

purification of DNA from leaf tissue of woody plants. *BioTechniques* **5**: 735–736 (1993). — SAMBROOK, J., FRITSCH, E. F. and MANIATIS, T. A.: A laboratory manual. 2nd ed. Cold Spring Harbor Laboratory, Cold Spring Harbor, NY, USA (1989). — SCHÄGGER, H. and VON JAGOW, G.: Tricine-sodium dodecyl-polyacrylamide gel electrophoresis for the separation of proteins in the range from 1 to 100 kD. *Anal. Biochem.* **166**: 368–379 (1987). — SHARMA, P. and LÖNNEBORG, A.: Isolation and Characterization of a cDNA encoding a plant defensin-like protein from Norway spruce. *Plant Mol. Biol.* **31**: 707–712 (1996). — STENLID, J.: Controlling and predicting the spread of *Heterobasidion annosum* from infected stumps and trees of *Picea abies*. *Scand. J. For. Res.* **2**: 187–198 (1987). — SWEDJEMARK, G. and STENLID, J.: Susceptibility of conifer and broad-leaf seedlings to Swedish S and P-strains of *Heterobasidion annosum* under greenhouse conditions. *Plant Pathol.* **44**: 73–77 (1995). — SWEDJEMARK, G. and STENLID, J.: Variation in spread of *Heterobasidion annosum* in clones of *Picea abies* grown at different vegetation phases under greenhouse conditions. *Scand. J. For. Res.* **11**: 137–144 (1996). — SWEDJEMARK, G. and STENLID, J.: Between-tree and between-isolate variation for growth of S-group *Heterobasidion annosum* in sapwood of *Picea abies* cuttings. *Can. J. For. Res.* **27**: 711–715 (1997). — SWEDJEMARK, G., STENLID, J. and KARLSSON, B.: Genetic variation among clones of *Picea abies* in resistance to growth of *Heterobasidion annosum*. *Silvae*

Genet. **46**: 369–374 (1998). — TERRAS, F. R. G., EGGERMONT, K., KOVALEVA, V., RAIKHEL, N. V., OSBORN, R. W., KESTER, A., REES, S. B., TORREKENS, S., VAN LEUVEN, F., VANDERLEYDEN, J., CAMMUE, B. P. A. and BROEKAERT, W. F.: Small cysteine-Rich Antifungal proteins from Radish: Their Role in Host Defense. *Plant Cell.* **7**: 573–585 (1995). — THOMMA, B. P. H. J. and BROEKAERT, W. F.: Tissue-specific expression of plant defensin genes *PDF2.1* and *PDF2.2* in *Arabidopsis thaliana*. *Plant Physiol Biochem.* **36**: 533–537 (1998). — VON ARNOLD, S.: Improved efficiency of somatic embryogenesis in mature embryos of *Picea abies* (L.) KARST. *J. Plant Physiol.* **128**: 233–244 (1987). — WALDEN, R., KONCZ, C. and SCHELL, J.: The use of gene vectors in plant molecular biology. *Methods in Mol. Cell Biol.* **1**: 175–194 (1990). — WALTERS, C., GRACE, L. J., DONALDSON, S. S., MOODY, J., GEMMELL, J. E., VAN DER MAAS, S., KVAALEN, H. and LÖNNEBORG, A.: An efficient Biolistic transformation protocol for *Picea abies* embryogenic tissue and regeneration of transgenic plants. *Can. J. For. Res.* **29**: 1539–1546 (1999). — WU, R., REMINGTON, D. L., MACKAY, J. J., MCKEAND, S. E. and O'MALLEY, D. M.: Average effect of a mutation in lignin biosynthesis in loblolly pine. *Theor. Appl. Genet.* **99**: 705–710 (1999). — YOSHIMURA, S., YOSHIMURA, A., IWATA, N., MCCOUCH, S., LLEVA ABENES, M., BARAOIDAN, M., WAH MEW, T. and NELSON, R. J.: Tagging and combining bacterial blight resistance genes in rice using RAPD and RFLP markers. *Mol. Breed.* **1**: 375–387 (1995).

Stability and Seed Movement for Loblolly Pine in the Western Gulf Region

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Summary

Fifteen test plantings of loblolly pine (*Pinus taeda* L.) were established throughout the Western Gulf Region to assess genotype by environment (G X E) interactions and to establish seed movement guidelines. Open-pollinated families from five selected trees plus a checklot from each of four seed zones were planted at each location. Seed zones tested were southeastern Texas, southern Louisiana, northern Louisiana and southern Arkansas, all in the USA.

Heterogeneity of regressions was significant for height and volume at age five and for volume at age 10. Data suggest that G X E interactions could be managed by stratifying environments. Significant concurrence was detected for volume at ages 5 and 10 indicating a significant portion of G X E interaction was due to changes in family rank. Family differences were significant at ages 5 through 15.

Regression estimates of slope and standard deviation for volume through age 10, indicated northern Louisiana and southeastern Texas families were intermediate in stability while southern Arkansas and southern Louisiana families were equally unstable. Families from southern Arkansas were least responsive to changes in site quality while those from southern Louisiana were most responsive. At age 15, northern Louisiana and southeastern Texas families remained intermediate in stability but southern Arkansas families exhibited increased

responsiveness and southern Louisiana families showed decreased responsiveness to site quality. All zones exhibited a linear trend with respect to site quality. Perhaps greater drought tolerance of southern Arkansas families enabled them to continue growing in dense stands where competition for water could be great. The rapid early growth and reduced subsequent growth of southern Louisiana families may highlight a consequence of seed movement without timely regulation of stand density.

Ecovalences and directional responses were large and negative if seed movement exceeded 125 miles north or south of origin. Ecovalences and coefficients of genetic prediction suggested coastal families should not be planted on poor sites. Favorable performances were observed for families planted in regions requiring specific adaptability often along their latitude of origin or areas of higher moisture. Local material showed adaptiveness to local planting conditions.

Key words: *Pinus taeda*, genotype x environment interaction, plant stability, stability parameters, seed movement.

Introduction

The Western Gulf Region of the southern United States includes the states of Mississippi, Louisiana, Texas, Arkansas and Oklahoma. These states vary widely in weather and soils and resultantly, in site productivity. State and federal agencies and private industry within the Western Gulf Region are planting genetically improved seedlings on diverse sites across large geographical regions. Realization of a consistent and predictable performance from superior seed depends on their use on appropriate sites. An assessment of stability and genotype by environment (G X E) interaction is fundamental to the development of a sound seed movement policy.

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YATES and COCHRAN (1938) introduced a regression technique assessing G X E interaction, and thus plant stability. More commonly used in modified form (FINLAY and WILKINSON, 1963; EBERHART and RUSSELL, 1966 and FREEMAN and PERKINS, 1971), this technique uses the average performance of all genotypes at each test site as an index of site quality and produces estimates of slope (b_1) and deviations from regression (s^2) to jointly explain G X E interaction. Some families have average stability with $b_1 = 1$ and small deviations from regression. These families are most desirable for large-scale plantings encompassing diverse environments due to their high degree of adaptability to new and varied environments. Families with $b_1 < 1$ and deviations from regression near zero are "stable" and not responsive to changes in site quality. A family with $b_1 > 1$ is "unstable" and responsive to improvements in site quality. As s^2 becomes smaller, family performance becomes more predictable.

Responsiveness to site quality may be described statistically with linear (FREEMAN and PERKINS, 1971) and nonlinear regression lines (MILLIKEN, 1989). A quadratic regression line is one type of nonlinear regression characterized by two slope terms (b_1, b_2) which can be jointly interpreted to explain growth trends. When both linear (b_1) and quadratic (b_2) regression coefficients are significant, the curve significantly departs from linearity. When a family has a positive b_2 its growth curve is concave upward with an increased responsiveness to highly productive sites. If b_2 is negative the curve is concave downward with decreased responsiveness to high quality sites.

MANDEL (1961) presents a second regression method for partitioning G X E interaction. This method provides a "slopes" term that estimates that portion of the G X E sums of squares explained by multiple regression lines and a residual term for that unexplained by multiple regression lines. MANDEL (1961) continues by separating the above "slopes" term into effects for concurrence, the tendency to share or intersect a common point, and non-concurrence. Concurrence suggests G X E interactions result from changes in rank as opposed to changes in scale.

WRICKE's ecovalence is another stability parameter assessing G X E interaction (SHELBOURNE, 1972). This statistic estimates the sums-of-squares contribution of each genotype to the overall G X E term. The smaller the contribution the more stable the genotype.

Both regression estimates for slope and variance and WRICKE's ecovalence have been used as practical indicators of plant stability. For western populations of loblolly pine, VAN BUIJTENEN (1978) used estimates of slope and standard deviation to characterize stability of geographic seed sources. For height, the Bastrop County, Texas seed source had $b_1 = 0.79$ and the Livingston Parish, Louisiana seed source $b_1 = 1.47$. These sources represented the extremes and were opposites in responsiveness to improved site quality. Also for western populations of loblolly pine, YEISER (1980) reported family responsiveness at age 5 ranging from $b_1 = 0.85$ to $b_1 = 1.25$ for height and $b_1 = 0.53$ to $b_1 = 1.51$ for volume. More recently, MCKEAND et al. (1989) reported extremes in responsiveness to site quality for stem volume of $b_1 = 0.42$ and $b_1 = 1.36$ for loblolly pine families from eastern populations. OWINO (1977) reported similar stability for wide and local crosses of family sets of loblolly pine for height. When OWINO contrasted regression coefficients with ecovalences, the latter showed greater variation. He suggested ecovalences may be more discriminating as indicators of stability. Following an assessment of 8-year-old genetic tests of eastern loblolly pine families, LI and MCKEAND (1989) and MCKEAND et al. (1989) concluded that the biological and

economical importance of G X E interaction and stability were minimal.

By regarding a character in two different environments as two different traits, BARADAT's (1976) coefficient of genetic prediction (CGP_{ij}) may be used to study G X E interaction. In this case, COV_{A1A2} represents the additive genetic covariance at locations one and two and $s_{p1.p2}$ is the product of phenotypic standard deviations at locations one and two. By pairing all possible environmental combinations, a matrix of correlations between genotypic means is produced which can be used to separate environments into similar groups. Additional information on GXE interaction can be found in NAMKOONG (1980), SHUKLA (1972) and STONECYPHER et al. (1996).

Because of site diversity, the years to reach maturity, and the relatively low financial return from forest regeneration, breeders and managers are concerned about GXE interaction and genotypic stability. Potentially, GXE interaction reduces the predictability of performance thus possibly leading to planting failure, lower genetic gains, and higher risk. By studying G X E interaction, seed movement policies can be developed that promote the long-term adaptability of improved tree crops thereby minimizing risk to investments in forest regeneration and management. The geographic seed source study reported here, was initiated by the Western Gulf Forest Tree Improvement Program (WGFTIP) to determine, in part, where and how far superior families and geographic sources could be moved without affecting their superiority. With this information a sound seed movement policy can be developed. This paper reports on:

- 1) The presence and magnitude of G X E interaction in selected families of loblolly pine (*Pinus taeda* L.) native to the Western Gulf Forest Tree Improvement Program region and
- 2) The stability of selected families of loblolly pine indigenous to the WGFTIP region.

Materials and Methods

The WGFTIP region was divided into eight geographic seed zones using permanent highways closely paralleling major physiographic changes in each state (Fig. 1). Five families from seven of the eight zones were outplanted in four-tree row plots in six blocks according to a randomized-complete-block-design. Because of the magnitude of the study, it was separated into two series of plantings replicated over two consecutive years. Only data from the first series were used in this report. Fifteen sites were tested each containing five families from each of four seed zones: southern Arkansas, northern Louisiana, southern Louisiana and southeastern Texas (Fig. 1).

Trees in 15 test plantings at ages 5 and 10 were recorded for survival and measured for total height (1 dm), and diameter at breast height (1 mm). The same measurements were taken on 13 test plantings at age 15. Stem volume per planted tree was computed as dm^3 at age 5 and as $m^3/ha/yr$ at ages 10 and 15.

An analysis of covariance was conducted on height and volume family means according to the techniques of FREEMAN and PERKINS (1971) and MANDEL (1961). The statistical model was:

$$Y_{ij} = u + L_i + F_j + E_{ij}$$

where u denotes the experiment mean, L the effect due to locations, F the effect due to families, and E the error within the i^{th} and j^{th} treatments. Regression estimates of slope, standard deviation, and intercept were interpreted to explain G X E interactions. A directional response and sum of squares contribution to the G X E interaction was calculated for each family at each location to determine how far and where a family or seed source could be moved and maintain its relative rank. The

directional response was computed as the direction a particular family mean at a given location deviates from the location, family and grand means.

To assess adaptability, the technique of SHELBOURNE (1972) was used to partition the contribution of each family or zone at each test planting to the ecovalence. Test plantings were then systematically eliminated according to their geographic distance from the source and the interaction re-examined with each elimination. When primarily positive interactions and small changes in ecovalences were encountered, the source was considered well adapted to the region. Coefficients of genetic prediction (CGP) were calculated according to BARADAT's (1976) and used to identify regions with similar family performances.

Results and Discussion

Bar graphs by zone were constructed for height and volume at ages 5, 10 and 15. Because of the similarity of trends, only volume is presented. GXE interaction is depicted by changes in rank (Figs. 2, 3 and 4). For example, the southern Louisiana seed zone performed poorly when planted in northeastern Texas but excelled in plantings in southern latitudes and in northern Mississippi. Furthermore, the Arkansas seed zone performed best in northeastern Texas and in Arkansas. Bar graphs illustrate the presence of GXE interaction and provide rudimentary interpretation of trends, but further quantification is needed to characterize growth patterns sufficiently for development of a seed movement policy.

At age 5, the heterogeneity of regressions was a significant source of linear and quadratic variation for height and volume; however, concurrence was significant for volume only (Table 1). These tests indicated that: (1) large differences existed among the slopes of regression lines characterizing individual family performance, (2) regression lines best describing the growth trends may be linear or quadratic, and (3) a major portion of the interaction for volume was due to changes in family rank.

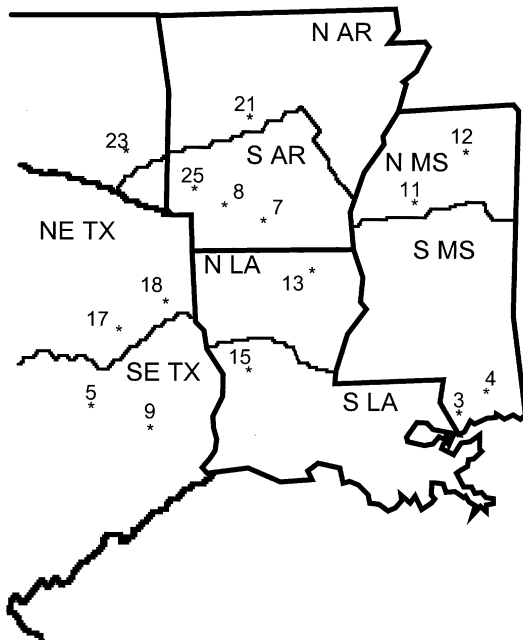


Figure 1. – The Western Gulf Region, eight geographic seed zones (NE TX = Northeastern Texas; SE TX = Southeastern Texas; N AR = Northern Arkansas; S AR = Southern Arkansas; N LA = Northern Louisiana; S LA = Southern Louisiana; N MS = Northern Mississippi, S MS = Southern Mississippi) and fifteen test locations (*).

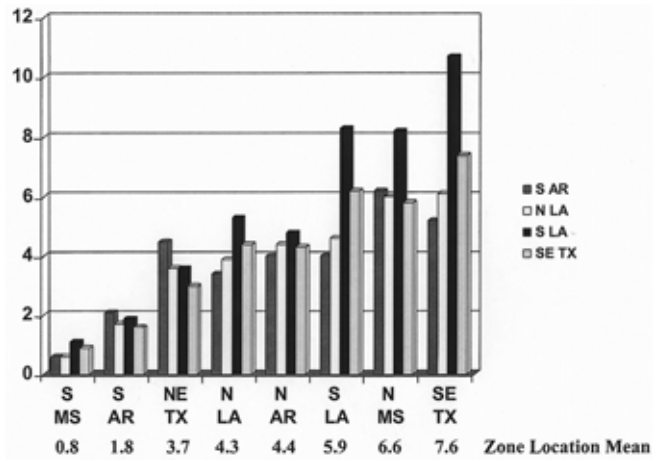


Figure 2. – Volume at age 5 (dm³/planted tree) for southern Arkansas (S AR), northern Louisiana (N LA), southern Louisiana (S LA), and southeastern Texas (SE TX) seed sources in eight planting zones in the Western Gulf Region.

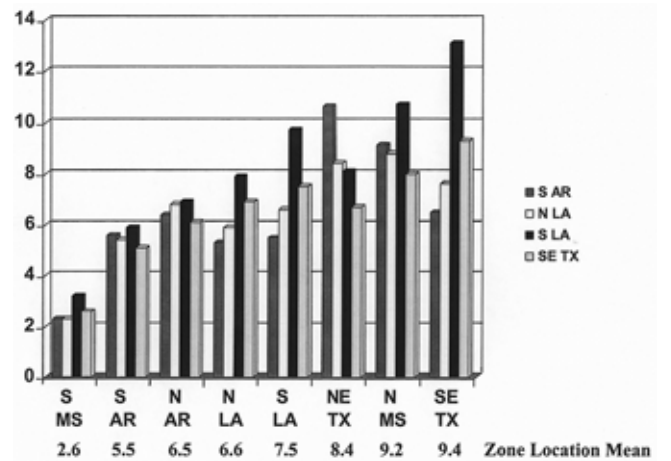


Figure 3. – Stem volume per planted tree at age 10 (m³/ha/yr) for southern Arkansas (S AR), northern Louisiana (N LA), southern Louisiana (S LA), and southeastern Texas (SE TX) seed sources planted in eight zones in the Western Gulf Region.

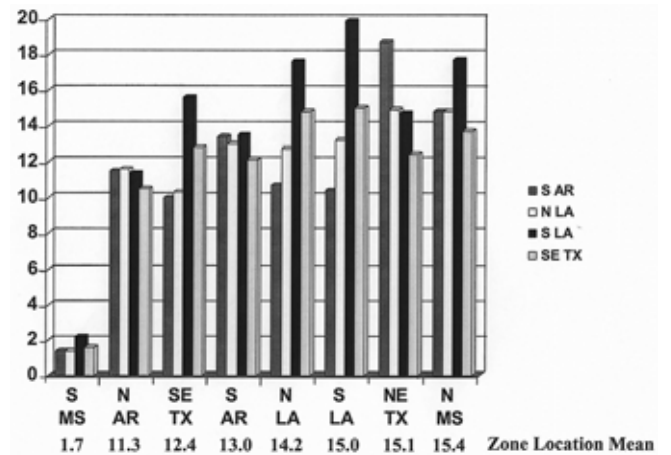


Figure 4. – Stem volume per planted tree at age 15 (m³/ha/yr) for seed sources from southern Arkansas (S AR), northern Louisiana (N LA), southern Louisiana (S LA), and southeastern Texas (SE TX) growing in eight planting zones in the Western Gulf Region.

The impact of the G X E interaction may be decreased and predictability of growth may be increased by stratifying sites into groups with similar family performance. For example, the G X E source of variation was approximately 17.5%, 27.6% and 30.7% of the total volume variation at ages 5, 10, and 15, respectively. Approximately 22.8%, 22.2% and 11.1% of the respective age interaction was explained by partitioning environments. Matching site conditions and family responsiveness enables managers to plant families providing a more consistent and predictable performance. Increased responsiveness to site quality is achieved by planting unstable families with linear estimates of $b_1 > 1.0$ or positive quadratic estimates of b_2 on high quality sites. Responsiveness decreases as site quality decreases.

At age 10, the strong age 5 patterns delineating family response to site quality had decreased with the heterogeneity term being a significant source of linear and quadratic variation for volume only (Table 1). Concurrence remained significant for volume. The lack of age 5 responsiveness of WHAPT-3 from southern Arkansas and UR-2 from northern Louisiana to high sites was again detected at age 10. In contrast, the quadratic growth curve for southern Louisiana family B-5-4 was absent at age 5 and significantly concave upward at age 10. The detection of significant quadratic growth responses at age 5 for some families and at age 10 for other families suggests undefined genes may be triggering increased growth at different stages of development. If so, managers should match families with stand density, site nutrition, etc. for growth activation of desired product classes to fully capture the potential contribution of GXE interaction. By age 15, linear

and quadratic trends were no longer significant suggesting opportunities to capitalize on GXE interaction were gone. These results may have occurred for three reasons. First, the ranking of location means used as the index of site quality changed over time (Fig. 5) possibly due to the interaction of genotypes with stand density and site index. Second, the most productive test, number 9, was destroyed prior to measurement at age 15. Factors one and two resulted in a different distribution of test conditions over time. Third, undefined genes for enhanced early growth were expressed by age 15. Although heterogeneity decreased with time, family differences remained significant through age 15.

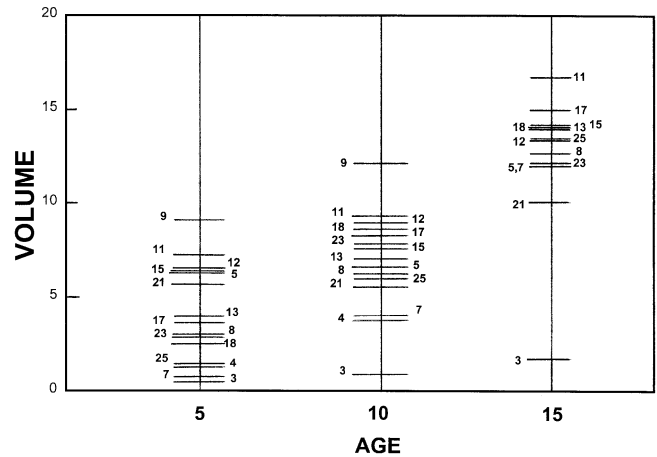


Figure 5. – An illustration of the ranking of test plantings for volume per planted tree at age 5 (m^3), 10 and 15 ($m^3/ha/yr$).

Table 1. – Analyses of variance and covariance at ages 5, 10 and 15 for height (HT) and volume (VOL) per planted tree for families of loblolly pine in the Western Gulf Region.

Sources of Variation	Degrees of Freedom	Mean Squares					
		5 HT	5 VOL	10 HT	10 VOL	15 HT	15 VOL
Location	14 ²	18.96*	122.93*	77.94*	129.15*	101.67*	265.09*
Family	19	1.02*	6.42*	3.22*	10.21*	3.53*	25.82*
Location by family interaction	257 ²	0.05	1.52	0.16	2.97	0.19	7.37
Heterogeneity of regressions ¹							
Linear	19	0.11*	7.00*	0.14	7.08*	0.20	5.12
Quadratic	19	0.11*	3.33*	0.18	6.08*	0.20	6.03
Error	219	0.04	0.89	0.16	2.35	0.19	7.74
Residual	238	0.04	0.96	0.15	2.51	0.18	7.68
Slope							
Concurrence	1	0.06	15.15*	0.18	7.60*	0.37	7.56
Non-concurrence	18	0.12	0.99	0.28	1.31	0.29	3.67
Total	291						

*) Significant at the 0.05 probability level.

¹) The location mean of test families was the covariate.

²) At age 15, 12 or 223 degrees of freedom existed for effects due to location and location by family interaction, respectively.

Family changes in stability over time were found to be especially noteworthy; some examples are presented in *Table 2*. Because similar trends were observed for height and volume, only volume will be presented. Based on regression estimates (b_1 , s) for volume, the southern Arkansas family DF-3252 was numerically most stable at ages 5 and 10 and intermediate at age 15. The poor early response by DF-3252 to increased site quality improved with time and was nearly proportionate at age 15. Southern Arkansas family WNAPT-6 was highly stable with a volume growth response proportionate to site quality at age 15. Throughout the study, WHAPT-3 was the southern Arkansas family with numerically, both the lowest stability and the highest early responsiveness to site quality. At age 5, northern Louisiana family UR-2 exhibited low stability. At age 10 and continuing through age 15, stability was intermediate and responsiveness to favorable growing conditions was consistently high. KS-309, from northern Louisiana, had low stability at ages 10 and 15. Throughout the study, SH-11 exhibited the highest stability among northern Louisiana families with a

growth response closely proportionate to site quality. From southeastern Texas, S3PT8 had high stability, S4PT8 had low stability and both families were responsive to site quality at age 5. At ages 10 and 15, S4PT8 was highly stable and K-79 was less stable than other southeastern Texas families. For both of these families, responsiveness to site quality increased from age 10 to 15. Southern Louisiana family B-2-7 demonstrated low stability throughout the study; responsiveness to site quality decreased with age. Family B-1-4 was highly unstable at age 5. At ages 10 and 15, B-5-4 was highly stable and showed decreasing responsiveness to improved growing conditions.

When families were grouped according to zone, the stability trends for height and volume were similar. Therefore, only volume is presented (*Table 3*). Through age 10, northern Louisiana and southeastern Texas families were numerically intermediate in stability. Their volume increased linearly with site quality. Southern Arkansas families were not responsive to improved site quality whereas southern Louisiana families were highly responsive to improved site quality (*Figs. 2 to 4*).

Table 2. – For selected families, mean volume per planted tree was regressed on the location mean at age 5 (dm³), 10 (m³/ha/yr) and 15 (m³/ha/yr), providing regression estimates of intercept (b_0), slope (b_1 , b_2), coefficient of determination (R^2) and standard deviation (s).

Age	Seed Source	Family	b_0	b_1	b_2	R^2	s	Mean	
5	S. Arkansas	DF-3252	0.50	0.72	–	0.85	0.78	3.41	
	S. Arkansas	WHAPT-3	1.02	0.54	–	0.63	1.09	3.20	
	S. Arkansas	WHAPT-3	-0.34	1.46	-0.11	0.82	0.79	3.20	
	N. Louisiana	SH-11	0.00	0.99	–	0.94	0.64	3.89	
	N. Louisiana	UR-2	0.20	0.83	–	0.87	0.85	3.57	
	N. Louisiana	UR-2	-0.66	1.41	-0.07	0.91	0.66	3.57	
	SE. Texas	S3PT8	-0.08	1.04	–	0.92	0.80	4.13	
	SE. Texas	S4PT8	0.05	0.95	–	0.73	1.44	3.84	
	S. Louisiana	B-1-4	0.08	1.21	–	0.94	0.82	4.97	
	S. Louisiana	B-2-7	-0.94	1.52	–	0.86	1.63	5.24	
	10	S. Arkansas	DF-3252	0.44	0.85	–	0.60	0.66	6.12
		S. Arkansas	WHAPT-3	1.97	0.62	–	0.36	2.24	6.11
S. Arkansas		WHAPT-3	-1.76	1.92	-0.10	0.52	2.03	6.11	
N. Louisiana		SH-11	0.44	0.91	–	0.84	1.09	6.43	
N. Louisiana		UR-2	0.49	0.90	–	0.75	1.44	6.54	
N. Louisiana		UR-2	1.91	1.74	-0.06	0.81	1.29	6.54	
N. Louisiana		KS-309	0.46	0.89	–	0.70	1.58	6.45	
SE. Texas		S4PT8	0.57	0.85	–	0.83	1.07	5.82	
SE. Texas		K-79	0.41	0.89	–	0.62	1.89	6.40	
S. Louisiana		B-5-4	-0.41	1.23	–	0.92	0.99	7.84	
S. Louisiana		B-5-4	1.29	0.64	0.04	0.94	0.88	7.84	
S. Louisiana		B-2-7	-1.33	1.35	–	0.69	2.50	7.76	
15	S. Arkansas	WNAPT-6	-0.29	1.01	–	0.71	2.44	12.18	
	S. Arkansas	DF-3252	-0.20	0.96	–	0.60	2.98	11.72	
	S. Arkansas	WHAPT-3	1.10	0.91	–	0.42	4.02	12.37	
	N. Louisiana	SH-11	0.45	0.95	–	0.70	2.45	12.12	
	N. Louisiana	UR-2	-1.38	1.17	–	0.83	1.97	13.07	
	N. Louisiana	KS-309	-0.68	1.04	–	0.65	2.85	12.20	
	SE. Texas	S4PT8	-0.01	0.94	–	0.87	1.66	11.13	
	SE. Texas	K-79	-1.61	1.08	–	0.57	3.57	11.77	
	S. Louisiana	B-5-4	0.43	1.09	–	0.78	2.17	13.91	
	S. Louisiana	B-2-7	0.18	1.04	–	0.51	3.86	13.06	

At age 15, northern Louisiana and southeastern Texas families remained numerically intermediate in stability. Responsiveness to site quality had increased for southern Arkansas families and decreased for southern Louisiana families with all zones exhibiting a linear trend with respect to site quality.

Table 3. – Regression of zone mean on the location mean volume per planted tree at ages 5 (dm^3), 10 ($\text{m}^3/\text{ha}/\text{yr}$) and 15 ($\text{m}^3/\text{ha}/\text{yr}$) provided estimates of intercept (b_0), slope (b_1 , b_2), coefficient of determination (R^2), standard deviation (s) and mean.

Zone	Volume					Mean
	b_0	b_1	b_2	R^2	s	
Age 5						
S. Arkansas	0.63	0.73	–	0.71	1.15	3.62
S. Arkansas	-0.27	1.33	-0.07	0.76	1.10	3.62
N. Louisiana	0.15	0.88	–	0.86	0.86	3.70
SE. Texas	-0.01	0.96	–	0.85	1.00	3.88
S. Louisiana	-0.61	1.40	–	0.91	1.10	5.07
S. Louisiana	0.19	0.86	0.06	0.92	1.04	5.07
Age 10						
S. Arkansas	1.11	0.76	–	0.52	1.89	6.23
S. Arkansas	-1.46	1.66	-0.07	0.60	1.75	6.23
N. Louisiana	0.54	0.88	–	0.74	1.74	6.41
SE. Texas	0.26	0.90	–	0.74	1.36	6.26
S. Louisiana	-1.27	1.37	–	0.81	1.69	7.92
S. Louisiana	1.31	0.47	0.07	0.85	1.54	7.92
Age 15						
S. Arkansas	0.69	0.90	–	0.49	3.23	11.88
N. Louisiana	-0.02	0.99	–	0.66	2.52	12.23
SE. Texas	0.01	0.95	–	0.70	2.24	11.73
S. Louisiana	-0.56	1.18	–	0.67	2.91	14.11

Regression coefficients characterizing volume for zones were different at ages 5 and 10. Families from southern Arkansas had a negative quadratic coefficient and did not exploit the potential of best sites. Southern Louisiana families exhibited a positive quadratic coefficient and showed increased growth on the most highly productively sites (Figs. 2 to 4). At age 15, regression lines for all families were similar (mean slope of $b_1=1.0$ and mean standard deviation of $s=2.72$). Thus, southern Louisiana families had fast early growth that slowed between ages 10 and 15 while southern Arkansas families exhibited the converse. Parallel lines at age 15 may have resulted from: (1) the activation of undefined growth genes in the southern Arkansas families or (2) the ability of drought tolerant families (WELLS and WAKELEY, 1966) to continue growing at higher stand densities when competition for water is great. Likewise, the simultaneous reduction in growth rate for southern Louisiana families may have resulted from a need for thinning. Should these trends continue (WELLS, 1983), managers attempting to increase yield through seed movement should carefully consider wood quality implications of rapid early – versus fast mid-rotational growth and regulate stand density through weed control, thinning and other moisture –, nutrient-, light- and space-providing treatments to maintain early genetic trends. Consequences of seed movement without regulating stand density may include lost growth or higher mortality in exotic sources. For example, tests 5, 15 and 21 had low mortality

(< 8%) after 15 years. In addition, the rank of all three tests declined with age (Fig. 5). At test 21 in northern Arkansas, mortality for coastal sources averaged 5% between ages 5 and 15 while northern Louisiana and southern Arkansas families averaged 1% mortality. While not inordinate, mortality for coastal families was greater than for noncoastal material and sufficient to contribute to a reduction in rank. At coastal plantings 5 and 15, reduction in rank was not accompanied by decreased survival. Perhaps seed movement out of dry regions into moist regions minimizes losses to mortality but reduced yield may still occur.

Trends in ecovalences and directional responses were similar for height and volume. Ecovalences at age 10 for an individual test varied from a high of +51.66 for B-5-7 planted in southeastern Texas to a low of -27.98 for WHAPT-3 planted in southeastern Texas (Table 4). A summary of the partitioned G X E interaction sums of squares and ecovalences shows families from northern Louisiana, southeastern Texas, southern Arkansas and southern Louisiana contributed 15%, 16%, 31%, and 37%, respectively to the G X E interaction sums of squares (Table 5). Therefore, northern Louisiana and southeastern Texas families were more stable than southern Arkansas and southern Louisiana families.

Local material showed adaptiveness to local planting conditions (Figs. 2 to 4). For example, of the five southern Arkansas families planted in five Arkansas tests, positive deviations from means occurred more frequently (16 times) and with a greater magnitude (16.49) than the nine negative deviations (Table 5). Similar trends were observed for other zones.

Sums of squares and directional responses were often large and negative when movement exceeded more than 125 miles for northerly families moved south and southerly families moved north. The same trend was observed for coastal families planted on poor sites. For example, southern Arkansas families showed poor adaptability to test sites in Louisiana and southeastern Texas (Figs. 2 to 4). Northern Louisiana families grew less than expected in coastal plantings in Texas and Louisiana. Southeastern Texas families grew slower than expected when planted in northeastern Texas. Southern Louisiana sources performed poorly in Arkansas, northeastern Texas, and on poor sites in southern Mississippi (Table 5, Figs. 2 to 4).

In contrast with south and north seed movements, favorable performances were observed for families planted in regions requiring specific adaptability often along their latitude of origin or areas of higher moisture. For example, the Arkansas seed source showed adaptability in Arkansas, northeast Texas and southern Mississippi to poor or droughty growing conditions (Table 5, Figs. 2 to 4). The northeast Texas test sites represent an east to west latitudinal movement against the moisture gradient but within regions known for droughty growing conditions. The southern Mississippi test site represents a long, south and east movement of families (Table 5, Figs. 2 to 4). This movement does not follow a longitude or latitude. Test sites in Arkansas and southern Mississippi have limited growth resources for which Arkansas families seem to be well adapted. On the other hand, northern Louisiana sources performed well in Arkansas and northeastern Texas. Families from southeastern Texas grew well in southeastern Texas, Arkansas, Louisiana and Mississippi. Southern Louisiana material performed well in southeastern Texas, Louisiana and northern Mississippi.

Trends in CGP's were similar for height and volume through age 15 so results are presented for volume only. At ages 5 and 10, large CGP's were observed among several southern plantings in Mississippi, Texas and Louisiana (Table 6, Figs. 2 to 4).

Table 4. – Location by family sums of squares, direction of response and ecovalence for volume per planted tree (m³/ha/yr) at age 10.

Zone	Family Test No.	Location ¹														Eco- valence	
		N AR		S AR			NE TX		N LA	S LA	N MS		SE TX		S M		
		23	21	25	8	7	17	18	13	15	11	12	5	9	3		4
S. Arkansas	WBRPT-6	0.05	0.02	0.23	2.11	0.15	3.54	11.26	2.69	3.80	0.00	2.98	1.52	4.81	0.32	1.01	34.64
		-	+	+	+	-	+	+	-	-	-	+	-	-	-	-	
S. Arkansas	WHAPT-3	0.02	0.22	0.45	3.95	0.28	3.91	29.17	0.17	1.18	5.17	1.79	0.46	27.98	0.22	0.33	75.40
		+	+	-	+	+	+	+	-	-	-	-	-	-	+	+	
S. Arkansas	WNAPT-6	0.49	0.45	0.35	0.70	0.01	0.12	7.06	0.86	4.75	2.11	7.12	0.55	15.47	0.01	0.08	40.20
		-	+	-	+	-	+	+	-	-	+	+	-	-	+	+	
S. Arkansas	DF-3252	0.05	0.01	0.03	0.94	0.08	0.18	25.01	0.97	1.16	1.11	1.91	2.06	11.97	0.14	0.55	46.31
		+	+	-	+	+	+	+	-	-	+	+	-	-	+	+	
S. Arkansas	DF-1158	1.96	3.10	0.18	0.01	2.37	0.58	3.54	0.01	0.33	6.28	2.28	0.09	19.9	1.70	*	42.32
		+	+	-	-	+	-	-	-	-	-	+	+	-	+	-	
N. Louisiana	H-29	1.77	1.00	0.78	2.42	0.08	5.08	4.53	1.07	0.51	1.40	1.85	0.92	1.72	0.51	0.53	24.28
		+	+	+	+	+	-	+	-	-	-	-	-	-	+	+	
N. Louisiana	KS-309	0.01	1.06	0.05	1.62	0.88	3.66	11.68	0.37	0.12	0.07	10.37	0.01	1.72	0.33	0.17	32.14
		-	+	-	-	-	+	+	-	+	-	-	+	-	+	+	
N. Louisiana	SH-11	0.12	0.00	0.02	3.75	1.00	2.78	0.14	0.53	0.04	4.43	*	0.01	0.05	0.00	0.31	13.21
		+	+	+	+	-	+	-	+	+	-	-	-	-	-	+	
N. Louisiana	KS-727	0.31	0.01	0.13	2.75	2.32	0.18	5.51	0.01	0.09	0.22	5.35	0.97	1.68	0.33	1.30	21.29
		+	+	+	+	+	-	-	-	-	+	+	-	-	-	-	
N. Louisiana	UR-2	0.01	0.44	0.20	0.01	0.16	0.29	3.28	0.21	0.85	3.37	4.09	0.30	12.81	0.00	0.31	26.39
		+	+	-	-	-	-	+	+	-	+	+	-	-	-	-	
SE. Texas	S3PT8	0.67	0.12	0.00	3.60	0.00	1.11	4.00	0.14	0.02	0.01	3.49	0.36	6.10	0.04	0.11	19.71
		-	+	+	+	+	+	-	+	+	+	-	+	+	-	+	
SE. Texas	S4PT8	*	0.04	*	0.40	1.89	*	1.70	1.44	*	0.84	0.89	3.56	*	0.43	*	11.20
		+	+	+	+	+	-	-	+	+	+	-	+	-	+	+	
SE. Texas	K-79	0.02	0.17	0.53	1.34	0.65	0.30	27.30	0.12	4.53	0.56	2.29	0.07	0.84	0.03	8.54	47.34
		-	+	+	-	-	+	-	+	+	-	-	-	+	+	+	
SE. Texas	S5PT8	0.02	0.06	0.10	1.86	0.01	0.36	2.99	0.77	2.09	0.06	1.82	1.28	4.37	0.31	0.02	16.00
		-	+	+	-	+	+	-	+	-	-	+	+	+	+	+	
SE. Texas	C17A	0.01	0.08	1.30	0.82	0.15	1.43	2.53	1.83	2.67	1.13	0.56	1.62	10.96	1.03	3.61	29.63
		+	+	+	-	+	+	-	+	+	-	+	+	-	+	-	
S. Louisiana	B-2-7	0.30	4.44	0.63	4.45	0.47	11.03	13.53	1.51	2.42	6.59	7.79	0.42	43.45	0.37	0.1	97.63
		-	-	-	+	-	-	-	+	+	+	-	+	+	-	-	
S. Louisiana	B-5-4	0.02	0.22	0.17	4.48	0.00	0.36	0.00	0.01	0.90	0.64	0.04	0.38	12.78	0.24	0.05	20.25
		+	-	-	-	+	-	-	-	+	-	-	+	+	-	-	
S. Louisiana	B-5-3	4.27	1.20	0.27	14.51	0.22	0.00	0.51	0.04	1.53	0.42	0.61	1.95	37.13	0.54	2.21	65.29
		-	-	+	-	+	-	-	+	+	+	-	+	+	-	-	
S. Louisiana	B-5-7	0.00	3.50	1.49	5.87	4.16	5.45	0.07	0.34	1.00	1.54	0.01	0.64	51.66	1.11	0.62	77.43
		+	-	-	-	-	-	+	-	+	+	+	+	+	+	-	
S. Louisiana	B-1-4	0.00	0.74	0.00	2.39	0.11	0.12	7.25	0.00	0.78	4.81	9.42	0.11	1.01	1.33	1.67	29.79
		-	-	-	-	+	+	-	-	+	+	+	-	+	-	-	
G X E Interaction Sums of Squares																767.33	

*) Did not occur at this location.

¹) N AR = Northern Arkansas; S AR = Southern Arkansas; NE TX = Northeastern Texas; N LA = Northern Louisiana; N MS = Northern Mississippi; SE TX = Southeastern Texas; S LA = Southern Louisiana; S MS = Southern Mississippi.

Table 5. – Totals for each zone of family origin and planting zone illustrating the sums of squares, direction of response (+,-) and number of family by location combinations contributing to the G X E interaction for volume per planted tree (m³/ha/yr) at age 10.

Family Origin ¹	Planting Zone ¹														Eco- valence	
	AR	NE TX		N LA		N MS		SE TX		S LA		S MS				
S AR	16.49	1.72	80.25	4.12	0.00	4.70	16.4	14.34	0.09	84.70	0.00	11.22	2.48	1.88	238.87	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	-	
	16	9	8	2	0	5	5	5	1	9	0	5	6	3		
N LA	16.97	3.93	25.93	11.2	0.74	1.45	13.03	18.12	0.01	20.18	0.16	1.45	1.85	1.94	117.30	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	-	
	17	8	5	5	2	3	4	5	1	9	2	3	5	5		
SE TX	8.46	5.38	3.20	38.52	4.30	0.00	1.96	9.69	18.13	11.03	7.20	2.11	10.47	3.65	123.88	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	-	
	16	7	4	5	2	3	6	4	9	1	5	2	8	2		
S LA	5.07	48.84	0.19	38.13	1.55	0.35	22.79	9.08	149.42	0.11	6.63	0.00	0.00	8.24	290.39	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	-	
	7	18	2	8	5	3	7	3	9	1	5	0	0	10		
G X E Interaction Sums of Squares																767.33

¹) N AR = Northern Arkansas; S AR = Southern Arkansas; NE TX = Northeastern Texas; N LA = Northern Louisiana; N MS = Northern Mississippi; SE TX = Southeastern Texas; S LA = Southern Louisiana; S MS = Southern Mississippi.

Table 6. – Coefficients of genetic prediction illustrating the correlation among tests for volume per planted tree at age 5 (dm³), 10 (m³/ha/yr) and 15 (m³/ha/yr).

Location ¹	SE	S	N	N	SE	S	N	N	SE	S	N	N				
													TX	LA	LA	MS
Test Number	5	9	15	13	11	5	9	15	13	11	5	9 ²	15	13	11	
	Age 5				Age 10				Age 15							
S MS	3	.68	.52	.59	*	.55	.71	.62	.66	.55	*	.57	-	*	.55	*
S MS	4 ²	*	.55	.62	*	*	*	.54	*	*	*	-	-	-	-	-
SE TX	5	-	.77	.82	.75	.72	-	.88	.81	.86	.61	-	-	.85	.85	.63
SE TX	9 ²	-	-	.79	.48	.72	-	-	.80	.77	.69	-	-	-	-	-
S LA	15	-	-	-	.69	.59	-	-	-	.82	.63	-	-	-	-	.70
N LA	13	-	-	-	-	.56	-	-	-	-	.66	-	-	-	-	.72

¹) SE TX = Southeastern Texas; S LA = Southern Louisiana; S MS = Southern Mississippi; N LA = Northern Louisiana.

²) Test destroyed prior to measurement at age 15.

*) CGP's < 0.50.

For ages 5, 10 and 15 tests in southeastern Texas, Louisiana and northern Mississippi were highly correlated (Table 6, Figs. 2 to 5). These tests are largely intermediate to highly productive (Figs. 2 to 5) with intermediate to high survival (> 72%). We conclude that no special adaptability was required for these growing conditions.

In conclusion, significant G X E interactions in the Western Gulf Region can be managed by stratifying environments. Local material showed adaptiveness to local planting conditions. Opportunity exists to increase early yields by moving coastal families to highly productive sites not more than 125 miles north. Favorable performances were observed in families planted in regions requiring specific adaptability often along their latitude of origin or areas of higher moisture. When selecting a seed movement strategy to increase yield, wood quality implications of increasing growth early versus late in the rotation and weed control, thinning and other space-providing treatments should be carefully assessed if genetic trends are to be maintained. Otherwise, lost growth or high mortality may occur in exotic material.

Literature

BARADAT, PH.: Use of juvenile-mature relationships and information from relatives in combined multitrait selection. Proc. IUFRO Joint Meeting on Advanced Generation Breeding. Bordeaux, France. p. 121-138 (1976). — EBERHART, S. A. and RUSSELL, W. A.: Stability parameters for comparing varieties. Crop Sci. 6: 6-40 (1966). — FINLAY, K. W. and WILKINSON, G. N.: The analysis of adaptation in a plant-

breeding programme. Aust. J. Agric. Res. 14: 742-754 (1963). — FREEMAN, G. H. and PERKINS, J. M.: Environmental and genotypes grown in different environments and measures of these environments. Hered. 27: 15-23 (1971). — LI, B. and MCKEAND, S. E.: Stability of loblolly pine families in the southeastern U. S. Silvae Genet. 38: 96-101 (1989). — MANDEL, J.: Non-additivity in two-way analysis of variance. American Statistical Association Journal 56(296) 878-889 (Dec. 1961) (1961). — MCKEAND, S. E., WEIR, R. J. and HATCHER, A. V.: Performance of diverse provenances of loblolly pine throughout the southeastern United States. South. J. Appl. For. 13: 46-51 (1989). — MILLIKEN, G. A.: Analysis of covariance: multiple covariates. Proc. 14th Annual SAS Users Group Intern. Conf., April 1989, San Francisco, Cali. pp. 51-60 (1989). — NAMKOONG, G.: Breeding for variable environments. Forest Industry Lecture Series, No. 6. For. Prog. The University of Alberta. 12 p. (1980). — OWINO, F.: Genotype X environment interaction and genotypic stability in loblolly pine. II. Genotypic stability comparisons. Silvae Genet. 26: 21-26 (1977). — SHELBOURNE, C. J.: Genotype-environment interaction: its study and its implications in forest tree improvement. New Zealand For. Ser. Rep., No. 683, 27 pp. (1972). — SHUKLA, G. K.: Some statistical aspects of partitioning genotype-environmental components of variability. Heredity 29: 237-245 (1972). — STONECYPHER, R. W., PIESCH, R. F., HELLAND, G. G., CHAPMAN, J. G. and RENO, H. J.: Results from genetic tests of selected parents of Douglas-Fir (*Pseudotsuga menziesii* [MIRB.] FRANCL) in an applied tree improvement program. For. Sci. Mongr. 32: 35 (1996). — VAN BULJTENEN, J. P.: Response of "Lost Pines" seed sources to site quality. Proc. Fifth N. Am. For. Bio. Workshop. Gainesville, Fla. pp. 228-234 (1978). — WELLS, O. O.: Southwide pine seed source study-loblolly pine at 25 years. South. J. Appl. For. 7(2): 63-70 (1983). — WELLS, O. O. and WAKELEY, P. C.: Geographic variation in survival, growth, and fusiform rust infection of planted loblolly pine. For. Sci. Monogram 11: 40 (1966). — YATES, F. and COCHRAN, W. G.: The analysis of groups of experiments. J. Agric. Sci. 28: 556-580 (1938). — YEISER, J. L.: Genotype by environment interaction in loblolly pine (*Pinus taeda* L.). Ph. D. Dissertation, Texas A & M University. 80 pp. (1980).