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Provenance Variation of Eastern Cottonwood in the Lower Mississippi Valley

By G. S. FOSTER

Research Forester, Forestry Research-Crown
Zellerbach Corp., Box 400, Bogalusa, LA, 70427, USA

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Abstract

Variation patterns were analyzed for eleven traits in a provenance study of eastern cottonwood (*Populus deltoides* BARTR.) planted in Mississippi. Two models of variation patterns were used to analyze the data: 1) stands and clones-within-stands and 2) clones pooled across stands.

Stand level variation declined with age of the test while the level of variation among clones-within-stands increased with advancing test age. Variation levels for the stand effect were smaller than clones-within-stands effects for all traits except beetle damage. At the stand level, volume (age seven) appeared to have an ecotypic distribution with no evidence for clones.

Broad-sense heritabilities were larger for stands (range of 0.29 to 0.91) than clones-within-stands (range of 0.19 to 0.77); and using the second model, the heritabilities for clones were generally intermediate as compared to stands and clones-within-stands. Comparing predicted gain between the two models, clonal selection, irrespective of stand origin, was superior to stand and clone-within-stand selection for all traits but beetle damage.

Genetic correlations between height, d.b.h., and volume were large (greater than 0.50) among the various ages with the correlation between volume at age four and volume at age seven equal to 0.96. This almost perfect correlation provided opportunities for correlated response in age seven volume, based on selection for volume at age four, which was 89 percent that of direct selection for age seven volume.

Key words: clone, heritability, gain, selection, correlations.

Zusammenfassung

In einer Provenienzstudie bei *Populus deltoides* BARTR. in Mississippi wurden die Variationsmuster von 11 Merkmalen analysiert. Um die Daten zu analysieren, wurden für die Variationsmuster 2 Modelle benutzt: 1) Bestände und Klone innerhalb der Bestände, 2) Klongruppen quer durch die Bestände. Die Variation im Bestandesniveau nahm mit dem Testalter ab, während die Variation zwischen den Klonen innerhalb der Bestände mit zunehmendem Testalter anstieg. Die Variationsniveaus für Bestandeseinflüsse waren geringer als die der Klone innerhalb der Bestände, und zwar für alle Merkmale, außer den Schäden durch Käfer. Auf dem Bestandesniveau schien das Volumen im Alter 7 eine ökotypische Verteilung zu haben, ohne den Beweis für das Vorhandensein eines Klones. Die Heritabilitäten im weiteren Sinne waren für die Bestände größer (Rang von 0,29—0,91) als für Klone innerhalb der Bestände

(Rang von 0,19—0,77). Bei Benutzung des 2. Modelles waren die Heritabilitäten für Klone generell intermediär, verglichen mit den Beständen und den Klonen innerhalb der Bestände. Vergleicht man den vorausgesagten genetischen Gewinn der beiden Modelle, so war die Klonselktion ohne Rücksicht auf die Bestandesherkunft, der Bestandes-Selektion und der Selektion von Klonen innerhalb von Beständen für alle Merkmale, außer dem Käferschaden, überlegen. Die genetischen Korrelationen zwischen Höhe, BHD und Volumen waren hoch (größer als 0,50); bei den verschiedenen Altersstufen, d. h. zwischen den Volumen im Alter 4 und 7, betrug die Korrelation 0,96. Diese insgesamt perfekte Korrelation zeigt, daß bei einer Selektion auf das Volumen im Alter 4 bereits 89% der Pflanzen selektiert worden wären, die im Alter 7 durch direkte Selektion ausgelesen wurden.

Introduction

The ability to vegetatively propagate eastern cottonwood (*Populus deltoides* BARTR.) (hereafter referred to as cottonwood) using stem cuttings provides the avenue for clonal selection. The magnitude of genetic gain through clonal selection depends both on the heritability of the trait and the amount and distribution of the variation. Previous studies demonstrated substantial heritabilities for most growth traits as well as large clonal variances (MOHN and RANDALL, 1971; RANDALL and COOPER, 1973).

Despite the extensive natural range of cottonwood, few provenance studies have been established to study variation patterns for the species. BRIDGWATER (1972) studied variation patterns for six growth and wood traits along three major rivers extending from eastern Oklahoma westward. He found significant variation among stands and clones within stands for all six traits. YING and BAGLEY (1976) investigated variation patterns in cottonwood, including provenances located over much of the natural range. Variation among provenances, families in provenances, and clones in families was significant for all 13 traits studied. In 1971, Cooper sampled stands of cottonwood along the Mississippi River from Memphis, TN to Baton Rouge, LA. Variability in resistance to *Septoria* leaf spot (COOPER and FILER, 1976), *Melampsora* rust (COOPER and FILER, 1977), and cottonwood leaf beetle (*Chrysomela scripta* F.) (OLIVERIA and COOPER, 1977) have been reported from this study. The following report describes genetic and environmental variability for growth traits expressed in a genetic test of clones from COOPER's original collection. The objectives of

Table 1. — Scores for level of damage^a to cottonwood trees due to an infestation of cottonwood leaf beetles_D.

