) and date of leaf fall (LF1); second year height (HT2), date of leaf fall (LF2), *Melampsora* spp. leaf rust score (MLR), number of branches per decimeter of tree height (BRPD) and survival (SURV). Analyses of variance were performed for each character, to test for significance of differences among stand and among family within-stand means. Geographic variation (among stand) was quantified and characterized. Family mean heritabilities and genetic correlation coefficients were estimated for each character and selected pairs, respectively.

Significant ($P < .05$) differences among stand means were found for all characters except SURV and among family means for GHT, HT1, DIA, LF1, LF2, MLR and BRPD. Significant location by stand interactions were found for all characters, while location by family interactions were significant for LF1 only. Continuous northwest-to-southeast patterns of variation were found for all characters except BRPD. Heritability estimates were zero for SURV ($.00 \pm .14$); moderate for HT2 ($.19 \pm .15$) and DIA ($.30 \pm .13$); and high for GHT ($.49 \pm .07$), HT1 ($.35 \pm .10$), LF1 ($.39 \pm .11$), LF2 ($.61 \pm .07$), MLR ($.38 \pm .11$) and BRPD ($.69 \pm .06$). Genetic correlation coefficients between characters showed second year diameter (DIA) to be the most useful character on which to base selections at age two.

Key words: Genetic variation, geographic variation, juvenile characters, heritability, genetic correlation, *Populus deltoides*.

Zusammenfassung

Bei *Populus deltoides* BARTR. aus den südlichen Great Plains wurde die genetische Variation von Merkmalen im ersten und zweiten Jahr geschätzt. Frei abgeblühte Samen von vier Bäumen in jedem der 40 natürlichen Bestände (159 Familien) wurden im Juni 1982 gesammelt und im Juli 1982 in einem Gewächshaus ausgesät. Die Sämlinge wurden sieben Wochen später in zwei Baumschulen in Oklahoma ausgepflanzt, und in den ersten zwei Jahren wurden folgende Daten erhoben: Gewächshaushöhe (GHT), Einjahreshöhe (HT1), Datum des Laubabfalles (LF1), Zweijahreshöhe (HT2), Datum des Laubabfalles (LF2), *Melampsora* spp. Blattrostbefall (MLR), Anzahl Äste pro dm Baumhöhe (BRPD) und Überlebensfähigkeit (SURV). Für jedes Merkmal wurden Varianzanalysen durchgeführt, um die Signifikanzen der Unterschiede zwischen Beständen und Familien innerhalb der Bestände zu testen. Die geographische Variation (zwischen Beständen) wurde quantifiziert und charakterisiert. Familienheritabilitäten im engeren Sinne und genetische Korrelationskoeffizienten wurden für jedes Merkmal und selektierte Paarungen geschätzt. Signifikante Unterschiede für $P < 0,05$ zwischen Bestandesmittelwerten wurden für alle Merkmale außer SURV und zwischen Familien für GHT, HT1, DIA, LF1, LF2, MLR und BRPD gefunden. Signifikante Standort × Bestand-Interaktionen wurden für alle Merkmale gefunden, während Standort × Familien-Interaktionen nur für LF1 festzustellen waren. Kontinuierliche Nordwest/Südost-Variationsmuster wurden für alle Merkmale außer BRPD gefunden. Heritabilitäts-Schätzwerte waren für SURV null (0,00 $\pm$ 0,14), für HT2 (0,19 $\pm$ 0,15) und DIA (0,30 $\pm$ 0,13) gemä-
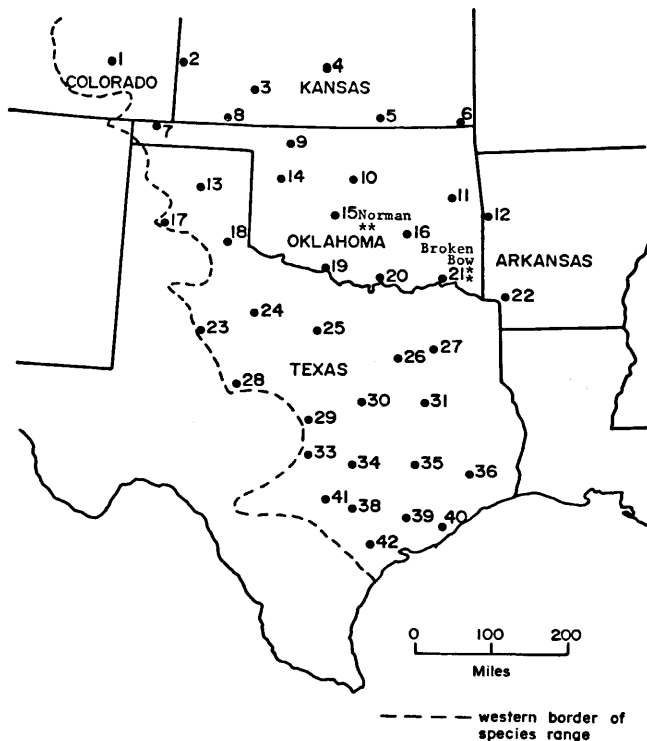
Figure 1. — Southwestern portion of the eastern cottonwood native range, seed collection sites (stands) and nursery locations.

