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Genotype × Environment Interactions and Seed Movements for Loblolly Pine in the Western Gulf Region*)

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Summary

Fifteen plantations were established throughout the western gulf region to analyze genotype by environment (GXE) interactions in loblolly pine. Open pollinated families from five selected trees plus a checklot from each of four seed zones were planted at each location. The seed zones tested were southeastern Texas, southern Louisiana, northern Louisiana and southern Arkansas.

Significant heterogeneity effects indicated that the GXE interaction for height and volume could be reduced by stratifying environments. Regression estimates of slope and standard deviation indicated southeastern Texas and northern Louisiana sources were intermediate in stability. Southern Arkansas and southern Louisiana families were equally unstable. Southern Louisiana families were most responsive and southern Arkansas families least responsive to improved site quality. Ecovalences and coefficients of genetic prediction suggested that southern Louisiana families may be well adapted to high site index areas in northern Mississippi, but the same sources should not be moved more than 125 miles northwest to Southeastern Texas. Results also showed that southern Arkansas sources could be moved to northeastern Texas.

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

Zusammenfassung

Es wurden fünfzehn Versuche mit *Pinus taeda* L. in der westlichen Golfregion angelegt, um die Genotyp-Umwelt-Interaktion zu analysieren. Frei abgeblühte Familien von fünf selektierten Bäumen sowie einer Kontrolle aus je vier Samenzonen wurden in allen Versuchen angepflanzt. Geprüft wurden die folgenden Samenzonen: Südost-Texas, Süd-Louisiana, Nord-Louisiana und Süd-Arkansas.

Signifikante Heterogenitätseffekte zeigten, daß die Genotyp × Umwelt-Interaktion für Höhe und Volumen vermindert werden kann, indem man eine Abstufung von Standort zu Standort vornimmt. Regressionsschätzungen von Gefälle und Standardabweichung zeigen, daß die Herkünfte Südost-Texas und Nord-Louisiana von mittlerer Stabilität sind, Familien aus Süd-Arkansas und Süd-Louisiana waren ähnlich unstabil. Familien aus Süd-Louisiana waren mehr an bessere Standorte angepaßt als Familien aus Süd-Arkansas. Ökovalenzen und Koeffizienten zur genetischen Vorhersage machten deutlich, daß Familien aus Süd-Louisiana wahrscheinlich gut an fruchtbare Böden in Nord-Mississippi angepaßt sind, aber dieselbe Herkunft sollte nicht weiter als 125 Meilen nordwestlich von Südost-Texas angepflanzt werden. Die Ergebnisse zeigen auch, daß Familien aus Süd-Arkansas mit gutem Erfolg in Nord-Texas angebaut werden können.

Introduction

Realization of the genetic potential of superior seed depends on its use on appropriate sites. Since state, federal, and industrial land holdings within the southern United States frequently span long distances and a variety of sites, guidelines governing seed movements are needed. Assessing plant stability and genotype by environment (G × E) interaction is the first step in developing a sound seed movement policy. This paper is a report of a study to determine:

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

2) The stability of selected families of loblolly pine indigenous to the WGFTIP region.

Literature Review

Genotype by environment interaction may be defined as the inconsistent relative performance of two or more genotypes over two or more environments. A regression technique assessing G × E interaction and thus plant stability was introduced by YATES and COCHRAN (1938), popularized by FINLAY and WILKINSON (1963), and modified by EBERHART and RUSSELL (1966) and FREEMAN and PERKINS (1971). This technique produces estimates of slope (b_1) and deviations from regression (s^2), which may be jointly interpreted to explain G × E interaction. A family with $b_1 > 1$ responds to improvements in site quality. As s^2 becomes smaller, family performance becomes more predictable. Stable families have estimates of slope near one and deviations from regression near zero.

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

Both Wricke's ecovalence and the regression estimates for slope and variance have been used as practical indicators of plant stability. In a study of geographic seed sources, VAN BUIJTENEN (1978) used estimates of slope and

*) This study was completed in partial fulfillment of the requirements of a Ph. D. degree at Texas A&M University, 1980.

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standard deviation to characterize stability. 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. Owino (1977) reported nonsignificant differences in the stability of wide and local crosses of family sets of loblolly pine for height. When he contrasted regression coefficients with ecovalences the latter showed greater variation. Owino suggested ecocalences may be more discriminating as indicators of stability. However, in a study of jack pine (*Pinus banksiana* Lamb.), Morgenstern and Teich (1969) found close agreement between ecovalences and regression estimates of slope and variance.