Score	Leaf damage (percent)				Terminal damage			Active growth	
	0-10	10-25	25-50	50-100	none	some	dead	yes	no
1	+				+			+	
2	+				+				+
3		+			+			+	
4		+			+				+
5			+		+			+	
6			+		+				+
7				+	+			+	
8				+	+				+
9				+		+			
10			+				+		
11				+			+		

^a Scored during last two weeks of October, 1976. Amount of damage was scored on the upper 60 cm of the main stem. Damage severity increases from 1 to 11.

^b Adapted from OLIVERIA and COOPER (1977).

this study were: ① to investigate variation patterns in growth traits of cottonwood clones located along a 500-mile segment of the Mississippi River between Memphis, TN and Baton Rouge, LA, ② to estimate inheritance patterns, predicted response to selection, and interrelationships among several growth traits, and ③ to investigate changes in the genetic and environmental parameters during stand development.

Materials and Methods

During fall, 1971, stem cuttings were collected from approximately 40 individual trees in each of 36 two- to four-year-old natural stands of cottonwood along the Mississippi River from Memphis, TN (34° 55' North latitude) to Baton Rouge, LA (30° 30' North latitude). The sample trees in each stand were chosen at random and were cloned and maintained in a nursery for four years. Cuttings from this nursery were used to establish two field tests, one at Chaulk Point, MS in 1974 and one at Fidler, MS (32° 45' North latitude) in February, 1976. This report contains data collected in the Fidler, MS test.

The test was installed using a 6 × 6 triple lattice configuration of the 36 stands. The 40 clones were randomized within each stand in each of three replications. A plot (experimental unit) contained two trees placed contiguously. Initially three 50.8 cm, unrooted cuttings were placed at each planting spot and were thinned to the best tree in July, 1976. Therefore, most clones were represented by six ramets in the study (3 replications × 2 tree plots) after thinning. Trees were planted at 3.66 m square spacings. The study was cultivated the first growing season.

Eleven traits were analyzed for each tree: ① survival (SURV): count of number of living trees per planting spot in July, 1976, ② cottonwood leaf beetle damage (OLIVERIA and COOPER, 1977) (BETL): amount of damage (Table 1), ③ tree height, ages 1, 2, 4 and 7 (HT1, HT2, HT4, and HT7): total height (m), ④ diameter (1.34 m high), ages 3, 4, and 7 (DBH3, DBH4, DBH7): d.b.h. (cm), and ⑤ volume index [(d.b.h.)² ht.] ages 4 and 7 (VOL4, VOL7): individual tree volume (m³).

The analyses for each trait employed two analysis of variance models. For both of these models, the features of the triple lattice were ignored, and a randomized complete block design was used. An important feature of a triple lattice design is that it can be analyzed using a randomized complete block analysis (Cox *et al.*, 1940). The first analysis of variance model utilized the entire sampling structure, i.e., stands and clones within stands.

$$Y_{ijkl} = \mu + B_i + S_j + C_{jk} + E_{ijkl} \quad (1)$$

where, μ = grand mean
 B_i = block effects, $i = 1 \dots b$
 S_j = stand effects, $j = 1 \dots s$
 C_{jk} = clone within stand j effects, $k = 1 \dots c$
 E_{ijkl} = residual

Subsequently, the second model was used including clones, without consideration of stands.

$$Y_{ijk} = \mu + B_i + D_j + E_{ijk} \quad (2)$$

where, μ = grand mean
 B_i = block effects, $i = 1 \dots b$
 D_j = clone effects, $j = 1 \dots d$
 E_{ijk} = residual

In addition to tests of significance, mean squares were equated to expected mean squares and variance components were calculated. Coefficients of variance components were adjusted (SEARLE, 1971) to account for data imbalance.

Broad-sense heritability was calculated on a clone-mean basis for the two models.