ßigt und für GHT (0,49 ± 0,07), HT1 (0,35 ± 0,10), LF1 (0,39 ± 0,11), LF2 (0,61 ± 0,07), MLR (0,38 ± 0,11) und BRPD (0,69 ± 0,06) hoch. Genetische Korrelationskoeffizienten zwischen Merkmalen zeigten, daß der Durchmesser im Alter von zwei Jahren (DIA) das brauchbarste Merkmal war, um im Alter 2 zu selektieren.

1. Introduction

Eastern cottonwood (*Populus deltoides* BARTR.) is native throughout much of the southern Great Plains region of the United States (*Figure 1*). Under proper management, it is fast growing and highly productive. In addition, the species is noted for good wood and fiber quality (CRIST et al. 1979).

Dry conditions usually limit the survival and growth of cottonwood in the southern Great Plains. However, mean annual precipitation varies remarkably in that region (31 cm in southeast Colorado to 134 cm in southeast Texas) and WALKER (1967) reported good eastern cottonwood growth on many sites in central Oklahoma. The combination of fast growth, good fiber quality and presence of suitable planting sites make eastern cottonwood a valuable species for wood and fiber production in the southern Great Plains.

Genetic improvement of eastern cottonwood has progressed in several regions of the United States (MOHN 1973, WILCOX and FARMER 1967, YING and BAGLEY 1976). However, genetic information about the southwestern portion of eastern cottonwood's native range is lacking (JOKELA and MOHN 1976). The following study documents the genetic parameters of juvenile growth of the southern Great Plains eastern cottonwood population.

2. Materials and Methods

In June 1982 open-pollinated eastern cottonwood seed was collected from as many as five trees in each of 42 natural stands within the southwestern portion of the eastern cottonwood range. The stands were systematically located along major rivers and were assumed to constitute a random sample of stands in the southern Great Plains. Ten stands were located in Oklahoma, 23 in Texas, six in Kansas, two in Arkansas and one in Colorado (*Figure 1*). A lack of seed bearing trees precluded the inclusion of two Texas stands (i.e. 32 and 37).

Within a stand, seed was collected directly from randomly selected trees with between seed tree spacing of at least 60 meters. A total of 197 open-pollinated families (seedlots) were collected. A germination test was run to determine which families to enter in the experiment. The four families of each stand with the highest percent germination were selected for use.

In July 1982 approximately 15 seeds from four trees per stand, except three trees from stand 41, were sown in a sterile peat-sand mixture in 5.1 × 5.1 × 12.7 cm pots. The pots were located in the Oklahoma State University Department of Forestry greenhouse at Stillwater, Oklahoma. A randomized complete block experimental design was utilized, with families as treatments, ten replicates and six-tree row plots.

Following seedling emergence, each pot was thinned to three plants and four weeks later to one plant. Moderate selection for vigor was practiced in thinning. All seedlings were moved into a shade house, after seven or eight weeks of growth, for outplanting acclimation.