By regarding a character in two different environments as two different traits, Baradat's (1976) coefficient of genetic prediction (CGP) also may be used to study G × E interaction. In this case, $COV_{A_1A_2}$ represents the additive genetic covariance at locations one and two and $\sigma_{P_1} \cdot \sigma_{P_2}$ is the product of phenotypic standard deviations at locations one and two. Correlations between genotypic means in all possible environmental combinations result in a matrix of values which can be used to separate environments into similar groups.

Materials

A geographic seed source study was initiated by the WGFTIP to determine, in part, where and how far superior families and geographic sources could be moved without affecting their superiority. The WGFTIP region was divided into eight zones (*Fig. 1*). Five open-pollinated families from selected trees from seven of the eight zones were planted in each of the eight zones. The design was four-tree row plots in six randomized blocks. The study was separated into two series each replicated over two consecutive years. The first-year planting of the first series provided the data for this report. Geographic seed zones for this series were southeastern Texas (SE TX), southern Louisiana (S LA), northern Louisiana (N LA), and southern Arkansas (S AR).

Trees in 15 test plantings were measured at age 5 for total height to the nearest 0.1 meter, diameter at breast height to the nearest 0.1 centimeter and total volume in cubic decimeters per planted tree.

Methods

An analysis of covariance was conducted on family means according to the technique of Freeman and Perkins (1971). The statistical model used was:

$$Y_{ij} = \mu + L_i + F_j + E_{ij}$$

where μ 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 × E interactions. For determination of how far and where a source could be moved and maintain its superiority, a directional response and sum of squares contribution to G × E interaction was determined for each family

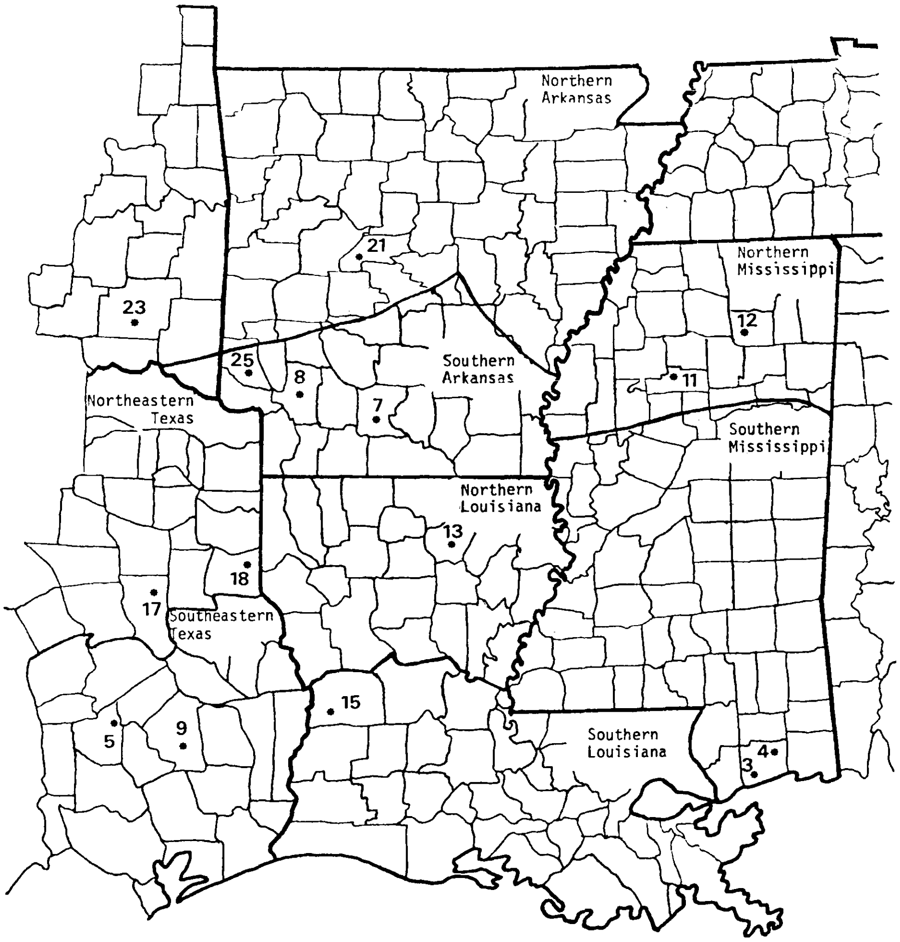

Figure 1. — The Western Gulf Forest Tree Improvement region, eight geographic seed zones and fifteen test locations (●).

Table 1. — Mean squares from analyses of covariance for height, diameter, and volume. The location mean is used as an index of site quality and is the covariate.