Using model 1,

$$H_S^2 = \frac{\hat{\sigma}_S^2}{\hat{\sigma}_S^2 + \frac{\hat{\sigma}_{C/S}^2}{c} + \frac{\hat{\sigma}_b^2}{bc}} \quad (3)$$

and

$$H_{C/S}^2 = \frac{\hat{\sigma}_{C/S}^2}{\hat{\sigma}_{C/S}^2 + \frac{\hat{\sigma}_b^2}{b}} \quad (4)$$

where, H_S^2 = broad-sense heritability of stands
 $H_{C/S}^2$ = broad-sense heritability of clones within stands
 $\hat{\sigma}_S^2$ = variance among stands
 $\hat{\sigma}_{C/S}^2$ = variance among clones within stands
 $\hat{\sigma}_b^2$ = error variance

Pooling stands, model 2,

$$H_D^2 = \frac{\hat{\sigma}_D^2}{\hat{\sigma}_D^2 + \frac{\hat{\sigma}_b^2}{b}} \quad (5)$$

where, H_D^2 = broad-sense heritability for clone means
 $\hat{\sigma}_D^2$ = variance among clones

In the same manner, predicted genetic gain (G) was calculated for the two models.

Selecting stands and clones within stand,

$$G_S = i_S H_D^2 \hat{\sigma}_{P_S} \quad (6)$$

$$\text{and } G_{C/S} = i_{C/S} H_{D(S)}^2 \hat{\sigma}_{P_{C/S}} \quad (7)$$

where, G_S = gain for stand selection
 i_S = standardized selection intensity for stands
 $\hat{\sigma}_{P_S}$ = phenotypic standard deviation
 $G_{C/S}$ = gain for clone in stand selection
 $i_{C/S}$ = standardized selection intensity for clones in stands
 $\hat{\sigma}_{P_{C/S}}$ = phenotypic standard deviation for clones in stands

Therefore, predicted gain from selecting the best clones in the best stands is G_S plus $G_{C/S}$.

Using the second model, genetic gain from selecting the best clones regardless of stands is,

$$G_D = i_D H_D^2 \hat{\sigma}_{P_D} \quad (8)$$

where, G_D = gain for clonal selection
 i_D = standardized selection intensity for clones
 $\hat{\sigma}_{P_D}$ = phenotypic standard deviation for clones

Analysis of covariance, using the second model, provided estimates of covariance components, from which genetic and phenotypic correlations were calculated. Calculation of the correlations followed JOHNSON *et al.*, (1955):

$$\hat{r}_{g(x,y)} = \frac{\hat{\sigma}_{D(x,y)}}{\sqrt{\hat{\sigma}_{D(x)}^2 \hat{\sigma}_{D(y)}^2}} \quad (9)$$

$$\text{and } \hat{r}_{p(x,y)} = \frac{MCP_{D(x,y)}}{\sqrt{MS_{D(x)} MS_{D(y)}}} \quad (10)$$

where, $\hat{r}_{g(x,y)}$ = genetic correlation of traits x and y
 $\hat{\sigma}_{D(x,y)}$ = covariance component for clones for traits x and y
 $\hat{\sigma}_{D(x)}^2$ and $\hat{\sigma}_{D(y)}^2$ = variance components for clones for traits x and y
 $\hat{r}_{p(x,y)}$ = phenotypic correlation of traits x and y
 $MCP_{D(x,y)}$ = mean cross product for clones for traits x and y
 $MS_{D(x)}$ and $MS_{D(y)}$ = mean squares for clones for traits x and y

If two traits are genetically correlated, direct selection of one trait will produce a correlated response in the other trait. Correlated response was calculated as (FALCONER, 1960):

$$CR_{(y)} = i_{D(x)} \sqrt{H_{D(x)}^2} \sqrt{H_{D(y)}^2} \hat{r}_{g(x,y)} \hat{\sigma}_{P_{D(y)}} \quad (11)$$

where, $CR_{(y)}$ = correlated response in trait y
 $i_{D(x)}$ = standardized selection intensity for clones for trait x
 $H_{D(x)}^2$ and $H_{D(y)}^2$ = broad-sense heritabilities for traits x and y
 $\hat{r}_{g(x,y)}$ = genetic correlation of traits x and y
 $\hat{\sigma}_{P_{D(y)}}$ = phenotypic standard deviation of trait y

Results and Discussion

A basic understanding of the genetic architecture of natural variation for traits in a species is imperative before initiating an effective tree improvement program. Once this structure is understood and the level of inheritance is known for a trait, response to selection for the trait can be predicted. Due to the structure of genes in a genome, traits may be interdependent. The result of this interdependence is that the expression of traits may be correlated; and if selection pressure is placed on one trait, a correlated response results for the correlated traits.

Survival of the study trees at the end of seven years was essentially 100 percent. Total height at seven years averaged 18.37 m with a range of 9.49 to 22.57 m (Table 2) while individual tree volume at seven years averaged 0.146 m³ with a range of 0.013 to 0.314 m³.