In late August 1982, following a 14 day acclimation period, half of the seedlings (five replicates) were planted in the Oklahoma Division of Forestry nursery near Norman, Oklahoma. In early September 1982 following an 11 day acclimation period, the remaining half of the seedlings were planted in a temporary nursery near Broken Bow, Oklahoma (*Figure 1*). The nursery phase experimental design was a randomized complete block, with families and locations as treatments, five replicates within-location and four-tree row plots. Seedling mortality and the need for border material made it necessary to reduce plot size from six to four seedlings.

Spacing at each nursery was 46 cm within rows by 99 cm between rows. All 159 seedlots of the greenhouse phase were represented in each replicate of the nursery phase. During the first month of establishment, both nursery sites were irrigated when necessary. Complete weed control was maintained at Norman, while only partial control was achieved at Broken Bow.

Data were collected on each tree for the following characters: greenhouse height (GHT); first year height (HT1) and date of leaf fall (LF1); second year height (HT2), date of leaf fall (LF2), diameter at one foot (DIA), *Melampsora* spp. leaf rust score (MLR), number of branches (BR) and survival (SURV).

Greenhouse height was measured seven weeks after sowing. First year height was measured following the first growing season (December 1982), while second year height, number of branches and survival data were collected following the second growing season (December 1983). Number of branches was converted to number of branches per decimeter of tree height (BRPD).

First and second year dates of leaf fall were recorded as the number of days past November 1, 1982 for LF1 and October 31, 1983 for LF2 — when one or zero leaves remained on the tree. *Melampsora* spp. leaf rust score was recorded, on October 10, 1983 at Norman and October 15, 1983 at Broken Bow, as the percentage to the nearest 10 percent of a tree's total (upper) leaf surface area that was covered with *Melampsora* spp. urediospores. The score was estimated by visual inspection.

Table 1. — Analysis of variance format, components of expected mean squares and F-tests.

Source of Variation	Degrees of Freedom	Mean Squares	Expected Mean Squares
Location	1		
Rep (Loc)	8		
Stand	39	M_5	$V_e + C_6 V_{1f(s)} + C_7 V_{f(s)} + C_8 V_{1s} + C_9 V_s$
Loc*Stand	39	M_4	$V_e + C_4 V_{1f(s)} + \qquad C_5 V_{1s}$
Family (Stand)	119	M_3	$V_e + C_2 V_{1f(s)} + C_3 V_{f(s)}$
Loc*Fam (Stand)	119	M_2	$V_e + C_1 V_{1f(s)}$
Error	****	M_1	V_e

F-tests:

$F_{stand} = (M_5 + M_2) / (M_4 + M_3)$ with $[(M_5 + M_2)^2] / [(M_5{}^2 / 39) +$
$(M_2{}^2 / 119)]$ and $[(M_4 + M_3)^2] / [(M_4{}^2 / 39) + (M_3{}^2 / 119)]$
degrees of freedom (Cochran and Cox 1957)

$F_{loc*stand} = M_4 / M_3$ with 39 and 119 degrees of freedom

$F_{family\ (stand)} = M_3 / M_2$ with 119 and 119 degrees of freedom

$F_{loc*stand} = M_2 / M_1$ with 119 and error **** degrees of freedom

Note: V_e = experimental error variance

$V_{1f(s)}$ = location * family within-stand interaction variance component

$V_{f(s)}$ = family within-stand variance component

V_{1s} = location * stand interaction variance component

V_s = stand variance component

C_i = coefficient in expected mean square as computed by the S.A.S. (1982b) procedure VARCOMP

**** The error degrees of freedom varied depending on the character being analyzed (i.e. 1182 for MLR to 1253 for SURV).

Each character was subjected to the analysis of variance procedure and F-tests, using a significance level of 0.05. The analysis of variance format and F-tests in terms of expected mean squares are shown in Table 1. All effects were considered to be random.

