Inheritance and Correlation of Growth of Shortleaf Pine in Two Environments[1])

By C. G. TAUER and R. W. MCNEW

Associate Professor, Department of Forestry and Professor,
Department of Statistics, Oklahoma State University,
Stillwater, Oklahoma 74078, USA

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Abstract

Natural variation in Oklahoma populations of shortleaf pine was examined using an open-pollinated progeny/provenance test. Results at age ten showed relatively small stand and stand by location contributions to total variance. Genetic differences in height, DBH, and volume growth were primarily due to mother trees, as shown by the performance of their progenies. Genotype by environment interaction was of little importance on the sites tested. Narrow-sense family-mean heritability estimates for survival were low, but estimates for age ten height, DBH, and volume were high. Genetic correlations over time suggest that selection for age ten volume using age two or four height would be reliable. No relationship was found between survival and growth rate. Genetic correlations between growth traits in the two environments showed generally consistent performance over locations and over locations across time.

Key words: Natural Variation, Genetic Correlation, Heritability, Genetic Gain, Genotype by Environment Interaction.

Zusammenfassung

In einem Provenienzversuch mit frei abgeblühten Nachkommenschaften von *Pinus echinata* MILL. wurde die natürliche Variation der Populationen in Oklahoma geprüft. Die Ergebnisse im Alter 10 zeigten von Bestand zu Bestand eine relativ geringe Beeinflussung der Gesamtvarianz durch den Standort. Genetische Unterschiede in Höhe-, BHD- und Volumenwachstum waren in erster Linie den Mutterbäumen zuzuschreiben, wie die Leistung ihrer Nachkommenschaften zeigt. Genotyp × Umwelt Interaktionen waren auf den getesteten Standorten von geringer Bedeutung. Familienmittel-Heritabilitäts-Schätzwerte im engeren Sinne waren für das Überlebensprozent gering, aber Schätzwerte für die Höhe, den BHD und das Volumen im Alter 10 waren hoch. Genetische Korrelationen über die Zeit hinaus zeigen, daß eine Selektion für das Volumen im Alter 10 zuverlässig ist, wenn man die Höhe im Alter 2 oder 4 als Grundlage benutzt. Zwischen Überlebensprozent und Wachstumsrate wurde keine Beziehung gefunden. Genetische Korrelationen zwischen Wachstumsmerkmalen in zwei Lagen zeigten über Jahre hinweg generell übereinstimmende Leistungen von Standort zu Standort.

Introduction

Studies reported by WELLS (1969, 1973, 1978), WELLS and WAKELEY (1970) and DORMAN (1976), among others, have shown that shortleaf pine *(Pinus echinata* MILL.) possesses a considerable amount of natural variation. Follow-up studies designed to estimate the proportion of that variability which is heritable, and therefore useful in a tree improvement program, have not been reported. Consequently, one of the first needs of the Oklahoma shortleaf pine improvement program was to estimate the genetic parameters pertinent to shortleaf pine populations in Oklahoma.

Results of a 20-year-old shortleaf pine seed source study (TAUER 1980) suggest that use of local sources of shortleaf pine in Oklahoma is appropriate. The Oklahoma sources grew as fast (.05 probability level) as any source tested, although a southern Arkansas source consistently produced a greater total volume (based on number of trees planted) of wood. This source might also be used for an improvement program in Oklahoma.

WELLS and WAKELEY (1970) divided Oklahoma shortleaf pine into two major seed zones, but they suggested that seed from the southern zone could be used for that zone and the northern zone as well. These seed zone recommendations should be given closer scrutiny because Oklahoma populations of shortleaf pine represent the extreme western edge of the species, and considerable differentiation migh be present.

When the shortleaf pine improvement program began in Oklahoma, a parallel study of the natural variation in the species was initiated. The study was designed to sample variation among stands and among families within stands, to examine genotype by environment interactions, to estimate heritabilities of various growth traits and to estimate genetic correlations among traits within and between environments. The seedling stage of this study was reported by BRIDGWATER (1969) while age ten results are reported here.

Materials and Methods

Open-pollinated seed were collected from ten shortleaf pine trees in each of 15 stands *(Figure 1).* The 15 stands, representative of the range of environments for commercial production of shortleaf pine in Oklahoma, were selected from an earlier study of 48 stands in which the objective was to systematically and intensively sample the entire southeastern Oklahoma range of the species. The earlier study has been described by MCCULLOUGH (1968) and POSEY and ROBINSON (1969). Minimum stand size sampled for both studies was 16.2 hectares. Trees selected in these stands had to be dominants or codominants, growing in closed conditions, separated by a minimum of 91.4 meters to reduce the likelihood of relatedness, and have cones. Within these constraints, the trees were otherwise selected at random.

Seed of the 150 open-pollinated families were grown in a replicated nursery test near Broken Bow, Oklahoma *(Figure 1).* First-year nursery measurements were reported by BRIDGWATER (1969). The seedlings were outplanted at Stilwell, Adair County and Broken Bow, McCurtain County *(Figure 1)* as 1—0 stock. Due to various forms of attrition, the field plantings contain 100 families with an average of 6.67 families per stand (range of 3 to 9 families). Each planting contains six replicates of four-tree open-pollina-

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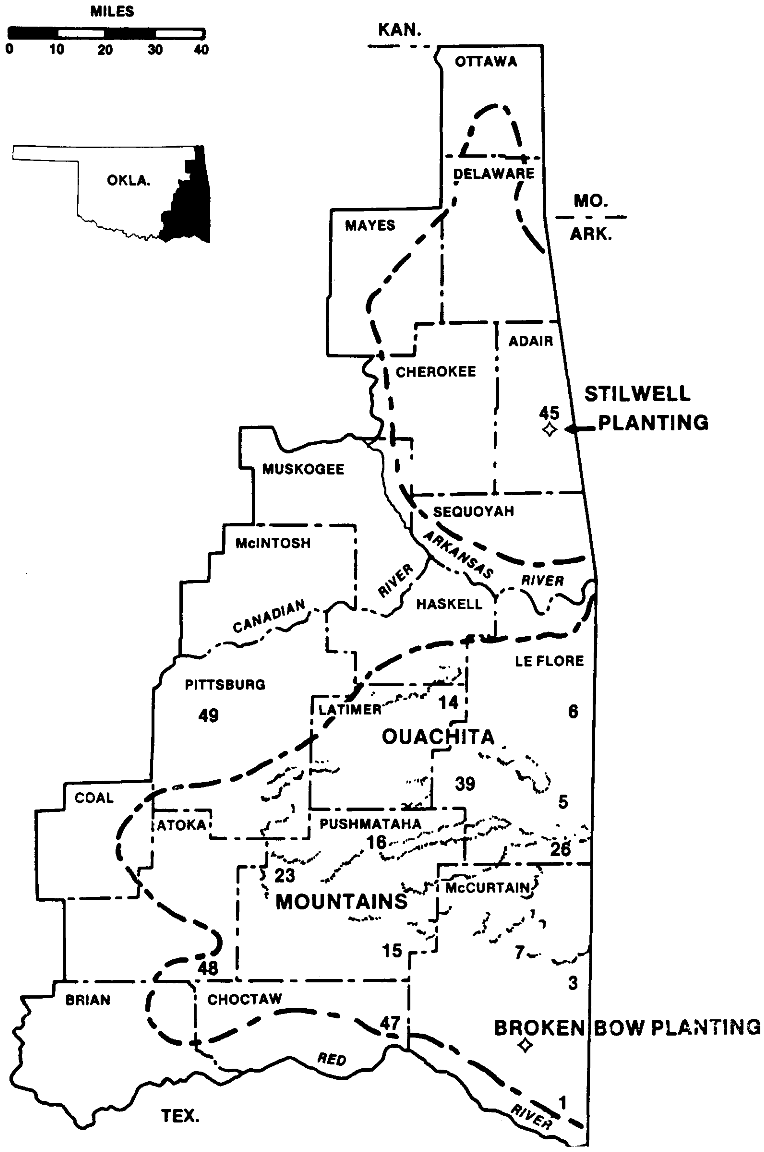

Figure 1. — Collection (numbers) and testing (◇) locations of the shortleaf open-pollinated progeny and seed source test, and the range of shortleaf pine (—·—·—) in Oklahoma.

ted family row-plots arranged in a randomized complete block design disregarding stands. Initial spacing was three by three meters.

The two planting sites were thought to represent the range of sites of commercial interest in Oklahoma. The Broken Bow planting is on an excellent site, (SI 65 to 70, 50-year base) and the Stilwell planting is on what was thought to be a commercially marginal site of unknown site index.

Tree heights and survival were recorded at ages one, two, four and ten years and diameter at breast height (DBH) was recorded at age ten. Straightness and crown ratings, using the system described by the North Carolina State University Cooperative Tree Improvement Program (undated), were recorded at ages four and ten years. Volume at age ten was computed using the formula given by GINGRICH (1962) for estimating merchantable volume with a minimum top diameter of 7.7 centimeters.

Data were analyzed using standard analysis of variance (Statistical Analysis System 1979, Procedure VARCOMP) procedures. Estimates of genetic correlations for traits over time and environments, and heritabilities were computed using the formulas listed in *Table 1.* The genetic correlation between two traits in different locations was estimated by the ratio of the estimated additive genetic covariance to the square root of the product of the estimated additive genetic variances of the two traits in the respective locations; the additive genetic covariance was estimated as 4 times the among-family within-stand mean cross-product of family means for the two traits. Standard errors were approximated using methods described by KENDALL and STUART (1969). It was assumed that members of open-pollinated families were true half-sibs. Violation of this assumption would bias the estimates upward due to closer relatedness. All statistical tests of significance were made at the .05 probability level.

Results of analyses by location and pooled over locations are presented for documentation and interpretation. A majority of the ensuing discussion will concentrate on the pooled results since the pooled analysis provides the most

Table 1. — Format of the Analysis of Variance and Cross Products by Location and Over Location.

ANOVA: OVER LOCATIONS, PLOT $\bar{x}$ BASIS

SOURCE	degrees of freedom	EXPECTED MEAN SQUARES AND CROSS PRODUCTS
LOCATION	1	
REP (LOC)	10	
STAND	14	$\sigma_{e_{ij}} + k_6\sigma_{lxf(s)_{ij}} + k_7\sigma_{f(s)_{ij}} + k_8\sigma_{lxs_{ij}} + k_9\sigma_{s_{ij}}$
LOC x STAND	14	$\sigma_{e_{ij}} + k_4\sigma_{lxf(s)_{ij}} + k_5\sigma_{lxs_{ij}}$
FAMILY (STAND)	85	$\sigma_{e_{ij}} + k_2\sigma_{lxf(s)_{ij}} + k_3\sigma_{f(s)_{ij}}$
LOC x FAMILY (STAND)	85	$\sigma_{e_{ij}} + k_1\sigma_{lxf(s)_{ij}}$
ERROR	949	$\sigma_{e_{ij}}$

If i = j then $\sigma_{ij} = \sigma_i^2$ (or σ_j^2), and the family mean heritability for trait i is

$$h_i^2 = \frac{\sigma^2_{f(s)_i}}{1/12\ \sigma^2_{e_i} + 1/2\sigma^2_{lxf(s)_i} + \sigma^2_{f(s)_i}}$$

ANOVA: BY LOCATION, PLOT $\bar{x}$ BASIS

SOURCE	degrees of freedom	EXPECTED MEAN SQUARES AND CROSS PRODUCTS
REP	5	
STAND	14	$\sigma_{e_{ij}} + k_{11}\sigma_{f(s)_{ij}} + k_{12}\sigma_{s_{ij}}$
FAMILY (STAND)	85	$\sigma_{e_{ij}} + k_{10}\sigma_{f(s)_{ij}}$
ERROR	494*	$\sigma_{e_{ij}}$

*452 at Stilwell location

If i = j then $\sigma_{ij} = \sigma_i^2$ (or σ_j^2) and, the family mean heritability for trait i is

$$h_i^2 = \frac{\sigma^2_{f(s)_i}}{1/6\ \sigma^2_{e_i} + \sigma^2_{f(s)_i}}$$

while k_1 through k_{12} are respective coefficients of the expected mean squares.

The genetic correlation for traits i and j in the same environment is

$$r_{g_{ij}} = \frac{\sigma_{f(s)_{ij}}}{\sqrt{\sigma_{f(s)_{ii}}\ \sigma_{f(s)_{jj}}}}$$

and, the genetic correlation for trait i in environment 1 and j in environment 2 is

$$r_{g_{i(1)j(2)}} = \frac{\text{covariance of trait i in environment 1 and trait j in environment 2}}{\sqrt{\sigma_{f(s)_{ii(1)}}}\ \sqrt{\sigma_{f(s)_{jj(2)}}}}$$

precise estimates of many statistical parameters and as interactions of family or stand with environment were small.

Results and Discussion

The ranges of mean stand performance at age ten years by location are listed below:

	Broken Bow		Stilwell	
Trait	Mean	Range	Mean	Range
Height (m)	7.1	6.7 — 7.5	6.3	6.0 — 6.6
DBH (cm)	14.9	13.9 — 15.5	15.7	14.7 — 16.8
Volume/Tree (dm^3)	48.1	39.6 — 53.8	45.3	36.8 — 53.8
Survival (%)	90	83 — 94	60	50 — 70

Growth rates at the two locations were surprisingly similar considering the apparently contrasting planting sites. The most apparent difference between sites was in survival, with the marginal Stilwell site showing 30 percent lower survival. The lower survival is apparently due, at least in part, to an error in early cultural treatment of the Stilwell site. Two incompatible chemicals were applied too close together in time, causing damage and some mortality. The lower survival may also reflect the relative dryness of the Stilwell site. The larger average diameter of the Stilwell trees almost certainly reflects the lower stocking after mortality. Thus, the similar volume per tree across sites is not indicative of the large difference in volume per hectare. The Stilwell planting produced 17.5 cubic meters per hectare less volume than the Broken Bow planting.

Variation Among Stands

The possibility of relationships between age ten stand growth variables and stand origin data, including latitude, longitude, elevation and average annual rainfall, was investigated. Age ten height and volume were moderately but significantly negatively correlated with origin elevation ($r = -.52$ and $r = -.62$, respectively), which suggests that stands originating at high elevations grow slower. The range of elevations for the 15 stands was from 123 to 690 meters. There was no suggestion of a north to south or west to east source influence on growth rates.

Variance components and tests of statistical significance by location and across locations *(Table 2)* indicate some stand influences on height growth at early ages, but these were greatly diminished by age ten. Stand contribution to variance at age ten was non-significant for height, DBH, volume, crown and straightness. However, rather large biological differences among stands are suggested by the data in *Table 3*, and additional testing might be considered before completely discounting stand effects.

The stand by location interaction was significant for DBH and volume, suggesting a possible change in stand rankings between locations. Ranking changes of a limited degree occurred *(Table 3)*. For example, coastal plain stands 1 and 47 ranked 3 and 1 for volume in the Broken Bow planting (coastal plain site) and 14 and 11 in the Stilwell planting. Stand 49, an outlier population of northern origin, ranked number 1 in the northern planting but 14 in the southern (Broken Bow) planting. In contrast, 11 of the 15 stands evaluated performed similarly across locations for both DBH and volume. Rankings based on volume and DBH showed that of the six best performing stands at the Broken Bow location, four (stands 7, 14, 16 and 48) were among the top six in the Stilwell planting. Some of the interaction must be due to unequal variance among stands at each location, leading to the conclusion that genotype by location interaction may be a minor consideration in a breeding program for shortleaf pine in Oklahoma. However, it is important to note that only two locations were sampled.

Of the several traits measured at age ten years, survival was the only one for which the stand component made a significant contribution to variance. This significant contribution was consistent over time, as it was also noted for survival at ages one, two and four years. The stand by location interaction component for survival was not significant, suggesting that there are real and consistent differences among the stands in survival. With the exception of stands 16, 26 and 49 (outlier), stands showing high survival in one test location also show high survival at the other location. However, the stand contribution to total variance for survival in the pooled analysis *(Table 2)* was less than two percent of the total variance for all ages at which survival was recorded. Ignoring survival differences among stands would thus probably be of limited consequence in a breeding program for shortleaf pine in Oklahoma. Yet survival is a critical factor on many Oklahoma sites, and even small differences may be useful.

Table 2. — Variance as Percent of Phenotypic Variance and Family Mean Heritabilities With Sandard Errors for Shortleaf Pine in Oklahoma.

VARIABLE		LOCATION	σ^2_s	σ^2_{sxl}	$\sigma^2_{f(s)}$	$\sigma^2_{lxf(s)}$	σ^2_e	$h^2 \pm$ S.E.
HEIGHT								
age	1	B.B.[@]	0.6		23.2*		76.2	.646±.058
		Stilwell	2.4		9.6*		88.0	.396±.103
		Pooled	0.7	1.0	11.2*	5.5*	81.6	.540±.100
age	2	B.B.	0.5		20.3*		79.2	.605±.065
		Stilwell	6.9*		4.4		88.7	.232±.133
		Pooled	2.8*	2.1*	9.3*	0.7	85.0	.556±.097
age	4	B.B.	2.0		14.4*		83.6	.509±.081
		Stilwell	6.0*		4.8		89.2	.244±.133
		Pooled	2.3*	2.7*	8.2*	0	86.8	.531±.104
age	10	B.B.	0		27.3*		72.7	.692±.051
		Stilwell	0.9		8.8*		90.3	.370±.109
		Pooled	0	1.5	14.9*	6.6*	77.0	.606±.086
DBH								
age	10	B.B.	3.5		24.5*		72.0	.672±.054
		Stilwell	2.2		10.4*		87.4	.417±.101
		Pooled	0	6.5*	13.7*	2.7	77.1	.637±.079
CROWN								
age	4	B.B.	0		17.4*		82.9	.558±.073
		Stilwell	1.1		4.6		94.3	.227±.136
		Pooled	0	0.7	10.4*	0.7	88.1	.576±.094
age	10	B.B.	0		6.3*		93.7	.288±.117
		Stilwell	2.3*		0.3		97.4	.017±.174
		Pooled	0	0.9	0	3.6	95.5	- .034±.229
STRAIGHTNESS								
age	4	B.B.	0.4		18.1*		81.5	.572±.070
		Stilwell	6.5*		0.8		93.7	.049±.169
		Pooled	4.3	0	3.7	5.3*	86.7	.271±.161
age	10	B.B.	0		4.2		95.8	.209±.130
		Stilwell	2.5		3.3		94.2	.173±.145
		Pooled	0.6	0.5	2.1	1.7	95.1	.196±.178
SURVIVAL								
age	1	B.B.	1.3		0		98.7	- .042±.171
		Stilwell	2.2		5.2		92.6	.252±.123
		Pooled	1.2*	0.8	1.0	2.5	94.4	.102±.193
age	2	B.B.	1.1		0.3		98.6	.019±.161
		Stilwell	3.5*		5.7		90.8	.273±.119
		Pooled	1.3*	1.6	1.4	2.8	92.9	.136±.185
age	4	B.B.	0.9		2.0		97.1	.108±.147
		Stilwell	3.7*		6.5		89.8	.302±.115
		Pooled	1.5*	1.5	0.7	4.4	91.9	.069±.199
age	10	B.B.	0.9		0.9		98.1	.050±.156
		Stilwell	3.7*		4.1		92.2	.213±.129
		Pooled	1.6*	1.5	1.0	2.3	93.5	.099±.193
VOLUME								
age	10	B.B.	1.7		28.0*		70.2	.705±.048
		Stilwell	3.0		10.8*		86.2	.429±.098
		Pooled	0	5.5*	17.1*	2.7	74.6	.692±.067

[@]B.B. = Broken Bow
* "F" test significant at 0.05 probability level or lower.

These data suggest that the stands of shortleaf pine in Oklahoma have developed a modest degree of genetic differentiation, presumably in response to environmental stresses. At the same time, these stands have retained a

Table 3. — Relative Performance at Age 10 of Shortleaf Pine Growth from Seed Collected from 15 Stands in Oklahoma, Presented by Location as a Percent of Plantation Mean.

	BROKEN BOW PLANTING				STILWELL PLANTING			
STAND	HEIGHT	DBH	VOLUME	SURVIVAL	HEIGHT	DBH	VOLUME	SURVIVAL
1	104.6	104.4	114.7	96.9	97.5	95.4	87.8	83.0
3	99.1	100.1	97.1	103.1	99.0	99.4	95.9	117.7
5	97.8	96.4	88.3	96.4	95.9	94.3	82.3	91.7
6	99.0	99.1	97.1	99.9	99.0	96.5	89.8	104.9
7	101.6	102.8	107.7	102.2	100.7	101.7	104.2	112.3
14	103.6	101.1	101.8	96.0	106.7	103.1	113.3	101.5
15	97.5	96.2	90.5	100.1	100.5	97.6	101.7	88.2
16	101.1	101.7	104.2	104.5	100.5	100.3	101.7	88.2
23	100.4	100.9	101.3	102.7	101.4	102.4	107.2	100.7
26	99.7	100.5	99.4	102.9	99.8	100.9	99.1	71.4
39	93.9	94.1	82.5	102.2	97.9	101.3	100.5	115.3
45	99.7	100.5	100.7	96.8	99.0	101.4	101.4	85.4
47	103.2	104.3	112.7	92.3	98.5	96.8	93.7	89.1
48	104.4	103.3	114.4	100.3	102.5	102.8	109.9	114.9
49	96.0	92.9	84.3	98.5	104.7	106.7	124.9	116.3

general common adaptability, with limited outliers providing some exceptions, for example stand 49. These results, in conjunction with the practical and economic constraints of tree improvement, suggests the best improvement plan would be to ignore the relatively small stand and stand by location variance contributions, and develop a single breeding population for general adaptability to the array of shortleaf pine sites found in Oklahoma.

Variation Among Families

The ranges in family-mean performance at age ten by location are:

Trait	Range of Family Means: Broken Bow	Range of Family Means: Stilwell
Height (m)	5.5 — 8.6	5.3 — 7.0
DBH (cm)	12.2 — 17.3	12.4 — 17.8
Volume/Tree (dm^3)	22.6 — 76.4	22.6 — 65.1
Survival (%)	71 — 100	29 — 96

The ranges in family mean growth rates over locations were quite similar, with the best families on the better site modestly outgrowing the best families on the poorer site (Stilwell), as might be expected. The great difference in survival was due, at least in part, to an error in cultural treatment on the Stilwell site. The amount of variability among families at each location was considerable, and suggests a breeding program confined to Oklahoma populations is practical.

The data presented in *Table 2* show that genetic differences in ten year height, DBH and volume growth in these shortleaf pine stands were primarily due to mother trees, as shown by the performance of their progenies. Stand, stand by location, and family in stand by location contributions to the total variance for those traits ranged from 0 to 7 percent, while the family contributions were 14, 15, and 17 percent for DBH, height and volume, respectively. These data support the earlier conclusion that stand variation is of limited importance, and that selection should concentrate on families.

Crown score, as rated at age ten years, showed no genetic variation among families. At age four this trait showed considerable family variation and made a significant contribution to total variance. Crown development following crown closure does not relate well to crown development of young trees.

Straightness score, at both age four and ten years, showed only limited genetic variation among families. The family contribution to variance at both age 4 and 10 was non-significant, although a genotype by environment interaction was noted at age four.

Survival differences among families were not significant for age one, two, four or ten years, and the contribution to total variance for this trait ranged from 0.7 to 1.4 percent.

Although the families were tested on two relatively diverse sites, almost no genotype by environment interactions (i.e. F(S)xL) were found to be significant. There was no significant genotype by environment interaction for either DBH or volume, the traits of most interest. However, testing at only two sites may not be sufficient to evaluate material for use throughout the shortleaf pine range in Oklahoma. For example, family performance over location, although generally consistent, showed some considerable exceptions for volume where only 12 of the top 25 families at Broken Bow were in the top 25 at Stilwell.

Heritability and Genetic Gain

Narrow-sense family-mean heritability for survival was estimated to be fairly low, less than 0.14 at all four ages (*Table 2*). These estimates suggest that although survival is a problem on Oklahoma sites, efforts to improve the trait through family selection would yield limited short term results. More progress might be made by stand selection for this trait. The apparent lack of a genetic correlation between survival and growth parameters suggests that a program of volume improvement could include selecting for survival ability without difficulty or conflict.

Family-mean heritability estimates for straightness were low at ages four and ten years, .27 ± .16 and .19 ± .18,

Table 4. — Genetic Correlations Among Traits Over Locations, With Standard Errors in Parenthesis, for Shortleaf Pine at Age 10.

TRAIT	AGE	HEIGHT 1	HEIGHT 2	HEIGHT 4	HEIGHT 10	DBH 10	STRAIGHTNESS 4	STRAIGHTNESS 10	CROWN 4	CROWN 10	SURVIVAL 1	SURVIVAL 2	SURVIVAL 4	SURVIVAL 10	VOLUME 10
HEIGHT	1		.92	.86	.44	.56	.27	.02	.46		.99	1.01	1.24	1.03	.49
			(.06)	(.08)	(.19)	(.16)	(.32)	(.41)	(.20)		(1.13)	(.84)	(1.89)	(1.12)	(.16)
	2			.98	.81	.74	.20	-.02	.28		.62	.63	.96	.80	.70
				(.04)	(.15)	(.13)	(.32)	(.40)	(.21)		(.77)	(.62)	(1.43)	(.89)	(.13)
	4				.90	.84	.40	.15	.35		.85	.66	.94	.90	.83
					(.12)	(.10)	(.37)	(.41)	(.22)		(.94)	(.63)	(1.50)	(1.00)	(.10)
	10					.87	.33	.45	-.24		.03	-.14	.07	.16	.94
						(.06)	(.33)	(.50)	(.19)		(.51)	(.46)	(.63)	(.53)	(.03)
DBH	10						.33	.59	.18		.37	.23	.54	.44	.98
							(.31)	(.46)	(.19)		(.63)	(.46)	(.99)	(.69)	(.01)
STRAIGHTNESS	4							1.50	.49		.08	.39	.30	.26	.26
								(.81)	(.27)		(.92)	(.95)	(1.34)	(1.03)	(.29)
	10								1.00		.85	.95	.90	.89	.52
									(.56)		(1.50)	(1.32)	(2.02)	(1.57)	(.45)
CROWN	4										.38	.45	.24	.32	.04
											(.69)	(.60)	(.80)	(.67)	(.19)
	10														
SURVIVAL	1											.97	.66	.78	.11
												(.08)	(.81)	(.46)	(.49)
	2												.96	.92	-.01
													(.19)	(.14)	(.40)
	4													.91	.27
														(.22)	(.70)
	10														.19
															(.53)

respectively. Since straightness in pine is often under considerable genetic control, the low estimates in this study may reflect the inherent nature of shortleaf pine, or may be due to the rating system used to score the trait. Straightness is a difficult trait to quantify, and the single value assigned each tree may not be an adequate measure of the trait. Whatever the case, it is apparent that careful selection will be necessary to improve straightness in these stands of shortleaf pine.

At age ten the heritability estimate for crown was negative *(Table 2)*. Crown at age four showed considerable family variation and a family-mean heritability estimate of .58 ± .09. It seems most probable that the crown rating scheme used, devised for young trees, is not an appropriate rating system for older trees. Selection for a favorable crown type at an early age may not be effective nor relate to later crown form.

Narrow-sense family-mean heritability estimates for height, DBH, and volume *(Table 2)* were relatively high. The associated standard errors of these estimates *(Table 2)* show that the estimates are reasonably precise. A family-mean heritability estimate of .69 ± .07 for age ten volume, coupled with the large amount of variation observed for the trait, suggests that a breeding effort to increase volume through family selection in Oklahoma shortleaf pine would be rewarding.

Expected genetic gain in volume at age ten was computed to estimate the result of family selection. The estimate was based on selecting the best ten percent of the families at each location (i = 1.755). Estimated gain is 20.4 dm^3 per tree at age ten, representing a 43 percent gain in volume. This gain represents the volume increase expected at age ten when growing the select families over both test locations, and is a reasonable representation of the kind of gain to be expected when growing the select families over the majority of similar Oklahoma sites. Additional gains, although not estimated, can be expected by selecting the best individuals in the select families. Estimated individual tree within family heritability for volume was 0.29.

Genetic Correlations Over Time and Environments

Genetic correlations (r_g) among traits with standard errors are presented in *Table 4.* These correlations suggest that early height measurements, at least after the first year, are generally highly correlated with ten year height, DBH and volume. A genetic correlation of .70 ± .13 for second year field height with ten year volume suggests that one might effectively select for age ten volume on the basis of second year height. Selecting for age ten volume using height at age four would be even more reliable, though more time consuming, as the genetic correlation between these traits is .83 ± .10. This high, positive genetic correlation also holds between age two and age four height and ten year DBH, with r_g values of .74 ± .13 and .84 ± .10, repectively.

No consistant identifiable relationships were found between survival at any age and age ten height, DBH or volume. These genetic correlations displayed large standard errors and varying signs. These apparently unreliable values might be due to the extremely low family variance estimates for survival, suggesting limited genetic control of the trait. The same is probably true of the genetic correlations estimated for crown and straightness with other traits. Large standard errors, changing signs of the genetic correlations, and negative variances for these traits make meaningful interpretation of the relationships impossible.

Genetic correlations between traits in the two environments are presented in *Table 5.* The growth parameters of major importance, height, DBH and volume, have estimates that show generally consistent performance over locations and even over locations across time. At age ten, the correlations between locations for height, DBH and volume were 1.01, .89 and .81, respectively. These values support the earlier discussion concerning the limited importance of genotype by environment interactions, and the suggestion that stand influences in Oklahoma shortleaf pine

Table 5. — Genetic Correlations, (r_g) Between Age 10 Shortleaf Pine Traits in Two Environments. (Top number is r_g for column variable in location one and row variable in location two, bottom number is r_g for column variable in location two and row variable in location one, diagonals are r_g for same trait over environments.)

		HEIGHT				DBH	STRAIGHTNESS		CROWN		SURVIVAL				VOLUME
TRAIT	AGE	1	2	4	10	10	4	10	4	10	1	2	4	10	10
HEIGHT	1	.75	.69	.72	.35	.43	.18	-.12	.42	-.10		1.72	.61	.91	.34
			.95	.79	.34	.53	.46	-.07	.53	-1.16	.28	.35	.25	.25	.56
	2		1.08	1.21	.88	.89	.34	-.33	.40	-.40		2.95	1.31	1.72	.64
				.89	.54	.56	-.03	.19	.21	-.33	.40	.45	.40	.46	.74
	4			1.08	.98	.96	.43	.06	.47	-.28		4.35	1.78	2.55	.70
					.77	.73	.04	.30	.20	.51	.41	.40	.34	.44	.96
	10				1.01	.98	.34	-.35	.11	-.75		.35	.34	.45	.88
						.68	.39	.59	-.44	2.36	-.22	-.31	-.23	-.25	.71
DBH	10					.89	.34	.10	.50	-.06		1.43	.63	.72	.64
							.10	.65	-.18	2.09	-.03	-.13	-.06	-.08	.79
STRAIGHTNESS	4						.88	1.34	.68	1.04		-6.87	-4.06	-4.30	1.16
								.88	.38	1.48	-.30	-.23	-.20	-.28	.16
	10							.66	.61	.11		-1.03	-.38	-.36	.93
									1.19	1.58	-.30	-.15	-.34	-.36	-.38
CROWN	4								1.16	1.00		.91	-.00	.33	-.04
										-.27	.06	.10	.00	-.06	.38
	10									-.06		7.57	2.51	3.23	3.16
											-.11	.06	-.11	-.23	-.47
SURVIVAL	1											2.05	.92	1.29	-.18
	2											2.37	1.06	1.51	-.28
													1.25	2.11	1.08
	4												.69	-.34	-.19
														1.06	.59
	10													1.52	-.25
															.63
VOLUME	10														.81

may be of limited concern. The correlations also suggest that selection for both environments can be effectively accomplished in either environment.

The genetic correlations between locations for straightness, crown, and survival were inconsistent and of varying sign, and some values were greater than one due to sampling error. These erratic values probably reflect limited genetic control over these traits, and disallow reaching meaningful conclusions about relationships between them.

Summary and Conclusions

Considerable genetic variation for height, DBH and volume is present in Oklahoma stands of shortleaf pine. Family variability offers the greatest opportunity for improvement in volume production, and stand to stand variation appears to be of limited importance. These growth traits are highly heritable on a family mean basis and there is limited genotype by environment interaction, suggesting a tree improvement program in Oklahoma using one breeding population is feasable, and considerable volume gains can be expected. High genetic correlations of height at age two and age four with ten year volume suggest that selection for age ten volume can be accomplished reliably at age four or five.

The isolated population of shortleaf pine (stand 49) appears to possess interesting genetic variation. More intensive examination of this and other isolated populations may provide extremely useful variability or gene frequencies.

Significant stand to stand variation in survival was noted even though heritability estimates for survival on a family-mean basis were quite low. Improvement of survival may therefore be difficult, but the importance of the trait on most Oklahoma sites may warrant further investigation.

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