Differences among stands and clones within stands were significant for essentially all the traits (Table 3). D.b.h. at age 7 was the exception since stand related variability was nonsignificant. The among-stands component accounted for an average of five percent of the total variation with a range of one to eleven percent. The change in percent of total variation over time, even though remaining significant, declines with advancing stand development (Table 3). YING and BAGLEY (1976) found just the opposite pattern in their study with the importance of geographic regions increasing from ages one to seven years for height. Little

Table 2. — Clone means and ranges for eleven traits of cottonwood clones.

Trait ^a	Means	Range
HT1 (m)	2.97	1.88 - 4.12
HT2 (m)	6.82	4.07 - 7.88
HT4 (m)	13.21	6.35 - 16.22
HT7 (m)	18.37	9.51 - 22.57
DBH3 (cm)	10.49	5.33 - 14.40
DBH4 (cm)	13.51	5.59 - 18.80
DBH7 (cm)	16.92	6.48 - 23.93
VOL4 (m ³)	0.067	0.008 - 0.144
VOL7 (m ³)	0.146	0.013 - 0.314
SURV (number)	2.56	0.83 - 3.00
BETL (score)	6.44	1.83 - 10.50

^a HT1, HT2, HT4, HT7 = total height at ages 1, 2, 4 and 7; DBH3, DBH4, DBH7 = d.b.h. at ages 3, 4, and 7; VOL4 and VOL7 = individual tree volume at ages 4 and 7; SURV = first year survival; BETL = amount of damage from cottonwood leaf beetle (see Table 1 for scores).

Table 3. — Variance components and percent of total variation (in parentheses) using stand and clones-within-stands.

Trait ^a	σ_B^2	σ_S^2	$\sigma_{C/S}^2$	σ^2
HT1	0.0019** (1)	0.0256** (9)	0.0300** (11)	0.2209 (79)
HT2	0.0359** (5)	0.0782** (11)	0.1189** (16)	0.5063 (68)
HT4	0.0584** (3)	0.2039** (9)	0.6553** (29)	1.3101 (59)
HT7	0.0809** (2)	0.2318** (5)	1.6370** (37)	2.4930 (56)
DBH3	0.0419** (1)	0.1813** (5)	1.0258** (30)	2.1568 (64)
DBH4	0.0761** (2)	0.1207** (2)	2.0839** (39)	3.0110 (57)
DBH7	0.0387** (1)	0.0600 ^{NS} (1)	4.3271** (51)	4.0606 (47)
VOL4	0.000015** (2)	0.000027** (4)	0.000247** (39)	0.000345 (55)
VOL7	0.000023** (1)	0.000053** (2)	0.001565** (51)	0.001424 (46)
SURV	0.0009** (1)	0.0055** (2)	0.0665** (24)	0.2093 (73)
BETL	0.3646** (7)	0.3471** (7)	0.3309** (6)	4.3189 (80)

^a Traits explained in Table 2.

** Statistically significant at the 1 percent level.

NS Not statistically significant at the 1 percent level.

Number of blocks (b) = 3 for SURV and BETL and 2.99 for all other traits.

Number of stands (s) = 36 for SURV and BETL, 35.76 for DBH3; 35.88 for all other traits.

Number of clones per stand (c) = 38.89 for SURV, BETL, HT2, DBH3, and VOL4; 39.91 for HT1, DBH4, and HT4; 38.79 for all other traits.

Degrees of freedom (DF) for blocks = 2; DF for stands = 35; DF for clones in stands = 1364, for all traits except the following: 1363 for HT7, DBH7, and VOL7. DF for error = 2798, for all traits except the following: 2787 for HT1; 2786 for DBH4; 2785 for HT4; 2784 for HT2; 2783 for VOL4; 2775 for HT7; DBH7, and VOL7; and 2768 for DBH3.

or no relationship exists between the traits and latitude of stand in this study. As evidenced by VOL7, the most northerly stand (# 1) and one of the most southerly (# 30) stands rank first and second with no discernable latitudinal pattern for the remaining stands.

Table 4. — Variance components and percent of total variation (in parentheses) using clones only.