Family mean heritability estimates were calculated for each character using Formula 1 (Wright 1976). Genetic correlation coefficient estimates, between selected characters (X and Y), were computed using Formula 2 (Falconer 1981). Standard errors for heritability and genetic correlation coefficient estimates were aproximated using methods described by Kendall and Stuart (1958).

$$h^2 = \frac{V_{f(s)}}{V_{e/j} + V_{1*f(s)}/k + V_{f(s)}} \qquad (1)$$

$V_{f(s)}$ = family within-stand variance component
$V_{1*f(s)}$ = location * family within-stand variance component
V_e = experimental error variance
j = C_3 (Table 1)
k = j/C_2 (Table 1)

$$r_{g[x,y]} = \frac{COV_{f(s)\ [x,y]}}{(V_{f(s)\ [x]} * V_{f(s)\ [y]})^{1/2}} \qquad (2)$$

$COV_{f(s)\ [x,y]}$ = family within-stand covariance component of characters x and y
$V_{f(s)\ [x]}$ = family within-stand variance component of x
$V_{f(s)\ [y]}$ = family within-stand variance component of y

Formulae 1 and 2. — Family mean heritability and genetic correlation coefficient.

Pearson (simple) correlation coefficients (S.A.S. 1982a) were calculated for overall stand means of each character with each of seven stand origin variables including latitude (°N), longitude (°W), mean number of frost free days, mean

annual precipitation (cm), elevation (m) and mean annual minimum and maximum temperatures (°C).

3. Results and Discussion

3.1 Means and Analysis of Variance

Table 2 presents the means and their standard errors for each character at each location and over locations. It seems apparent from these means that a location effect was present, with trees at Norman growing larger in height and diameter. Analyses of variance and F-tests (P < .05) for each character verify the presence of a significant location effect for all characters except Melampsora leaf rust score. The differing dates in assigning Melampsora scores may have obscured a possible location effect.

In addition to being a better cottonwood site, a portion of the survival and growth advantage at Norman was probably due to the complete weed control achieved at that site. Eastern cottonwood survival and growth can be substantially retarded by weed competition (Fowells 1965).

The later dates of leaf fall and greater number of branches per unit height at Norman seems also to be related to the site quality and the degree of weed control achieved at that site. Greater weed competition at Broken Bow apparently resulted in less favorable growing conditions, which has been suggested to cause earlier growth cessation

Table 2. — Location means and their standard errors.

Character	Norman Nursery Mean	s.e.	Broken Bow Nursery Mean	s.e.	Overall Mean	s.e.
SURV (%)	79.4	- -	67.5	- -	73.3	- -
HT1 (cm)	27.4	0.22	23.0	0.20	25.3	0.15
HT2 (cm)	223.5	1.31	185.4	1.31	205.8	0.97
DIA (mm)	16.1	0.11	13.5	0.12	14.9	0.09
LF1 (days*)	38	0.2	24	0.3	31	0.2
LF2 (days**)	30	0.3	20	0.1	25	0.2
MLR (%)	29	0.6	31	0.5	30	0.4
BRPD (#/dm)	1.07	0.010	0.64	0.010	0.87	0.08
GHT (cm)	- -	- -	- -	- -	9.62	0.05

Note: * number of days past November 1, 1982
** number of days past October 31, 1983

and leaf fall (JOKELA and MOHN 1976). Also, the presence of weeds appears to limit branch production by competing for above ground sunlight and below ground water and nutrients.

Differences among stand means were significant for all characters except survival. This indicates that a growth rate advantage may be gained in the second year by planting seed from stands having the fastest growing progenies. However, juvenile cottonwood performance has been found to be an unreliable predictor of mature tree performance (MOHN and RADSLIFF 1983).

Differences among family within-stand means were significant for greenhouse height; first year height; and second year diameter, date of leaf fall, Melampsora score and number of branches per decimeter. In addition to improvement resulting from stand selection, it is evident that open-pollinated family selection would add markedly to the stand selections gains.

Significant location by stand interaction effects were found for all characters. Rankings of stand means for each character at each location indicates change in rank interactions for second year height, Melampsora score and number of branches per decimeter. This suggests that stand selections for these characters should be based on the individual location ranking that most closely approximates (environmentally) the anticipated planting site.

Stand by location interactions for first year height and date of leaf fall as well as second year diameter and date of leaf fall did not appear to have been caused by obvious rank changes. It seems more probable that differences in stand variance between locations or diverging stand means may have caused these significant interactions (LOWE et al. 1982).

Two year height at Broken Bow was greater for seedlings from south and east Texas whereas at Norman, seedlings from south and southeast Oklahoma grew best. It appears that gains in juvenile performance can be made through a judicious seed transfer in the northwesterly direction.

The location by family within-stand interaction effect was significant for first year date of leaf fall only. Thus, early family within-stand performance appears to be fairly stable across the two environments.

3.2 Simple Correlation Coefficients

Table 3 presents Pearson correlation coefficient estimates of stand means for each character with stand geographic and environmental variables. These correlation coefficients represent a quantification of the presence or absence of geographic (among stand) patterns of variation.

First year height and date of leaf fall and second year height, diameter, date of leaf fall and survival were similarly correlated with each of the stand origin variables. Each

character was strongly, negatively correlated with latitude, longitude and elevation. This suggests a northwest-to-southeast (or higher-to-lower elevaton) trend of variation. The strong, positive correlations for these characters with number of frost free days, mean annual precipitation, and mean annual minimum and maximum temperatures also support the suggested trend.

The correlation coefficients for greenhouse height were opposite in sign to those for first and second year height. Stand means from higher latitudes and longitudes were larger for seven weeks of greenhouse-growth, while after one season (including greenhouse phase) they were smaller (eg. GHT with Latitude, r = .45 and HT1 with Latitude, r = −.88). This reversing height growth trend seems to be related to the mid-season change in environment (greenhouse to nursery).

Melampsora leaf rust score was strongly, positively correlated with latitude, longitude and elevation and negatively correlated with number of frost free days, mean annual precipitation, and mean annual minimum and maximum temperatures. These coefficients also imply a northwest-to-southeast trend, except in the opposite direction of those for first and second year height and date of leaf fall, and second year diameter and survival.

A west-to-east pattern of variation for number of branches per decimeter of tree height was suggested by its simple correlations with longitude (r = .44) and mean annual precipitation (r = −.44). Several researchers have found similar patterns of geographic variation for these and other traits in eastern cottonwood and other forest tree species in the cental United States (BEY 1979, JOKELA and MOHN 1976, POSEY et al. 1969).

In general, seedlings from stands south and east of each nursery site grew larger in second year height and diameter and exhibited later dates of leaf fall (Table 3). Seedlings from stands north and west of the greenhouse and nursery locations grew taller in the greenhouse and had larger second year Melampsora leaf rust scores, while seedlings from western stands produced more branches per unit of tree height at age two (Table 3).

3.3 Heritabilities

Family mean heritability estimates with their approximated standard errors are presented in Table 4. The heritability estimate for greenhouse height is based on data from one location only, while all other estimates utilize data from both nursery locations.

The high heritability estimates for first and second year dates of leaf fall and number of branches per decimeter are in agreement with FARMER's (1966) observation that phenological and morphological characters of "lower Mississippi Valley (LMV)" eastern cottonwood seem to be under

Table 3. — Pearson correlation coefficients: stand means with stand origin data.

CHARACTER	Lat.	Long.	#Frost Free Days	Precip.	Elevation	Min. Temp.	Max. Temp.
GHT	.45*	.38*	-.41*	-.43*	.38*	-.48*	-.02
HT1	-.88*	-.58*	.85*	.60*	-.74*	.61*	.47*
HT2	-.57*	-.78*	.67*	.69*	-.85*	.45*	.61*
DIA	-.70*	-.82*	.78*	.77*	-.90*	.53*	.60*
LF1	-.91*	-.59*	.89*	.61*	-.77*	.69*	.47*
LF2	-.89*	-.59*	.89*	.63*	-.77*	.64*	.43*
MLR	.75*	.83*	-.82*	-.79*	.91*	-.58*	-.51*
BRPD	.03	.44*	-.17	-.44*	.24	-.03	.22
SURV	-.48*	-.63*	.55*	.58*	-.67*	.28	.39*

Note: * significantly different from zero at the .05 probability level

CHARACTER	h²	s.e.
GHT	.49	.07
HT1	.35	.10
HT2	.19	.15
DIA	.30	.13
LF1	.39	.11
LF2	.61	.07
MLR	.38	.11
BRPD	.69	.06
SURV	.00	.14

simple genetic control. In a Nebraska planting of a range-wide eastern cottonwood provenance test, YING and BAGLEY (1976) also found phenological traits to be under strong genetic (provenance, family, clone) control.

The decrease in estimated heritability for height between years one and two (HT1, $h^2 = .35 \pm .10$ and HT2, $h^2 = .19 \pm .15$) does not agree with YING and BAGLEY's (1976) observation that over time genetic factors become more dominant than site factors in determining growth rate. However, their observation was based on seven years of growth at one site.

The lower heritability estimate for second year height may be related to the reversal in the height growth trend from the greenhouse to the nursery (i.e. seedlings of southern origin beginning to outgrow seedlings of northern origin). FARMER and WILCOX (1965) reported heritabilities (individual tree) for third year height and diameter of "LMV" eastern cottonwood to be .35 and .16, respectively, which represents a reversal in magnitude from these estimates (HT2, $h^2 = .19$ and DIA, $h^2 = .30$). This difference may also be due in part to the reversing height growth trend from greenhouse to nursery.

3.4 Genetic Correlation Coefficients

Genetic correlation coefficient estimates between pairs of selected characters are presented in Table 5 with their approximate standard errors. Thirteen of the 28 possible correlation coefficients were estimated. These 13 were judged to be most valuable for genetic interpretation and most practical for immediate use in an eastern cottonwood breeding program.

The strong, negative correlation of greenhouse height with second year height ($r = -.75 \pm .36$) was probably a result of favorable greenhouse conditions for seedlings of northern origin, specifically conditions of a long (17 h) photoperiod and the environmental change following greenhouse height measurements. The weaker, negative correlation of first year height with second year height ($r_G = -.16 \pm .48$) probably reflects an intermediate point in the reversal of the height growth trend (from greenhouse to nursery). Under these conditions, it appears that at least two years of growth would be necessary before selection based on height could be made.

Second year date of leaf fall was positively correlated with first year leaf fall ($r_G = .68 \pm .16$), second year height ($r_G = .26 \pm .30$), diameter ($r_G = .31 \pm .23$) and number of branches per decimeter ($r_G = .37 \pm .14$). Families with later dates of leaf fall tended to attain a larger size through two years. Number of branches per decimeter of tree height was positively correlated with second year height ($r_G = .39 \pm .24$) and diameter ($r_G .69 \pm .14$), indicating that large seedlings produce more branches per unit tree height.

Melampsora leaf rust score was positively correlated with second year height ($r_G = .24 \pm .41$) and negatively correlat-

ed with second year diameter ($r_G = -.38 \pm .34$) and date of leaf fall ($r_G = -.55 \pm .17$). It is not clear from these data whether families with early leaf fall are more suseptible to Melampsora infection or Melampsora infection promotes early leaf fall.

The interpretation of several of these correlation coefficients appears questionable because of their large standard errors, especially MLR with HT2 ($r_G = .24 \pm .41$) and HT1 with HT2 ($r_G = -.16 \pm -.48$). Friend (1981) found Melampsora leaf rust incidence to be negatively correlated to both second year height ($r_G = -.41$) and diameter ($r_G = -.26$) of eastern cottonwood seedlings of southern United States origin.

Selections based on second year height would result in indirect selection favoring increased diameter, date of leaf fall, Melampsora susceptibility and number of branches per unit of tree height. Selections based on second year diameter would result in indirect selection for increased height, date of leaf fall, Melampsora resistance and number of branches per unit of tree height. With favorable genetic correlation coefficients and a moderately high heritability, second year diameter appears to be the best character on which to base eastern cottonwood selections at age two.

4. Conclusions

The southern Great Plains eastern cottonwood population was found to contain significant among stand and among family within-stand variation in juvenile characters. Much of the among stand variation fit into a continuous pattern of geographic variation, with northwest-southeast being the prominent orientation. Individual nursery stand means indicated that seed from south and east Texas would perform best at Broken Bow, while seed from south and southeast Oklahoma would perform best at Norman.

Genotype by environment interactions were found to be important only on a stand by location basis. However, many of the significant interactions (first year height and date of leaf fall and second year diameter, date of leaf fall and survival) appeared not to have been caused by changes in rank. Family by location interactions were generally lacking, probably in response to the significant levels of family within-stand genetic variation. Using clonal material, FARMER (1970) and MOHN and RANDALL (1973) found significant clone by location interactions but their results were based on a different level of genetic variation.

Heritability estimates based on family means were low-to-moderate for growth characters, and moderate-to-high for phenological and morphological characters and Melampsora spp. leaf rust incidence. Second year diameter, with a moderately high heritability ($h^2 = .30 \pm .13$) and favorable genetic correlation coefficients, seems to hold the greater promise as the selection criterion at age two.

	HT2		DIA		LF2	
	r_g	s.e.	r_g	s.e.	r_g	s.e.
GHT	-.75	.36	-.13	.27		
HT1	-.16	.48				
HT2			.68	.20	.26	.30
DIA					.31	.23
LF1					.68	.16
MLR	.24	.41	-.38	.34	-.55	.17
BRPD	.39	.24	.69	.14	.37	.14

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Additive and Dominance Genetic Effects in Pinus pinaster, P. radiata and P. elliottii and some Implications for Breeding Strategy

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Summary

Additive and dominance genetic variances were estimated for growth and stem straightness measured at around 8 years in control-pollinated progeny trials of *Pinus pinaster*, *P. radiata* and *P. elliottii* in South Africa. The progeny trials involved Design II matings among 13 female × five male parents in the case of *P. pinaster*, 11 × 5 for *P. radiata*, and 8× 8 for *P. elliottii*.

The levels of additive variance tended to be about the same or greater than the levels of dominance variance for growth of *P. pinaster* and *P. radiata*. Variance components for stem straightness of these two species were not reliably estimated. Additive variance was generally substantially greater than dominance variance for growth and straightness of *P. elliottii*.

An important finding was that the expected performance of full-sib families, as calculated by summing the general combining abilities of parents, proved to be a reasonable guide to the observed performance; even where levels of dominance variance were about the same as additive variance. Implications of this finding are discussed with particular reference to breeding strategies involving mass vegetative propagation.

Key words: Additive variance, dominance variance, *Pinus pinaster*, *Pinus radiata*, *Pinus elliottii*.

Zusammenfassung

In Südafrika wurden bei rund 8 Jahre alten frei abgeblühten Nachkommenschaftsprüfungen von *Pinus pinaster*, *Pinus radiata* und *Pinus elliottii* die additiven und die dominanten genetischen Varianzen für das Wachstum und die Geradschäftigkeit geschätzt. Die Nachkommenschaften umfassen im Design II Kreuzungen zwischen 13 weiblichen und 5 männlichen Eltern bei *Pinus pinaster*, 11 × 5 für *Pinus radiata* und 8 × 8 für *Pinus elliottii*.

Die Levels für die additive Varianz waren für das Höhenwachstum für *Pinus pinaster* und *Pinus radiata* genauso groß oder größer als die für die Dominanzvarianz. Die Varianzkomponenten für die Geradschäftigkeit dieser beiden Arten waren nicht zuverlässig zu schätzen. Bei *Pinus elliottii* war die additive Varianz sowohl für das Höhenwachstum als auch für die Geradschäftigkeit generell erheblich größer als die Dominanzvarianz.

Eine wichtige Feststellung war, daß die Leistungsfähigkeit der Vollgeschwisterfamilien, welche aus der Summe der generellen Kombinationseignungen der Eltern erwartet wurde, sich als ein guter Leitfaden für die beobachtete Leistungsfähigkeit erwies, besonders dort, wo die Levels der Dominanzvarianz etwa die gleichen waren, wie die, für die additive Varianz. Folgerungen aus dieser Erkenntnis werden besonders im Hinblick auf Züchtungsstrategien diskutiert, die eine vegetative Massenvermehrung mit sich bringen.

Introduction

Additive genetic effects are the only source of genetic variation which can be utilized in the cumulative improvement of trees by recurrent selection from one generation to the next. Non-additive genetic effects (such as dominance gene effects) can, however, be exploited when multiplying improved genetic material for use in establishing plantations. Afforestation using clones of superior individuals is clearly the most efficient method of exploiting

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