

Figure 1. — Illustration of IDH banding patterns in four megagametophytes from a shortleaf pine tree, a hybrid pine tree and a loblolly pine tree.

pooled results from all of the known hybrid seed lots produced an exact 50:50 ratio of parental bands. The 8 putative hybrid trees from the littleleaf infected shortleaf stand were classified by this technique as 6 loblolly-shortleaf hybrid trees, 1 loblolly pine tree and 1 shortleaf pine tree.

Processing single seed samples allowed for only 30 seeds per gel slab and limited us to testing only 3 trees per gel. Large testing programs would require a great many gels using this procedure which may result in a prohibitively high cost in terms of time or money. If a simple, single-banded, monomeric enzyme system, such as IDH, is being used it may be feasible to pool all ten megagametophytes from a single test tree and to use the pooled material as a single tissue sample. This pooling should result in a single-banded sample if the tree is homozygous for either parental band and a double-banded sample if the tree is a hybrid. The ratio of the two parental isoenzyme types in the ten seed sample will determine the relative darkness of the two bands on the gel. We tested this pooling technique on seeds from our known hybrid trees with complete success. All of the tested known hybrid trees produced two distinguishable bands. We then tested different mixtures of the two parent species megagametophytes to determine if both isoenzyme types would still be identifiable when the parent ratio was as high as 9:1. We found IDH activity to be sufficiently strong in the two tested pine species to produce both band types even when the ratios were skewed to this maximum point for a ten seed sample.

Electrophoretic assaying of IDH isoenzymes should be highly accurate for identifying first generation loblolly-shortleaf hybrid trees. However, identification of hybrid trees of more advanced generations may not be as reliable. It is reasonable to assume that natural back-crossing will occur between the first generation hybrids and one of the two parent species. Mendel's principle of segregation would allow for only one half of the progeny to contain both of the IDH bands if the segregation is unrestricted. Likewise, progeny produced as a result of crossing between two

first generation hybrid trees should be 50% heterozygous and 25% homozygous for each of the two parent types. Deviations from these expected segregation ratios is possible if the IDH gene is linked with a trait that increase the probability of individual tree survival in areas where either fusiform rust disease or littleleaf disease is a problem.

When this test is applied to new situations, a large portion of the local parental populations of both species should be tested for IDH homozygosity to minimize the probability of missing a low frequency IDH allele which may cause misclassification problems of both parent trees and hybrids. The possibility of misclassification must be considered even if no low frequency alleles are found. The probability of such a misclassification will undoubtedly be small, but nonetheless must be taken into account when trees are assigned a "hybrid" designation. Use of this test in conjunction with other forms of hybrid identification such as index calculations should increase the accuracy and reliability of the testing program.

Conclusion

An accurate and precise system for differentiating between first generation loblolly-shortleaf hybrids and the two parent species can be developed with simple starch gel electrophoresis. Trees in the South Carolina and Georgia portions of the two parent species ranges were distinguishable by differing IDH bands when either ten single seed samples or a single ten seed pooled sample was used. Use of this type of biochemical system eliminates many of the problems inherent in a taxonomic classification based on quantitative, morphological traits such as needle length or cone size that are subject to environmental modification.

Literature Cited

- BERGMANN, V. F. and RUETZ, W.: Short Note: Identifizierung von Hybridlärchensaatzgut aus Samenplantagen mit Hilfe eines Isoenzym-Markers. *Silvae Genetica* 36 (2): 102–105 (1987). — CONKLE, M. T., HODGKISS, P. D., NUNNALLY, L. B. and HUNTER, S. C.: Starch gel electrophoresis of conifer seeds: a laboratory manual. U.S.D.A., Forest Service Gen. Tech. Rep. PSW-64 18 pp. (1982). — FLORENCE, L. Z.: Prospects for using loblolly × shortleaf hybrids for resistance to fusiform rust. 12th South. For. Tree Imp. Proc. 1973: 302–309 (1973). — HARE, R. C. and SWITZER, G. L.: Introgression with shortleaf pine may explain rust resistance in western loblolly pine. U.S.D.A. Forest Service, Res. Note SO-88, 2 pp. South. For. Exp. Sta., New Orleans, La (1969). — HENRY, B. W. and BERCAW, T. E.: Shortleaf-loblolly hybrid pines free of fusiform rust after 5 year's exposure. *J. of Forestry* 54: 779 (1956). — LITTLE, E. L., JR., and RIGHTER, F. I.: Botanical descriptions of forty artificial pine hybrids. U.S.D.A., Tech. Bull. 1345, 45 pp. (1965). — SCHOFNIKE, R. E.: Professor of Forestry. Clemson University, Clemson, S.C.. — ZOBEL, B. J.: Are there natural loblolly-shortleaf pine hybrids? *J. of Forestry* 51: 494–495 (1953).