Trait ^a	σ_B^2	σ_D^2	σ^2
HT1	0.0019** (1)	0.0550** (20)	0.2209 (79)
HT2	0.0359** (5)	0.1950** (27)	0.5063 (68)
HT4	0.0584** (3)	0.8538** (38)	1.3101 (59)
HT7	0.0809** (2)	1.8594** (42)	2.4930 (56)
DBH3	0.0419** (1)	1.2013** (35)	2.1568 (64)
DBH4	0.0761** (1)	2.2026** (42)	3.0110 (57)
DBH7	0.0387** (1)	4.3781** (52)	4.0606 (47)
VOL4	0.000015** (2)	0.000272** (43)	0.000345 (55)
VOL7	0.000023** (1)	0.001616** (53)	0.001424 (46)
SURV	0.0009** (1)	0.0720** (26)	0.2093 (73)
BETL	0.3646** (7)	0.6780** (13)	4.3189 (80)

^a Traits explained in Table 2.

** Statistically significant at the 1 percent level.

Number of blocks (b) = same values as in Table 3.

d = (number of clones in stands) (number of stands) = 1440 for SURV and BETL; 1396.48 for HT1; 1395.37 for HT2; 1395.73 for HT4; 1390 for DBH3; 1396.09 for DBH4; 1395.01 for VOL4; and 1391.79 for all other traits.

DF for blocks and error are the same as in Table 3. DF for clones = 1399 for all traits except the following: 1398 for HT7, DBH7, and VOL7.

Variation among stands was a significant yet weak source of genetic variability, and it followed an ecotypic pattern of expression. The results of this study are in opposition with YING and BAGLEY'S (1976) and POSEY'S (1969) results since the later studies delineated strong clinal patterns for growth traits of cottonwood. This apparent conflict may be due to the populations sampled and the testing environments.

The genetic constitution of a population of trees reflects the environmental conditions under which the trees evolved (MORGENSTERN, 1978; CAMPBELL, 1979), and the expression of this genetic variability depends upon the environment in which the trees are grown (CAMPBELL and SORENSEN, 1978). YING and BAGLEY (1976) sampled a large and environmentally diverse portion of the species range [six Plant Hardiness Zones; 120—270 freeze-free days; 559—1321 mm of annual total precipitation (LITTLE, 1971)] and tested the sample trees in eastern Nebraska. POSEY (1969) also sampled populations from highly diverse environments [three Plant Hardiness Zones; 175—240 freeze-free days; 356—1245 mm of annual total precipitation (LITTLE, 1971)] and conducted the clonal test in eastern Oklahoma. In contrast, the sampled stands in this study came from a relatively small range of environmental conditions [two Plant Hardiness Zones; 210—270 freeze-free days; 1219—1524 mm of annual total precipitation (LITTLE, 1971)] and were tested in a relatively mild environment. I hypothesize that the environments within which the sampled stands evolved are fairly similar with no strong environmental gradient; therefore the trees within the stands were allowed to evolve in response to local environmental factors, producing ecotypes instead of a cline.

Considerable gene flow should be influencing the genetic variability patterns among stands. All sampled stands were located along the Mississippi River and subject to waterborne migration of plant parts (potential vegetative propagules) and seeds from more northerly sources. Yet no evidence for the anticipated north-south cline exists. Hypothetically, this anticipated clinal gradient may occur in untested traits or harsher test environments.

Clones within stands were a significant source of variation for traits (Table 3). This source of variation accounted for an average of 30 percent of the total variation with a range of 6 to 51 percent. The importance of this source of variation increased with advancing stand development (Table 3) which agreed with YING and BAGLEY'S (1976) results.

If the stand structure of the data set was ignored (second model), the pattern of the variability closely followed that of the clones-in-stand pattern in the first model. The clonal component was significant for all traits and averaged 35 percent of the total variation with a range of 13 to 53 percent (Table 4). The importance of the among-clones source increased with advancing stand development.

Broad-sense heritabilities were moderate to large for all the traits. Considering the first model, heritabilities at the stand level were quite large; yet they consistently declined with increasing stand development (Table 5). Heritability for height declined from a high of 0.91 to 0.79 from ages one to seven years. From ages three to seven years, the heritability for d.b.h. declined from 0.80 to 0.29. For volume, heritability declined from 0.74 at age four to 0.50 at age seven. First year survival (SURV) and degree of beetle damage during the first Fall (BETL) had heritabilities of 0.61 and 0.88, respectively.

Table 5. — Broad-sense heritability values for eleven traits using two models of analyses of variance.

Trait ^a	First model		Second model
	Stands	Clones/S	Clones
HT1	0.91	0.29	0.43
HT2	0.91	0.41	0.53
HT4	0.88	0.60	0.66
HT7	0.79	0.66	0.69
DBH3	0.80	0.59	0.62
DBH4	0.60	0.67	0.69
DBH7	0.29	0.76	0.76
VOL4	0.74	0.68	0.70
VOL7	0.50	0.77	0.77
SURV	0.61	0.49	0.51
BETL	0.88	0.19	0.32

^a Traits explained in Table 2.