Sources of Variation	Degrees of Freedom	Mean Squares		
		Height	Diameter	Volume
Family x Location interaction	257	0.05	0.23	1.53
Heterogeneity of regressions	19	0.11**	0.33	6.99**
Residual	238	0.04	0.23	1.09
Total	290			

**Significant at α = 0.01.

Table 2. — Regression of family mean height on the location mean height. A separate regression is presented for the most and least stable family within each zone.

Zone	Family	Mean	Slope	Standard Deviation
SE TX	S3PT8	3.92	0.95	0.18
SE TX	K-79	4.10	0.96	0.22
N LA	KS-309	3.89	0.96	0.13
N LA	UR-2	3.69	1.08	0.22
S LA	B-5-7	4.43	1.24	0.18
S LA	B-1-4	4.30	0.98	0.14
S AR	WHAPT-3	3.67	0.84	0.28
S AR	DF-3252	3.72	0.94	0.14

Table 3. — Regression of family mean volume on location mean volume. A separate regression is presented for the most and least stable family within each zone.

Zone	Family	Mean	Slope	Standard Deviation
SE TX	S3PT8	4.13	1.01	0.84
SE TX	C17A	3.79	0.79	1.19
N LA	H-29	3.28	0.68	0.75
N LA	SH-11	3.89	0.98	0.64
S LA	B-5-7	5.23	1.49	0.96
S LA	B-1-4	4.97	1.19	0.79
S AR	WHAPT-3	3.21	0.52	1.11
S AR	DF-3252	3.41	0.70	0.78

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

Test plantings were eliminated according to their distance from the source and the ecovalence 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. Baradat's (1976) coefficient of genetic prediction was used to identify regions with similar family performances.

Results and Discussion

The heterogeneity of regressions was a significant source of variation for height and volume (*Table 1*). This indicates large differences exist among the slopes of regression lines characterizing family performance. Thus G × E interaction can be reduced by stratifying environments. Separate regressions for families whose stabilities are particularly noteworthy are presented in *tables 2* (height) and *3* (volume). For both variables, family B-5-7 (southern Louisiana) exhibited a large standard deviation and slope suggesting that it is well adapted to above average sites. The other extreme was represented by WHAPT-3 (southern Arkansas) which demonstrated low responsiveness to site quality B-1-4 (southern Louisiana) may be a desirable intermediate. It had a slope near one, deviated little from the regression line and had a large mean. B-1-4 was considered the most stable and WHAPT-3 and B-5-7 the least stable families.

Families were grouped according to zone and characterized for stability (*Table 4, Fig. 2*). Northern Louisiana sources were slightly more stable in height than southeastern Texas sources. Southern Arkansas sources showed less stability than southern Louisiana sources. Volume data indicated northern Louisiana families were less stable than southeastern Texas families. Both variables showed southern Louisiana and southern Arkansas sources opposite in responsiveness to site quality. Southern Louisiana sources were most responsive to improved site quality while southern Arkansas families were least responsive.

Ecovalences and directional responses were calculated for height, diameter, and volume and interpreted for seed-movement recommendations. Similar trends were observed for all three variables, but only the trend for height is presented. Southern Louisiana sources grew slower than expected when planted in Arkansas, northeastern Texas and northern Louisiana (*Table 5*). Based on these results,

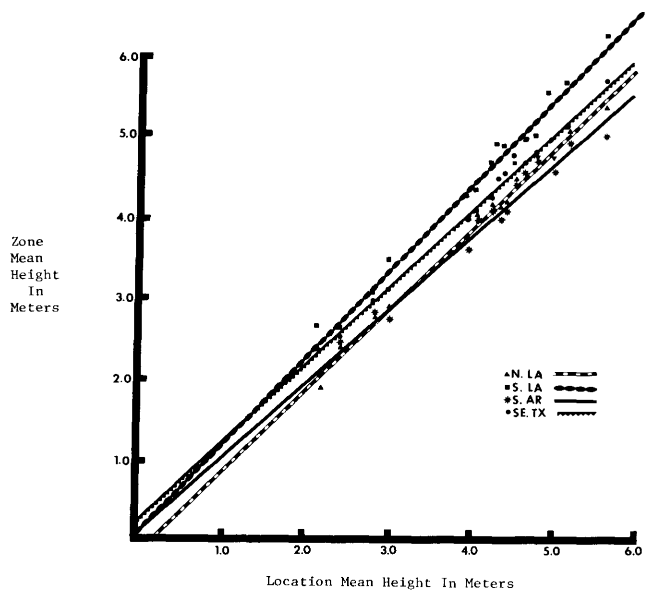

Figure 2. — Regression lines for zones within the WGFTIP region.

Table 4. — Regression of height and volume zone means on location means. A regression for each seed zone provides estimates of the mean ($\bar{y}$), slope (b_1), and standard deviation (s).

Zone	Height M			Volume DM^3 Per Planted Tree		
	$\bar{y}$	b_1	s	$\bar{y}$	b_1	s
SE TX	4.02	0.98	0.23	3.89	0.96	0.94
N LA	3.81	1.00	0.20	3.71	0.87	0.90
S LA	4.38	1.07	0.20	5.06	1.37	0.97
S AR	3.77	0.91	0.21	3.55	0.72	1.04

Table 5. — The height location by family sums of squares and directional response for southern Louisiana seed sources planted in Arkansas, northeastern Texas, Mississippi, and Louisiana.

Family	Location (Location Number)												
	N AR (23)	N AR (21)	S AR (25)	S AR (8)	S AR (7)	NE TX (17)	NE TX (18)	N LA (13)	S MS (3)	S MS (4)	N MS (11)	N MS (12)	S LA (15)
B-2-7	.00 −	.07 −	.06 −	.01 +	.10 −	.04 +	.07 −	.03 −	.01 +	.03 +	.02 +	.04 −	.13 +
B-5-4	.01 −	.02 +	.00 −	.01 −	.04 −	.00 −	.04 −	.01 −	.01 +	.02 −	.00 +	.04 +	.09 +
B-5-3	.03 −	.05 −	.00 −	.03 −	.00 −	.01 −	.31 −	.02 +	.13 +	.03 −	.10 +	.00 +	.04 +
B-5-7	.01 −	.02 −	.15 −	.02 +	.16 −	.00 −	.01 −	.01 −	.23 −	.01 +	.20 +	.11 +	.11 +
B-1-4	.01 −	.08 −	.00 −	.04 +	.02 −	.02 +	.00 −	.00 +	.01 +	.00 +	.03 +	.00 +	.00 +

Table 6. — Location means in ascending order for height in meters.

Location	Height
3	2.14
7	2.39
25	2.74
4	2.97
13	3.94
23	4.01
8	4.17
15	4.22
5	4.27
18	4.37
17	4.49
21	4.63
11	4.78
12	5.03
9	5.60

Table 7. — Coefficients of genetic prediction for height illustrating the correlation among northern and southern plantings and among northeastern Texas and Arkansas plantings.

Location (Location Number)	N LA (13)	S LA (15)	NE TX (17)	N AR (21)	N AR (23)
S MS (4)	.67	.79	.73	.62	.81
N LA (13)		.89	.77	.57	.82
S LA (15)			.85	.72	.84
NE TX (17)				.72	.78
N AR (21)					.80

the north-northwestward movement of southern Louisiana sources should not exceed Cherokee County, TX (location 17), at 32° north latitude and a distance of approximately 125 miles. Directional responses were not favorable for southern Louisiana families planted in southern Mississippi. This was probably due to low site quality and the inadaptability of southern Louisiana sources to poor sites *(Table 6)*. Positive directional responses were recorded for southern Louisiana families planted in northern Mississippi and in southern Lousiana. Both northern Mississippi plantings were on highly productive sites. Thus, the observed performance may be restricted to locations above average in site quality.

Southern Arkansas families recorded positive directional responses in northeastern Texas, southern Mississippi, and Arkansas. This probably resulted from the adaptability of southern Arkansas sources to poor and dry sites. Southeastern Texas and northern Louisiana families showed no regional preference.

Table 8. — Coefficients of genetic prediction for height illustrating the correlation among northern Mississippi plantings and southeastern Texas and southern Louisiana tests.

Location (Location Number)	SE TX (9)	N MS (11)	N MS (12)	S LA (15)
SE TX (5)	.81	.81	.76	.82
SE TX (9)		.78	.71	.86
N MS (11)			.86	.68
N MS (12)				.60

Coefficients of genetic prediction were computed for height, diameter and volume to identify outlying or similar environments. Four similar trends were observed for all three variables, but only the trend for height is presented.

First, large CGP's occurred among several northern and southern plantings *(Table 7)*. Since highly correlated plantings were on sites of intermediate quality, we concluded that the test material performed consistently among zones and that no special adaptability was required for the range of conditions present at these sites.

Second, high correlations existed among Arkansas and northeastern Texas plantings *(Table 7)*. Southern Arkansas sources, being well adapted to dry sites, were also well suited for the sandy test planting in northeastern Texas. This trend was noted in ecovalences. Third, southeastern Texas and southern Louisiana tests were highly correlated with northern Mississippi plantings *(Table 8)*. This may be due to similarities in site quality. Northern Mississippi plantings averaged approximately 5 meters for height. Southern Louisiana and southeastern Texas plantings averaged approximately 4.25 and 5.6 meters respectively. Ecovalences provided this trend for southern Louisiana families only. Fourth, family rankings at southern plantings were highly related as were family performances among northern plantings.

Acknowledgement

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Short Note: Studies on Antigenic Proteins of Pinus sylvestris from Six Swedish Provenances –A Pilot Study

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Abstract

Six populations of *Pinus sylvestris* (L.) from latitude 56—67° were analysed by the immunodiffusion technique. The samples (20—22) from each population were collected in a provenance trial belonging to the Institute for Forest Improvement at latitude 64°. The main results were as follows:

* One fraction of antigens (3) is twice as frequent in the northern samples (0.90) as in the southern ones (0.43)
* The range of variation within each group of samples is less than 10% of each mean value
* The sample from central Sweden takes an intermediate position (0.73)
* The latter sample also shows the highest level of polymorphism
* These results give a slight support to the hypothesis that there are two varieties of *Pinus sylvestris* in Sweden

Key words: Pinus sylvestris, provenances, antigenic proteins, serological methods.

Zusammenfassung

Sechs Populationen von *Pinus sylvestris* L. aus 56—67° geographischer Breite wurden mittels Immundiffusionstechnik untersucht. 20—22 Proben von jeder Population wurden in einem Provenienzversuch, der zum Institute for Forest Improvement auf 64° geographischer Breite gehört, gesammelt. Die Hauptresultate waren wie folgt:

— Eine Fraktion von Antigenen (3) ist in den nördlichen Proben zweimal so häufig (0,90) wie in den südlichen (0,43).

— Der Umfang der Variation in jeder der Probengruppen beträgt weniger als 10% des Mittelwertes.

— Die Probe von Zentralschweden nimmt eine mittlere Position ein (0,73).

— Die letzte Probe zeigt den höchsten Grad an Polymorphismus.

— Diese Resultate unterstützen die Hypothese, daß es in Schweden zwei Varietäten von *Pinus sylvestris* gibt.

Introduction

Pinus sylvestris is considered to have invaded Sweden from both the north and the south (KIELLANDER 1974). The migration streams seem to have met in central Sweden between the latitudes 60°—61°. In this region, a large and well-known variation in morphological characteristics can be found such as crown shape. Certain forest scientists consider Sweden to have two originally and morphologically different varieties of *Pinus sylvestris* (SYLVEN 1916, KIELLANDER 1974). The northern Swedish variety with a narrow and finebranched crown is called var. *lapponica*, while the southern Swedish broadcrowned variety is called var. *septentrionalis*. Other forest scientists such as SCOTT (1907) and LANGLET (1936) considered Sweden to have a single stepwise clinal variation of *Pinus sylvestris* from the south to the north of Sweden without any zone of introgression showing increased varibility of any kind.

Isozyme studies give som indications of an introgression zone between lat. 61°—61° (RUDIN unpubl.) by showing a higher proportion of heterozygotes. The serological methods and their great sensitivities open up further possibilities of casting some light on the two opposing hypotheses.

Serological techniques in plant protein investigations have been mostly used in chemotaxonomy for detecting the differences between species (for review see SMITH 1976). However, the serological differences have been detected not only at the level of different species, but also between populations of the same species as reported by LEE and FAIRBROTHERS (1969), CLARKSON and FAIRBROTHERS (1970) in *Typha* and in *Abies balsamea* var. *balsamea* and *A. fraseri*.

Investigations by HAGMAN (1977) and other authors, including PRUS-GLOWACKI and SZWEYKOWSKI (1979) (1980), additionally demonstrated the serological differences between individuals of the same species. This great sensitivity of serological methods, offers us the possibility of studying the variability of antigenic proteins at the level of single trees in some Swedish populations of *Pinus sylvestris*, and to cast some light on the two hypotheses referred to above.

Materials and Methods

Proteins from needles of 20 to 22 eight-year-old plants from each of six Swedish provenances *(Table 1)* were studied by means of immunodiffusion. Extraction of proteins from the needles, immunodiffusion procedures and interpretation of results were done as described in previous papers, (PRUS-GLOWACKI and SZYEYKOWSKI 1979, PRUS-GLOWACKI and SZWEYKOWSKI 1980). Antisera for immunodiffusion analysis was produced against needle proteins from 30 pine