Stability of Loblolly Pine Families in the Southeastern U. S.

By B. LI and S. E. McKEAND¹⁾

(Received 1st February 1988)

¹⁾ Research Associate and Associate Professor, Cooperative Tree Improvement Program, Department of Forestry, Box 8002, North Carolina State University, Raleigh, NC 27695-8002, USA. Paper number 11360 of the Journal Series of the North Carolina Agricultural Research Service. Research supported by the North Carolina State University-Industry Cooperative Tree Improvement Program.

Abstract

The response of 43 open-pollinated loblolly pine (*Pinus taeda* L.) families from different first-generation seed orchards in the southeastern U. S. were evaluated for 8-year height, DBH, volume and percent fusiform rust (*Cronartium quercuum* (BERK.) MIYABE ex SHIRAI f. sp. *fusiforme*)

infection at 21 test locations in coastal Georgia, Florida, Alabama, and Mississippi. Analyses of variance indicated highly significant ($p < 0.01$) genotype \times environment ($G \times E$) interaction and heterogeneity of regressions among families. However, regression stability analyses identified only a few interacting families which had regression coefficients significantly different from the expected value of one. Linear regressions of family mean performance at each test on an environmental index (mean of all families in each test) showed the general stability and adaptability of most selected loblolly pine families over test environments. Most selected families had better mean performance and greater response to favorable sites than unimproved check seedlots over test sites. The few families which were responsive and high yielding on different test sites could be used to maximize forest productivity and to obtain the best use of genetically improved stock under different environmental conditions.

Key words: Adaptability, environmental index, $G \times E$ Interaction, *Pinus taeda* L..

Introduction

Tree breeders' concern with genotype \times environment ($G \times E$) interaction has led to a greater interest in studies of genotypic stability across various environments. However, most stability studies in forestry have been done with only a few genotypes or seed sources, and those materials have been tested over a limited range of locations. MORGENSTERN and TEICH (1969) identified different stabilities in 12-year height growth among different Jack pine (*Pinus banksiana* LAMB.) provenances. GODDARD (1977) reported that the stability parameters (regression coefficients) of four open-pollinated slash pine (*Pinus elliottii* ENGELM.) families were significantly different from a value of one. Differences in stability were not found among groups of loblolly pine families by OWINO (1977). Regression estimates of slope and standard deviation by YEISER *et al.* (1981) indicated different stabilities among four loblolly pine seed sources in plantations of the Western Gulf region. Based on the adaptability and stability parameters in both height and rust resistance of loblolly pine families in Georgia, LA FARGE and KRAUS (1981) suggested that the best families are those that maintain a stable superiority in growth rate and resistance to fusiform rust over wide ranges of site quality and rust hazard. BARNES *et al.* (1984) compared four methods of evaluating $G \times E$ interaction for maximum wood density of *Pinus caribaea* MORELET and found the regression analysis had the potential for predicting genotypic performance on untested sites.

Traditional analysis of variance is a useful way to provide information on $G \times E$ interaction, but it does not identify interacting genotypes nor give any measure of stability in the dynamic response of genotypes to different environments. Expressing the performance of a genotype as a linear function of an environmental index (YATES and COCHRAN, 1938; FINLAY and WILKINSON, 1963; EBERHART and RUSSELL, 1966; PERKINS and JINKS, 1968 a, b) has considerable value for interpretation of interaction because it usually accounts for a substantial part of the $G \times E$ interaction variance (FREEMAN and PERKINS, 1971).

As tree improvement programs become more intense in the southeastern U. S., and more improved loblolly pine seeds are produced from seed orchards, the adaptability and stability of selected families to a wide range of environmental conditions must be determined. A better understanding of genotypic stability and adaptability of many

selected families over various locations will increase genetic gains by allowing breeders to optimally deploy families to sites. This paper reports the stability of 43 open-pollinated loblolly pine families in 21 test locations in coastal Georgia, Florida, Alabama and Mississippi.

Materials and Methods

A series of tests was established throughout the southeastern U. S. from 1975 to 1978 by using open-pollinated seeds from first-generation clones in the N. C. State University Tree Improvement Cooperative. One to six open-pollinated families from each of 14 cooperators (Table 1) were selected for use in the tests primarily based on their superior growth performance in each cooperator's progeny tests. A total of 43 families were used in the study. No attempt was made to put all families in each test. Unimproved local seedlots were also included in each test as checks. The checks were not from the same seedlot in each test.