Heritability of clones-within-stands was consistently smaller and increased with stand development as contrasted to heritability at the stand level (Table 5). For height, heritability increased from 0.29 to 0.66 from ages one to seven years; while heritability for d.b.h. increased from 0.59 to 0.76 from ages three to seven years. The heritability for volume increased from 0.68 at age four to 0.77 at age seven years. Heritability for SURV and BETL was 0.49 and 0.19, respectively.

Heritabilities from the second model for the traits were intermediate between the values for stands and clones-within-stands from the first model. In addition, the estimates from the second model increased with stand development (Table 5). For height, heritability increased from 0.43 to 0.69 from ages one to seven years; and from 0.62 to 0.76 from ages three to seven years for d.b.h. Estimates of heritability improved for volume from 0.70 at age four to 0.77 at age seven years. Finally heritabilities for SURV and

BETL were 0.51 and 0.32, respectively. Heritabilities estimated by MOHN and RANDALL (1971) for cottonwood increased with age of the stand, from 0.32 to 0.46 for height and from 0.21 to 0.35 for d.b.h. Those heritabilities were calculated on a plot-mean basis which generally gives a lower estimate than obtained from a clone-mean basis. BRIDGWATER (1972) reported heritability estimates, calculated on a clone-mean basis, for two test locations of 0.73 and 0.78 for height, 0.62 and 0.76 for d.b.h., and 0.59 and 0.72 for volume of cottonwood at age three years.

Predicted genetic gain from clonal selection depended upon the selection strategy, yet the level of response differed only slightly between the two strategies. With a goal of 45 selected clones, two strategies were used: (1) select the best five clones from each of the best nine stands or (2) select the best 45 clones from all the clones combined. As with heritabilities for the first model, predicted gains for height, d.b.h., and volume decreased with age for stand selection and increased with age for clones-within-stand selection (Table 6). The net effect using the first selection strategy is a general increase in predicted gain with increasing stand development, and the greatest gain occurred for traits measured at age seven years. The estimate for predicted gain of traits HT7, DBH7, VOL7, SURV, and BETL was 12.3, 18.7, 43.7, 14.4, and 17.3 percent gain, respectively (Table 6). Using the second selection strategy, predicted gains also increased with increasing stand development. Predicted gain from clonal selection for HT7, DBH7, VOL7, SURV, and BETL was 13.9, 24.2, 54.4, 16.8, and 16.3 percent, respectively (Table 6), slightly higher than for combined stand and clones-within-stands selection.

Height d.b.h., and volume were positively correlated at all measurement ages. The genetic and phenotypic correlations among these traits equaled or exceeded 0.50 (Table 7). Correlations with VOL7 were larger with d.b.h. than height at all ages, and the genetic correlation between VOL4 and VOL7 was 0.96. MOHN and RANDALL'S (1971) genetic and phenotypic correlations for diameter agree quite well with my results, but their correlations for height are

Table 6. — Phenotypic standard deviations ($\hat{\sigma}_P^2$) and predicted genetic gain in measurement units (in percent) for clonal selection for eleven traits, using two models of analysis of variance.

Trait ^d	Stand selection		Clone/stand selection		Stand + C/S selection	Clonal selection	
	$\hat{\sigma}_{PS}$	Gain _S ^a	$\hat{\sigma}_{PC/S}$	Gain _{C/S} ^b	Gain _{S+C/S}	$\hat{\sigma}_{Pn}$	Gain _D ^c
HT1 (m)	0.1682	0.19 (6.4)	0.3223	0.15 (5.1)	0.34 (11.5)	0.3589	0.35 (11.7)
HT2 (m)	0.2927	0.34 (5.3)	0.5369	0.36 (5.7)	0.70 (11.1)	0.6036	0.72 (11.4)
HT4 (m)	0.4817	0.54 (4.1)	1.0457	1.03 (7.8)	1.57 (11.9)	1.1366	1.69 (12.8)
HT7 (m)	0.5437	0.55 (3.0)	1.5719	1.71 (9.3)	2.26 (12.3)	1.6411	2.55 (13.2)
DBH3 (cm)	0.4757	0.48 (4.6)	1.3228	1.29 (12.3)	1.77 (16.9)	1.3876	1.94 (18.5)
DBH4 (cm)	0.4473	0.34 (2.5)	1.7582	1.94 (14.4)	2.28 (16.9)	1.7915	2.78 (20.6)
DBH7 (cm)	0.4544	0.17 (1.0)	2.3843	2.98 (17.6)	3.15 (18.6)	2.3950	4.10 (24.2)
VOL4 (m ³)	0.0060	0.006 (8.9)	0.0190	0.021 (31.3)	0.027 (40.2)	0.0197	0.031 (46.3)
VOL7 (m ³)	0.0103	0.007 (4.8)	0.0452	0.057 (39.0)	0.064 (43.8)	0.0458	0.079 (54.1)
SURV (number)	0.0949	0.07 (2.7)	0.3692	0.30 (11.7)	0.37 (14.4)	0.3766	0.43 (16.8)
BETL (score)	0.6266	-0.70 (10.8)	1.3306	-0.42 (6.5)	-1.12 (17.3)	1.4552	-1.05 (16.3)

^a Selection intensity was 9/36 stands ($i = 1.2711$).

^b Selection intensity was 5/40 clones per stand ($i = 1.6468$).

^c Selection intensity was 45/1440 clones ($i = 2.2516$).

^d Traits explained in Table 2.

Table 7. — Genetic (above diagonal) and phenotypic (below diagonal) correlations among eleven traits of cottonwood.

	HT1	HT2	HT4	HT7	DBH3	DBH4	DBH7	VOL4	VOL7	SURV	BETL
HT1 ^a		0.73	0.67	0.64	0.50	0.54	0.56	0.59	0.58	0.31	0.07
HT2	0.67**		0.88	0.81	0.59	0.63	0.63	0.73	0.69	0.06	0.16
HT4	0.58**	0.80**		0.89	0.65	0.71	0.72	0.79	0.76	0.07	0.13
HT7	0.49**	0.67**	0.81**		0.76	0.83	0.85	0.85	0.87	0.08	0.08
DBH3	0.52**	0.67**	0.69**	0.71**		0.96	0.92	0.93	0.91	0.09	0.11
DBH4	0.51**	0.63**	0.71**	0.78**	0.91**		0.96	0.96	0.95	0.10	0.10
DBH7	0.47**	0.57**	0.70**	0.81**	0.85**	0.91**		0.94	0.98	0.11	0.04
VOL4	0.54**	0.71**	0.79**	0.78**	0.91**	0.93**	0.89**		0.96	0.06	0.14
VOL7	0.47**	0.62**	0.72**	0.83**	0.85**	0.90**	0.96**	0.92**		0.09	0.07
SURV	0.22**	0.08*	0.08*	0.08*	0.08*	0.09**	0.09**	0.06*	0.07*		-0.05
BETL	0.14**	0.15**	0.11**	0.04 ^{NS}	0.11**	0.09**	0.04 ^{NS}	0.10**	0.04 ^{NS}	0.04 ^{NS}	

** Significant at the 1 percent level.

* Significant at the 5 percent level.

NS Not significant at the 5 percent level.

^a Traits explained in Table 2.

somewhat lower. Phenotypic correlations given by RANDALL and COOPER (1973) closely agree with my results; while phenotypic correlations given by YING and BAGLEY (1976) are slightly larger than these.

SURV was positively correlated with the growth traits at all measurement ages, but the correlations tended to be small. HT1 had a genetic correlation of 0.31 with SURV, therefore clones which had lower survival tended to grow less in height the first year. The genetic or phenotypic correlation of SURV and height, d.b.h., or volume measured at later ages was less than or equal to 0.11 (Table 7). One component of first year survival of cottonwood cuttings is rooting ability (COOPER, 1982), therefore the correlation between HT1 and SURV may be partially due to a positive correlation between HT1 and rooting ability of the clones. This hypothesis is partially supported by work of YING and BAGLEY (1976) in which they found a correlation of 0.17 between number of main roots per cutting and HT1.

Genetic variation among clones of cottonwood appears to exist for tolerance to damage by the cottonwood leaf

beetle (OLIVERIA and COOPER, 1977). Genetic and phenotypic correlations between the beetle damage score (BETL) and growth traits were small, yet consistently positive (Table 7). The phenotypic correlations between BETL and height, d.b.h., and volume, up to age four, were significant and ranged from 0.09 to 0.15. Since leaf beetle damage increased as the score increased, a positive correlation with tree growth indicates that trees grow better when beetle damage is heavier. However, the nonsignificant correlations with seven year growth traits indicate that the earlier results are meaningless with respect to long-term growth performance. Levels of beetle damage after the measurement year may not have been severe enough to provide continuing pressure on the trees, yielding no long-term relationship between levels of damage and growth.