The experimental design for each test was a randomized complete block with six replications of 10-tree plots of 30 to 50 seedlots. Stem height, diameter at breast height (DBH), and the presence or absence of fusiform rust were measured at eight years of age for each tree. Volume was estimated using the formula of GOEBEL and WARNER (1966) and was converted from cubic feet to cubic decimeters. Arithmetic means for each seedlot (family and check) were calculated for each trait within and across tests. A mean for all seedlots in a test was also calculated for each trait and is considered as the measure of site quality or environmental index for each trait. These test means included seedlots which were not included in the stability analyses.

There were 21 tests from coastal Georgia, Florida, Alabama, and Mississippi in the same latitudinal area (Figure 1) which were used in the analyses. The stability of 43 families plus the check seedlots that were tested in at least six locations was evaluated.

An analysis of variance was conducted on family plot means by using the method of FREEMAN and PERKINS (1971). FINLAY and WILKINSON's (1963) concept of regression coefficient and family performance for traits was used for estimating stability and adaptability. Family means from each test were regressed on the mean performance of all genotypes at each location (environmental index).

Regression coefficient (b) and the seedlot means were presented in Figure 2 as a generalized method of interpretation for analyzing the stability and adaptability of the families. The position of a particular genotype on the plot indicates the type of stability and performance over test sites. Genotypes with $b = 1.0$ have an average stability since their response to environments is parallel to the mean response of all genotypes in the tests. Genotypes with a high mean performance are well adapted to all environments. Genotypes with $b > 1.0$ have low stability but are responsive to improved environmental conditions. Genotypes with $b < 1.0$ have high stability and are not sensitive to changes in environmental conditions. The ideal genotype is the one with maximum yield potential in all environments (high mean performance), and maximum stability ($b = 0.0$).

Results and Discussion

The effects of test location by family interaction for height, DBH, volume and percent rust-free trees were highly significant at the 1% level (Table 3). Significant

Table 1. — Family means for height and DBH, number of tests, regression coefficients (b) and standard errors (in parentheses), and the coefficients of determination (R²) for the regression models.

Family	Origin ¹	# Tests	Height (m)			DBH (cm)		
			Mean	b _i	R ²	Mean	b _i	R ²
01014	P,GA	8	7.82	1.01 (0.085)	0.95	11.22	1.03 (0.070)	0.96
01064	P,GA	12	6.52	0.93 (0.098)	0.85	9.75	0.92 (0.130)	0.81
01523	P,SC	7	8.09	1.01 (0.112)	0.92	12.50	1.10 (0.179)	0.84
02008	C,VA	8	8.11	0.92 (0.091)	0.92	11.93	0.93 (0.067)	0.96
02040	C,VA	19	6.79	0.95 (0.081)	0.88	10.30	0.96 (0.095)	0.84
03007	P,SC	13	7.64	1.00 (0.073)	0.94	11.77	1.00 (0.076)	0.93
03036	P,SC	14	7.09	1.05 (0.039)	0.98	10.95	1.01 (0.065)	0.95
04006	C,VA	9	7.77	0.91 (0.091)	0.92	12.06	1.11 (0.089)	0.94
04018	C,VA	19	7.25	1.02 (0.069)	0.92	11.11	1.03 (0.068)	0.93
05005	C,GA	10	7.79	1.08 (0.109)	0.91	12.31	1.11 (0.107)	0.91
06009	P,NC	11	7.82	0.83* (0.069)	0.93	11.64	0.97 (0.072)	0.94
06020	P,NC	19	7.51	1.03 (0.059)	0.94	11.00	1.02 (0.050)	0.96
06022	C,NC	8	7.66	0.78* (0.088)	0.91	11.33	0.77 (0.119)	0.84
07002	C,SC	8	7.82	1.22 (0.127)	0.92	11.81	1.18 (0.155)	0.88
07034	C,SC	11	8.54	0.94 (0.133)	0.82	12.76	0.92 (0.159)	0.75
07056	C,SC	19	8.30	1.14 (0.070)	0.93	12.37	1.12 (0.086)	0.90
08001	C,NC	20	7.59	1.07 (0.085)	0.94	11.25	1.10 (0.057)	0.95
08059	C,NC	20	7.51	1.10 (0.055)	0.95	11.50	0.98 (0.068)	0.91
08061	C,NC	20	7.70	1.12* (0.042)	0.97	11.72	1.08 (0.051)	0.96
08068	C,NC	21	7.38	1.03 (0.048)	0.96	11.18	1.01 (0.070)	0.91
08076	C,NC	16	7.75	1.10 (0.064)	0.95	12.49	1.05 (0.073)	0.93
08102	C,NC	7	7.26	0.96 (0.039)	0.99	11.46	0.97 (0.093)	0.94
08509	C,AL	10	7.41	0.99 (0.094)	0.92	11.12	0.83 (0.106)	0.86
09017	P,NC	11	7.88	1.08 (0.073)	0.95	12.20	0.94 (0.102)	0.88
10002	C,GA	7	7.13	0.86 (0.164)	0.80	12.33	0.92 (0.163)	0.82
10005	C,GA	13	7.97	1.09 (0.066)	0.95	12.29	1.09 (0.061)	0.96
10006	C,GA	8	7.62	1.07 (0.116)	0.91	12.20	0.96 (0.108)	0.91
10010	C,GA	7	7.61	0.89 (0.172)	0.78	12.05	1.00 (0.193)	0.79
10014	C,GA	14	7.57	1.11 (0.096)	0.90	11.50	1.00 (0.100)	0.88
10046	C,GA	6	7.88	1.01 (0.107)	0.94	11.51	0.95 (0.106)	0.93
11009	C,SC	10	7.95	1.20* (0.077)	0.96	12.30	1.06 (0.116)	0.89
11010	C,SC	8	8.29	0.91 (0.078)	0.94	12.64	0.97 (0.118)	0.89
11016	C,SC	14	7.66	1.16 (0.085)	0.93	11.44	1.10 (0.100)	0.90
11061	C,SC	7	7.32	1.22 (0.150)	0.90	11.56	1.11 (0.113)	0.93
15042	P,GA	16	7.41	1.19* (0.079)	0.93	11.04	1.14 (0.085)	0.92
17004	C,AL	9	7.71	1.00 (0.089)	0.93	12.41	1.02 (0.103)	0.92
17005	C,AL	7	7.80	1.03 (0.095)	0.94	12.03	1.04 (0.053)	0.98
17016	C,AL	20	7.02	1.06 (0.074)	0.91	10.74	1.00 (0.068)	0.92
17019	C,AL	6	7.79	1.15 (0.144)	0.91	12.55	1.08 (0.144)	0.90
17037	C,AL	11	7.41	1.06 (0.139)	0.84	11.17	1.08 (0.132)	0.86
19016	C,AL	8	6.75	0.98 (0.157)	0.82	10.46	0.93 (0.158)	0.81
19017	C,AL	7	7.66	1.20 (0.128)	0.93	11.70	1.01 (0.127)	0.90
19024	C,AL	8	6.77	0.99 (0.100)	0.92	10.51	0.99 (0.109)	0.91
Check Seedlots		21	7.35	0.80 (0.136)	0.70	11.35	0.81 (0.163)	0.61
Overall Mean			7.60			11.63		

¹) Origin: Province (P = Piedmont, C = Coastal Plain), State.
 *) Significantly different from 1 at the 5% and 1% level, respectively.

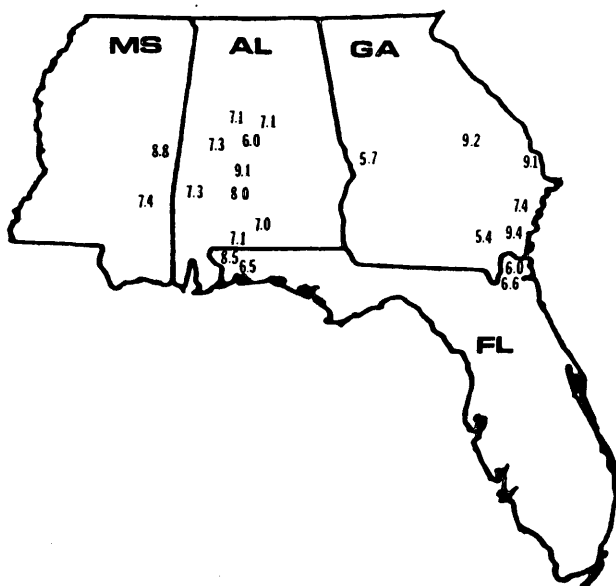


Figure 1. — Test locations in the study. Numbers indicate the mean height (m) at age eight years.

linear regression effects partitioned from the interaction sums of squares suggested that the $G \times E$ interaction was partially due to the heterogeneity of family response over various environments. Also, a small but significant portion of the $G \times E$ interaction was nonlinear.

The stability of a genotype across a range of environments has been measured by its among-environment variance (PLAISTED, 1960; SHUKLA, 1972), the regression of its mean to an environmental index (FINLAY and WILKINSON,

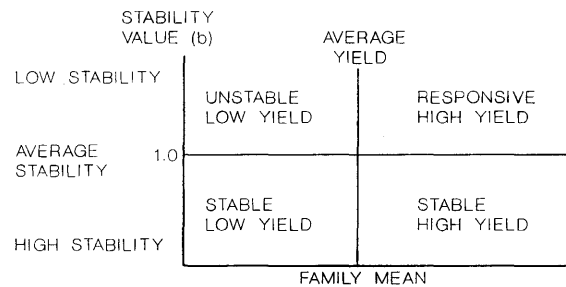


Figure 2. — A generalized interpretation of stability and adaptability for all genotypes by plotting regression coefficients (b) and family means over all tests.

1963; PERKINS and JINKS, 1968a), the residual mean square from the regression (EBERHART and RUSSELL, 1966; TAI, 1971), or combinations of these three methods. LIN *et al.* (1986) examined nine stability statistics currently in use and concluded that the regression procedure is valid for providing information on the relative stability among genotypes included in the experiment if the regression model fits the data. The use of the mean of all genotypes as the environmental index for regression has been criticized since it is biased by the genotypes under consideration (FREEMAN and PERKINS, 1971; HARDWICK and WOOD, 1972). The assumption of linearity of response was also questioned by NAMKOONG (1978). However, if the number of genotypes and environments is reasonably large and the environmental range is sufficiently wide, the linear regression using the mean of all genotypes should be biologically valid (FRIPP and CATEN, 1971; FRIPP, 1972). In this study, the 21 test means represented 30 to 50 families per test, and the test means ranged from 5.4 m to 9.4 m for height and 13% to 73% infection level for rust. The number of families tested and the range in site quality and rust infection were judged to be large enough to justify using the regression method. The coefficient of determination (R^2) for the regression was used in this study to determine how well the linear model fit the data. Essentially, the R^2 measured the genotypic sta-

bility as the deviation mean square from the regression as proposed by EBERHART and RUSSELL (1966). A stable family is defined as one having $b = 1.0$ and $R^2 = 1.0$.

For each loblolly pine family, the mean, regression coefficient (b) and standard error, and the coefficient of determination (R^2) are shown for height and DBH in Table 1 and volume and percent rust-free trees in Table 2. All R^2 values are highly significant except for family 10002 for percent rust infection. The b statistic was interpreted as the genotypic response and was used as a relative measure of stability over test sites since such a large part of the total variation was accounted for by the regression. Values for the regression coefficients ranged from 0.78 to 1.22 for height, 0.77 to 1.18 for DBH, 0.72 to 1.41 for volume, and 0.59 to 1.52 for percent rust-free trees. Regression coefficients (b) were significantly different from 1.0 for relatively few families, for height (5 of 43), for volume (8 of 43) and for percent rust-free trees (6 of 43) (Tables 1 and 2). The average stability of these loblolly pine families in this region is demonstrated by the majority of selected families having regression coefficients (b) not significantly different from one. The significant $G \times E$ interaction sums of squares in the analyses of variance was contributed by only a few interacting families.

Table 2. — Family means for volume and percent rust-free trees, number of tests, estimated regression coefficients (b) and standard errors (in parentheses), and the coefficients of determination (R^2) for the regression models.

Family	# Tests	Volume (dm ³)			% of Rust-Free Trees				
		Mean	b_i	R^2	Mean	b_i	R^2		
01014	8	31.40	0.91	(0.074)	0.95	55	1.24	(0.126)	0.92
01054	12	21.33	0.56**	(0.091)	0.81	53	1.44*	(0.161)	0.87
01523	7	39.16	1.03	(0.142)	0.88	50	1.18	(0.184)	0.85
02008	8	35.19	0.96	(0.062)	0.97	68	1.00	(0.129)	0.88
02040	19	25.17	0.85	(0.075)	0.87	50	1.23	(0.136)	0.81
03007	13	34.01	0.98	(0.071)	0.94	75	0.82	(0.113)	0.80
03036	14	28.92	0.91	(0.048)	0.96	57	1.28*	(0.102)	0.92
04006	9	35.72	1.00	(0.073)	0.95	52	1.32	(0.150)	0.89
04018	19	29.96	0.95	(0.063)	0.93	56	1.23	(0.164)	0.75
05005	10	38.92	1.21	(0.116)	0.92	57	1.36	(0.250)	0.74
06009	11	34.75	0.88	(0.085)	0.91	40	1.32	(0.224)	0.75
06020	19	30.61	0.97	(0.429)	0.96	57	1.28	(0.137)	0.82
06022	8	31.61	0.72*	(0.092)	0.88	57	1.13	(0.252)	0.71
07002	8	38.29	1.41*	(0.149)	0.92	50	0.83	(0.243)	0.57
07034	11	44.39	1.11	(0.156)	0.82	65	1.13	(0.201)	0.74
07056	19	41.73	1.34*	(0.083)	0.93	64	0.99	(0.133)	0.74
08001	20	32.02	1.13*	(0.047)	0.97	63	1.06	(0.132)	0.76
08059	20	33.01	1.00	(0.057)	0.94	65	1.20	(0.137)	0.79
08061	20	34.82	1.15**	(0.045)	0.97	56	1.39**	(0.107)	0.89
08063	21	30.69	1.02	(0.053)	0.94	65	0.97	(0.108)	0.79
08076	16	39.43	1.13	(0.064)	0.95	63	1.22	(0.160)	0.78
08102	7	32.80	1.05	(0.084)	0.96	34	1.07	(0.248)	0.72
08509	10	29.34	0.80	(0.090)	0.88	57	1.41	(0.272)	0.72
09017	11	38.05	1.07	(0.080)	0.94	63	1.02	(0.085)	0.93
10002	7	36.24	0.98	(0.165)	0.83	65	0.38	(0.194)	0.30
10005	13	40.58	1.23*	(0.067)	0.96	67	0.59	(0.198)	0.46
10006	8	38.01	1.08	(0.100)	0.93	75	0.70*	(0.110)	0.83
10010	7	36.64	1.11	(0.204)	0.80	53	0.91	(0.317)	0.51
10014	14	34.40	1.12	(0.100)	0.90	40	0.85	(0.113)	0.80
10046	6	34.16	0.93	(0.095)	0.94	58	1.05	(0.297)	0.65
11009	10	39.31	1.24**	(0.093)	0.95	82	0.84	(0.177)	0.58
11010	8	42.39	1.15	(0.132)	0.90	81	0.73	(0.210)	0.57
11016	14	34.08	1.18	(0.088)	0.93	74	0.74	(0.192)	0.50
11051	7	34.44	1.23	(0.116)	0.94	59	1.08	(0.286)	0.41
15042	16	30.96	1.01	(0.071)	0.93	73	0.60	(0.107)	0.65
17004	9	37.49	0.98	(0.089)	0.93	56	1.52**	(0.135)	0.93
17005	7	36.68	1.03	(0.068)	0.97	72	1.18	(0.129)	0.92
17016	20	27.66	0.93	(0.055)	0.93	53	1.21*	(0.098)	0.88
17019	6	38.78	1.09	(0.127)	0.92	70	0.89	(0.315)	0.54
17037	11	30.91	0.96	(0.134)	0.82	61	1.00	(0.175)	0.74
19016	8	25.24	0.72	(0.124)	0.80	33	1.23	(0.280)	0.70
19017	7	33.60	0.97	(0.098)	0.93	49	1.41	(0.225)	0.85
19024	8	26.04	0.88	(0.076)	0.94	43	1.08	(0.179)	0.81
Check	21	31.64	0.76	(0.145)	0.63	63	1.15	(0.150)	0.79
Overall Mean		34.13				59			

*, **) Significantly different from 1 at the 5% and 1% level, respectively.

Table 3. — Analyses of variance for height, DBH, volume and percent rust-free trees of loblolly pine at age eight in 21 test locations in the southeastern US.

Source	df	Mean Squares			
		Height	DBH	Volume	% Rust-free trees
Location	20	262.60**	571.31**	85515.61**	3.76**
Replication(Location)	107	5.75**	12.25**	1485.53**	0.09**
Family	42	11.82**	28.42**	4736.07**	0.72**
Location x Family	443	2.53**	6.88**	464.28**	0.05**
Linear regressions	42	3.53**	8.87**	1155.02**	0.11**
Dev. from regressions	401	2.43**	6.67**	391.93**	0.04**
Residual	2490	1.29	3.15	207.07	0.033

** Significant at $p < 0.01$.

The different types of stabilities can be illustrated by plotting means from three selected families against the test means for volume (Figure 3). Family 03007 represents a genotype of average stability, as defined by b approximating 1.0, and average performance for volume growth over all tests. Changes in its performance across test sites were proportional to changes in the test site averages and were essentially equal to the test average. Family 01064 represents a relatively stable genotype for volume compared with other families in this study but was a poor

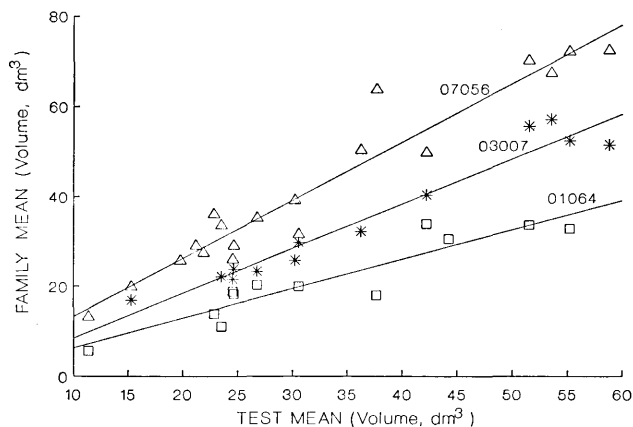


Figure 3. — The regressions of three family means for volume on the environmental index (test means).

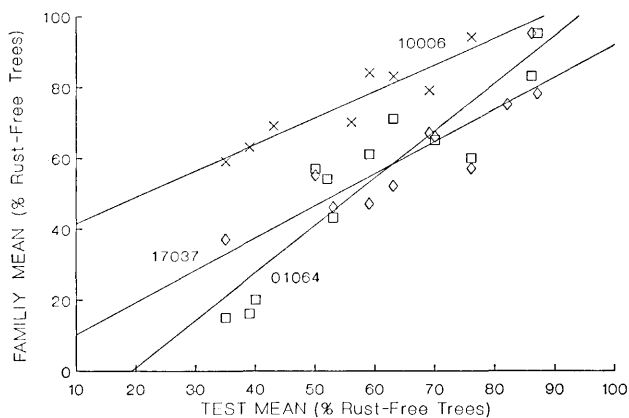


Figure 4. — The regression of three family means for percent rust-free trees on the environmental index (test means of percent rust-free trees).

performer for volume over all tests. Family 07056 represents a relatively unstable genotype that was sensitive to site changes and had greater adaptability to favorable sites.

The same patterns of differential reaction of families to various environments for percent rust infection is shown in Figure 4. Three families were used to illustrate the application of regression analysis in analyzing their relative stabilities and susceptibilities to rust in high and low rust-hazard sites. There were differences in rust resistance among the three families. Family 17037 represents a genotype with average resistance and average stability ($b = 1.0$) over all sites. Family 10006 was a stable genotype ($b = 0.70$) over all levels of rust infection, while family 01064 was very unstable ($b = 1.44$), and it was highly susceptible to rust.

To identify genotypes with different levels of mean performances and stabilities in the study, the relationship between regression coefficients and family means for volume was plotted (Figure 5). High family mean performance over all test environments indicated the general adaptability of the families. The regression coefficient further measured the stability of the genotype and indicated the kind of environmental condition to which the family was adapted. Most of the 43 selected loblolly pine families were classified as Average Stability genotypes because their linear response to site averages was approximately $b = 1.0$ (Figures 2 and 5). Family 03007 is an example of an Average Stability genotype with $b = 1.0$ and average performance in volume (Figure 5). There were some families such as 07056 with $b > 1.0$ and high mean performance (Figures 3 and 5) which can be classified as Responsive High Yield genotypes. These families were relatively unstable but performed relatively better on favorable sites. They were also above average on poor sites. Only a few families such as family 01064 were identified as Stable Low Yield genotypes for volume growth (Figures 3 and 5). The check seedlot was above average for stability ($b < 1.0$) in height, DBH and volume and was below average for mean performance (Tables 1 and 2).

A significant positive relationship ($r = 0.75$) between the b parameters and the family mean performance for volume (Figure 5) was noted in this study. This kind of relationship has been found in other crops (FINLAY and WILKINSON, 1963; GRAY, 1982), where better performing genotypes were more responsive to better sites.

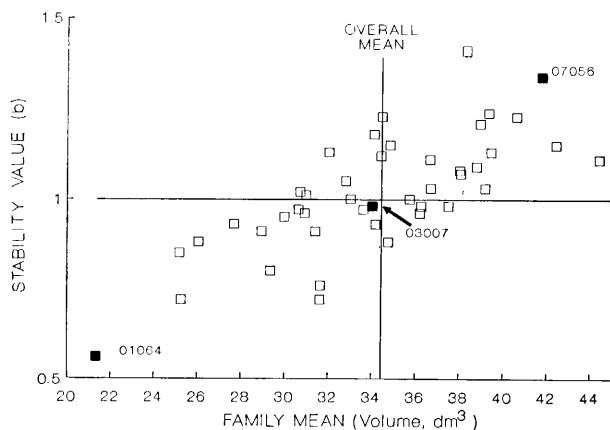


Figure 5. — The relationship of regression coefficients and mean performance for volume of loblolly pine families.

If there is genetic variation in stability and performance among families, tree breeders have the opportunity to select for different stabilities under different environmental conditions and determine the optimum genotypes and management systems for each environmental condition. For example, families in the Responsive High Yield group have greater specificity of adaptability to high quality environments and should respond well to intensive silvicultural practices. Although there were few of these families found in this study, it would be most valuable to use these families such as 07056 on high site index lands to maximize yield and to obtain the best use of genetically improved stock. If forests are being established on less favorable sites or over a large range of average sites, families in Responsive High Yield group or in the Average Stability group with above average performance would be very productive genotypes. The Average Stability group has general stability and adaptability to all environments.

Conclusion

The strong trend in this study for selected loblolly pine families to have average stability and perform in a predictable manner over a wide range of sites is very valuable information for tree breeders. Significant $G \times E$ interaction in the analyses of variance was contributed by very few families for height, DBH, volume and percent rust-free trees in the study. An important implication to the breeding program is that families usually need not be tested over environmental extremes to determine breeding values. With few exceptions, a family's performance on

good sites was highly correlated with its performance on poor sites. It may be valuable to test over environmental extremes to identify the few Responsive High Yield families which should be used to increase forest productivity on intensively managed sites.

Literature Cited

- BARNES, R. D., BURLEY, J., GIBSON, G. L. and GARCIA DE LEON, J. P.: Genotype-environment interactions in tropical pines and their effects on the structure of breeding populations. *Silv. Genet.* **33** (6): 186–198 (1984). — EBERHART, S. A. and RUSSELL, W. A.: Stability parameters for comparing varieties. *Crop Sci.* **6**: 36–40 (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, J. H. and PERKINS, J. M.: Environmental and genotype-environmental components of variability. VIII. Relations between genotypes grown in different environments and measures of these environments. *Heredity* **27**: 15–23 (1971). — FRIPP, Y. J.: Genotype-environmental interactions in *Schizophyllum commune*. II. Assessing the environment. *Heredity* **28**: 223–238 (1972). — FRIPP, Y. J. and CATEN, C. E.: Genotype-environmental interactions in *Schizophyllum commune*. I. Analysis and character. *Heredity* **27**: 393–407 (1971). — GODDARD, R. E.: G-E interaction in slash pine. Third world consultation on forest tree breeding. FAO/IUFRO, Canberra, Aust., March, 1977. 8 pp. (1977). — GOEBEL, N. B. and WARNER, J. R.: Volume tables for small diameter loblolly pine, shortleaf and virginia pine in the upper South Carolina piedmont. Forest Research Series No. 7, Clemson Univ. Clemson, SC. (1966). — GRAY, E.: Genotype \times Environment interactions and stability analysis for forage yield of orchard grass clones. *Crop Sci.* **22**: 19–23 (1982). — HARDWICK, R. C. and WOOD, J. T.: Regression methods for studying genotype-environment interactions. *Heredity* **28**: 209–222 (1972). — LA FARGE, T. and KRAUS, J. F.: Genotype \times environment interactions of loblolly pine families in Georgia, U.S.A. 1981. *Silv. Genet.* **30**: 156–162 (1981). — LIN, C. S., BINNS, M. R. and LEFKOVITCH, L. P.: Stability Analysis: Where do we stand? *Crop Sci.* **26**: 894–900 (1986). — MORGENSTERN, E. K. and TEICH, A. H.: Phenotypic stability of height growth of jack pine provenances. *Can. J. Genet. Cytol.* **11**: 110–117 (1969). — NAMKOONG, G.: Genotype by environment interaction: some theoretical considerations. In: Proc. Fifth North American Forest Biology Workshop. Univ. Fla., Gainesville (1978). — OWINO, F.: Genotype \times environment interaction and genotypic stability in loblolly pine. II. Genotypic stability comparisons. *Silv. Genet.* **26** (1): 21–25 (1977). — PERKINS, J. M. and JINKS, J. L.: Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. *Heredity* **23**: 339–356 (1968a). — PERKINS, J. M. and JINKS, J. L.: Environmental and genotype-environmental components of variability. IV. Non-linear interactions for multiple inbred lines. *Heredity* **23**: 339–356 (1968b). — PLAISTED, R. L.: A shorter method for evaluating the ability of selections to yield consistently over locations. *Am. Potato. J.* **37**: 166–172 (1960). — SHUKLA, G. K.: Some statistical aspects of partitioning genotype-environmental components of variability. *Heredity* **29**: 237–245 (1972). — YATES, F. and COCHRAN, W. G.: The analysis of groups of experiments. *J. Agric. Sci. (Cambridge)* **28**: 556–580 (1938). — YEISER, J. L., VAN BUIJTENEN, J. P. and LOWE, W. J.: Genotype \times environment interactions and seed movement for loblolly pine in the Western Gulf Region. *Silv. Genet.* **36** (6): 196–200 (1981).

Tree Improvement Strategies: Modelling and Optimization: the Model*)

By L. E. PAQUES

I.N.R.A., Station d'amélioration des Arbres forestiers,
Ardon, 45160 Olivet, France

(Received 3rd February 1988)

Abstract

A model of a complete cycle of tree improvement is proposed that combines in the equivalent annual rent (E.A.R.), both genetic and economic factors affecting tree

*) Based on a thesis presented to North Carolina State University in partial fulfillment of the requirements for the degree of Master of Science.