Selection of cottonwood clones based on early performance would shorten the testing cycle and therefore the time needed to move the clones into commercial usage. If VOL7 was the desired character for improvement, selection for DBH4 or VOL4 would theoretically result in 87 and 89 percent of the gain predicted if VOL7 was selected directly (Table 8). Selection for HT1, HT2, HT4, or DBH3

Table 8. — Correlated response for individual tree volume at age seven (VOL7) from direct selection for other traits.

Selected trait (x) ^b	VOL7		Selected trait			Correlated response (VOL7)		Percent of direct selection for VOL7
	$\bar{\sigma}_{PD}(y)$	$\sqrt{i_D^2}(y)$	$i_D^a(x)$	$\sqrt{i_D^2}(x)$	$\bar{r}_g(x,y)$	m ³	percent	
HT1	0.0458	0.88	2.2516	0.66	0.47	0.028	19	35
HT2	0.0458	0.88	2.2516	0.73	0.62	0.041	28	52
HT4	0.0458	0.88	2.2516	0.81	0.72	0.053	36	67
DBH3	0.0458	0.88	2.2516	0.79	0.85	0.061	42	77
DBH4	0.0458	0.88	2.2516	0.83	0.90	0.068	47	86
VOL4	0.0458	0.88	2.2516	0.84	0.92	0.070	48	89

^a Selection intensity was 45/1440 clones ($i = 2.2516$).

^b Traits explained in Table 2.

would also yield substantial indirect response in VOL7 but at a considerably lower level.

These results have important implications for a tree improvement program for cottonwood within the sampled area. Predicted genetic gains from clonal selection and propagation were largest when clonal selection was not confined to a subset of stands (Table 6). In addition, predicted gain in growth traits increased with advancing stand development, yielding the largest response to selection (VOL7) at age seven years (Table 6). Due to a large genetic correlation though, selection for DBH4 or VOL4 provides nearly the same level of gain for VOL7 as when selecting directly for it (Table 8). Therefore if increased VOL7 is the goal of selection, a small amount of predicted gain is forfeited (six to seven percent) by selecting for either DBH4 or VOL4 while the length of the testing period is reduced by 43 percent.

The potential exists for selection to improve first year survival (SURV) yet the impact of this trait on VOL7 was low. Clones vary widely for SURV and these problems in initial survival may be due to many factors (COOPER, 1982). The low correlation between SURV and VOL7 may be somewhat misleading when interpolating to volume per unit land area. VOL7 represents the average volume per living tree on a plot basis and therefore does not reflect mortality. Using multiple cuttings per planting spot (with a subsequent thinning to one tree per spot) resulted in very high survival on a plot basis. If planting practices and environmental conditions resulted in significant plot mortality, the correlation between initial survival and volume per unit land area would be important.

Predicted heritabilities and gains are applicable only to sites which are similar to the Fidler test site. Genotype \times environment interaction can be important when testing cottonwood in diverse environments (RANDALL and MOHN, 1969; RANDALL and COOPER, 1973). For application of results to a range of planting sites, heritabilities and gains would have to be reduced appropriately for genotype \times environment interaction.

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Genetic Variation in Dormancy Relations of Balsam Poplar Along a Latitudinal Transect in Northwestern Ontario

By R. E. FARMER JR. and R. W. REINHOLT¹⁾

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Summary

Dormancy relations of balsam poplar clones from five populations along a transect from northern Wisconsin to Hudson's Bay were examined in a forcing study. The material exhibited unconditional physiological dormancy in autumn but required a relatively short chilling period to overcome this dormancy. Most of the variance in response to chilling was due to differences among clones within populations. Bud break was promoted by a range of temperatures which were equally effective in terms of response to degree hours.

Key words: chilling requirements, clones, bud break.

Zusammenfassung

In einem Treibhausversuch wurde die relative Winterruhe von Balsampappel-Klonen aus 5 Populationen entlang einer Linie vom nördlichen Wisconsin bis zur Hudson Bay untersucht. Das Stecklingsmaterial zeigte eine uneingeschränkte physiologische Ruhepause im Herbst, erforderte jedoch eine relativ kurze Frostperiode, um diese Ruhepause zu überwinden. Der größte Teil der Variation in der Reaktion auf Frostbedingungen war auf Unterschiede zwischen den Klonen innerhalb der Populationen zurückzuführen. Der Knospentrieb wurde durch einen Temperaturbereich begünstigt, der zeitlich genauso effektiv war, d. h. wie die Reaktion auf die Anzahl Stunden.

Introduction

Dormancy of North American forest trees has been most frequently examined within the context of provenance in-

¹⁾ The authors are respectively Professor and Research Assistant, School of Forestry, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada.