Genotype × Environment Interactions of Loblolly Pine Families in Georgia, U. S. A.

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Summary

Genotype × environment interactions were found for height and the number of fusiform rust galls per tree in three loblolly pine progeny tests in Georgia, U. S. A. Test 1, measured at age 6, was planted at two locations in the Piedmont, and Tests 2 and 3, measured at age 5, were each planted at two Piedmont locations and at a third location in the Upper Coastal Plain.

Despite the genotype × environment interactions, adaptability and stability analyses of Tests 2 and 3 suggested that the best families are those which maintain a stable superiority in growth rate and resistance to rust over wide ranges of site quality and rust hazard. Genetic gain does not seem to be greatly diminished when the best families are selected on the basis of average performance at all locations, even when there are strong interactions for a few families.

Key words: Genotype × environment interaction, *Pinus taeda* L., *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*, stability, adaptability.

Zusammenfassung

In drei Nachkommenschaftsprüfungen von *Pinus taeda* in Georgia, USA, wurden für Höhe und Anzahl von Fusiform-Rostgallen je Baum Interaktionen zwischen Genotyp und Umwelt gefunden. Test 1, an zwei Standorten in Piedmont ausgepflanzt, wurde im Alter von 6 Jahren, Test 2 und 3, außer an den zwei o. a. Standorten noch in der höhergelegenen Coastal Plain ausgepflanzt, wurden im Alter von 5 Jahren gemessen und bonitiert.

Ungeachtet der Genotyp-Umwelt Interaktion zeigten Stabilitäts- und Anpassungsfähigkeitsanalysen bei den Tests 2 und 3, daß die besten Familien diejenigen waren, die eine stabile Überlegenheit in Höhenwachstum und Rostresistenz bei unterschiedlichen Standortqualitäten und Rostrisiken zeigten.

Der genetische Gewinn scheint nicht stark vermindert zu werden, wenn die besten Familien auf der Basis ihrer durchschnittlichen Leistung auf allen Standorten selektiert werden, selbst wenn bei einigen Familien starke Interaktionen auftreten.

Introduction

As more seed from genetically improved loblolly pine (*Pinus taeda* L.) families becomes available from seed orchards, increased attention is being given to the performance of these trees in different environments (Goddard and Vande Linde, 1967; Kraus, 1970; Snyder and Allen, 1971; Owino, 1975, 1977 a, 1977 b; Owino and Zobel, 1977). If strong genotype × environment interactions are found in progeny tests at several locations, then it might be desirable to develop special varieties suited for each environment. The development of such well-adapted varieties would theoretically increase genetic gains. However, this would require that we be able to accurately classify the site at each environment in which the trees are to be grown.

Other important traits might require less advance preparation. For example, resistance to fusiform rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) requires only that we have a reasonable estimate of the degree of risk of infection at each location to be planted. Land managers who have data or observations on existing stands in the area to be planted already have such information. Documentation of the presence or frequency of the alternate host (*Quercus* spp.) in the area would be helpful. Survey data are now available for several southern states (Powers *et al.*, 1974; Phelps 1974; Walterscheidt and Van Arsdel, 1976), but such surveys might need to be still more precise to be useful for this purpose. It would be simpler to breed genotypes of broad adaptability to a wide range of environments, i. e., stable genotypes which maintain above-average yields in most environments.

This paper reports the genotype × environment interactions found in three loblolly pine progeny tests at different locations in the Piedmont and Upper Coastal Plain of Georgia.

Materials and Methods

Test 1

In January, February, and March 1969, 72 seed lots of loblolly pine were planted at two locations in the Georgia Piedmont. Each planting was designed as an 8 × 9 rectangular lattice with three repetitions of the three basic replications. The trees were planted at a spacing of 2.6 × 2.6 meters in 5-tree row plots. One plantation was located in Heard County at 33.4° N. 85.2° W on forest land which had been clearcut 2 years before planting; the second was in Putnam County at 33.2° N, 83.3° W on an abandoned old field.

The seedlots in both plantations were identical and consisted of 66 single cross progenies from 16 female parents crossed to either 4 or 5 male testers plus six standard check lots.

Test 2

In January 1973, 18 seed lots of loblolly pine were planted at three locations, two in the Piedmont and the third on the Upper Coastal Plain. Each planting was a randomized complete-block design with 16-tree square plots replicated four times. The trees were planted at a spacing of 2.5 × 2.5 meters. One plantation was located in Troup County at 33.2° N, 85.0° W in an old field typical of the Piedmont in west Georgia. The second plantation was in Greene County at 33.6° N, 83.3° W, also in the Piedmont, on land clearcut and site-prepared. The third plantation was in Houston County at 32.3° N, 83.6° W in the Upper Coastal Plain of central Georgia. This site was formerly a peanut field, and the most productive of the three.

All three plantations had 15 half-sib families and three standard check lots in common.

Test 3

Also in January 1973, 16 seed lots of loblolly pine were planted at three locations. Two of the plantings were adjacent to the Troup and Greene County plantings in Test 2 and the third was part of the same Houston County planting used in Test 2. The experimental design was the same as that used for Test 2. This test consisted of 13 halfsib families, and the same three standard check lots used in Test 2.

Statistical Analysis

Test 1 was assessed after 6 years, and Tests 2 and 3 after their fifth growing season in the field at which time total height was measured and the numbers of fusiform rust infections were counted. For analysis, the numbers of infections per tree in Tests 2 and 3 were transformed to $\sqrt{x + 0.5}$.

A combined analysis of variance for each trait in Test 1 was performed. From the expected mean squares of this analysis, variance components were estimated for locations (σ^2_l), families (σ^2_f), family × location interactions (σ^2_{fl}), and the error variance (σ^2_e).

For Tests 2 and 3, regressions of the mean performance for any single trait of a family (or variety) at each location were used on the mean performance of all families at each location, also termed the environmental index. This method was initially developed by Yates and Cochran (1938) but was not applied until Finlay and Wilkinson (1963) used it to analyze the performance of 277 barley varieties at three locations in Australia over a period of 3 years.

By means of this regression analysis, genotype × environment interactions may be broken down into different components: one involving adaptation, the other stability. Finlay and Wilkinson (1963) used a combination of regression analysis and analysis of variance, but they used the regression coefficient (b) as a measure of both adaptation and stability in three categories of variation: (1) varieties with $b < 1.0$ were specifically adapted to unfavorable environments and above average in stability, (2) those with $b > 1.0$ were specifically adapted to favorable environments and below average in stability, and (3) those with $b = 1.0$ were either poorly or well adapted to all environments, depending on the mean yield of all varieties, and average in stability.

Eberhart and Russell (1966) went further than Finlay and Wilkinson because their method permitted the calculation of the variance of the mean square of deviations from regression for each variety ($\bar{s}^2_d$) in addition to the regression coefficient. They defined a stable variety as one having $b = 1.0$ and $\bar{s}^2_d = 0$. According to these constraints, varieties with $b = 1.0$ or $\bar{s}^2_d = 0$, would all be unstable. Although their basic model was that of Finlay and Wilnkinson, they made no allowance in their definitions for adaptation to changing environments.

Bilbro and Ray (1976) suggested a compromise method in which the analysis of variance structure proposed by Eberhart and Russell would be appropriate, but b would be the measure of adaptation and s^2_d would be the measure of stability. In their own study they substituted the coefficient of determination, r^2, for s^2_d because it accomplished essentially the same purpose and differences between r^2 values for different varieties could be tested statistically.

In the present analysis, the statistical model proposed by Eberhart and Russell is used, but with adaptation as defined by Finlay and Wilkinson and stability as defined by Bilbro and Ray. That is, the regression coefficient, b, is used to measure adaptation, and the variance of the mean square of deviations from regression, s^2_d, is used to estimate relative stability. If b was significantly less than 1.0, the family was considered to be well adapted to unfavorable environments; if b was significantly greater than 1.0, the family was judged to be well adapted to favorable environments; if $b = 1.0$, it was considered to be either poorly or well adapted to all environments, depending on its mean performance relative to that of the other families in that test.

Table 1. — **Trait means for 6-year-old loblolly pine families at two locations in Georgia (Test 1).**

Parental identification	Average height at:		Trees rust-free at:		Galls per tree at:	
	Putnam Co.	Heard Co.	Putnam Co.	Heard Co.	Putnam Co.	Heard Co.
	Meters		*Percent*		*Number*	
			FEMALES			
Barrow 1	4.67	3.94	33.4	18.9	1.24	2.43
Meriwether 6	4.64	4.07	65.6	21.4	.78	2.12
Morgan 39	4.55	3.94	38.1	15.0	1.18	2.34
Harris 4	4.46	3.88	25.6	10.5	1.62	3.49
Heard 5	4.46	3.98	65.2	17.2	.76	2.61
Chattahoochee 1	4.43	4.25	43.6	9.7	1.05	3.33
Coweta 1	4.42	4.09	55.5	22.2	.78	2.35
Heard 1	4.41	4.11	37.9	15.2	1.14	3.10
Morgan 57	4.40	3.99	50.4	21.2	1.02	2.55
Sumter 2	4.39	4.27	64.4	16.1	.85	3.16
Green 5	4.36	4.05	64.8	32.8	.72	1.75
Floyd 31	4.35	4.04	39.5	16.4	1.19	2.71
Coweta 3	4.34	4.26	74.4	49.3	.71	1.26
Floyd 35	4.34	4.14	22.8	12.4	1.61	3.80
Taliaferro 4	4.32	4.07	44.1	8.5	1.08	3.08
Chattahoochee 2	4.18	4.10	46.7	24.9	1.02	2.78
			MALES			
Grady 6	4.62	4.12	32.5	5.8	1.46	4.67
Sumter 1	4.46	4.18	48.1	16.8	1.06	2.42
Greene 9	4.43	4.02	51.1	19.9	.99	2.34
Meriwether 7	4.34	4.15	56.3	29.0	.86	2.01
Heard 8	4.25	3.91	54.8	29.0	.87	1.95
			CHECK LOTS			
Ga. For. Comm. S.O., O.P.	4.33	4.14	45.1	11.5	1.29	2.44
C.D. 3 (West-Central Ga.)	4.34	4.02	47.7	20.6	1.18	2.80
C.D. 7 (North-West Ga.)	3.79	3.85	49.0	16.2	1.04	2.53
C.D. 10 (East-Central Ga.)	4.30	3.95	58.0	10.3	.81	3.80
G.C.I.A., Coastal Plain check	4.88	4.06	27.4	12.0	1.89	2.76
G.C.I.A., Piedmont check	4.36	3.97	30.3	20.2	1.37	3.30

Table 2. — **Estimated variance components and standard errors (in parentheses) for combined analysis of loblolly pine single cross progenies planted at two locations (Test 1).**

Variance component	Trait					
	Height		Rust infection		Galls/tree	
σ^2_m	0.12	(0.10)	42.76**	(26.96)	0.25	(0.21)
σ^2_f	0	(.06)	42.06**	(19.55)	.10**	(.06)
σ^2_{fxm}	.14	(.09)	7.89	(7.04)	.04	(.04)
σ^2_{mxl}	.05	(.05)	0	(1.74)	.18	(.12)
σ^2_{fxl}	.18**	(.10)	13.27**	(8.20)	.03	(.03)
σ^2_{fxmxl}	0	(.10)	0	(8.43)	.07*	(.04)
σ^2_e	4.59		397.07		1.50	

* Significant at the 5 percent level.

** Significant at the 1 percent level.

Results and Discussion

Test 1

The average performances of the loblolly pine families and check lots in this test are shown in *Table 1*. The Putnam County site is obviously more productive based on tree height and the lower incidence of fusiform rust infection. Rust infection at both locations is over 50 percent, indicating that there has been ample opportunity for discrimination of resistant vs. susceptible families.

Combined analysis of the data from both plantations and estimates of variance components show only one interaction of any consequence (*Table 2*). The location × female (σ^2_{fl}) component for height was highly significant and large relative to σ^2_f. The same interaction component was also highly significant for percentage of rust infection but relatively small compared to the variance among females. These results are substantiated by the correlations between plantations. For height of female progenies, $r = 0.42$ n. s. but for percent rust infection, 0.67**, which indicates major changes in relative height among families in the two plantations, but minor changes in percentage of rust infection.

Table 3. — Family-plantation means for two studies at three locations.

Progeny identification	Plantation location			Combined average	Plantation location			Combined average
	Troup	Greene	Houston		Troup	Greene	Houston	
	Height (meters)				*Galls/tree*			
				TEST 2				
2-SO-65-1	2.8	2.8	4.9	3.5	0.9	0.3	3.1	1.4
GCIA Coastal Loblolly	2.9	2.9	4.8	3.4	0.5	0.5	3.1	1.4
GCIA Piedmont Loblolly	2.7	2.9	4.2	3.3	0.7	0.3	5.3	2.1
Carroll 6	2.9	2.8	4.7	3.4	0.3	0.1	0.5	0.3
Chattahoochee 3	2.9	3.0	4.6	3.5	2.4	0.9	15.5	6.3
Floyd 3	2.9	3.0	3.9	3.3	1.5	0.9	7.9	3.0
Floyd 27	2.3	3.0	4.5	3.3	1.2	0.7	3.1	1.7
Greene 12	2.5	2.7	4.7	3.3	0.5	0.3	2.4	1.1
Harris 2	2.7	3.0	4.6	3.4	0.7	0.5	2.7	1.3
Heard 7	2.9	2.8	4.9	3.5	1.2	0.9	5.7	2.6
McIntosh 1	3.1	2.8	5.1	3.7	0.9	0.9	4.3	2.1
Meriwether 9	2.5	2.6	4.7	3.3	0.5	0.5	3.1	1.4
Morgan 10	2.8	2.7	4.6	3.4	0.5	0.5	3.1	1.4
Putnam 7	2.5	2.7	4.4	3.2	0.5	0.3	3.1	1.3
Putnam 17	2.7	2.6	4.5	3.3	1.5	0.5	5.3	2.4
Putnam 20	2.7	2.9	4.9	3.5	0.3	0.1	1.5	1.3
Troup 5	2.9	3.0	5.0	3.6	0.7	0.7	4.0	1.8
Troup 10	2.8	2.8	4.1	3.2	0.5	0.5	2.4	1.1
Mean	2.7	2.8	4.6	3.4	0.9	0.5	4.0	1.8
				TEST 3				
2-SO-65-1	2.5	3.2	4.9	3.5	0.5	0.3	3.1	1.3
GCIA Coastal Loblolly	2.9	2.7	4.8	3.5	0.3	0.7	3.1	1.4
GCIA Piedmont Loblolly	2.6	2.5	4.2	3.1	0.7	0.7	5.3	2.2
Carroll 7	2.5	2.4	4.4	3.1	0.1	0.3	2.4	0.9
Chattahoochee 1	2.6	2.7	4.3	3.2	0.5	0.7	4.3	1.8
Floyd 1	2.5	2.7	4.4	3.2	0.3	0.5	1.7	0.9
Harris 1	2.5	3.0	4.6	3.3	0.3	0.3	2.4	1.0
Heard 12	2.2	3.3	4.4	3.3	0.3	0.5	4.3	1.3
Meriwether 7	2.7	3.0	4.3	3.3	0.5	0.5	2.7	1.2
Morgan 7	2.4	2.4	4.5	3.1	0.3	0.3	1.7	0.8
Morgan 25	2.9	2.8	4.1	3.3	0.3	0.3	1.2	0.6
Putnam 13	2.6	1.5	4.3	3.1	0.5	0.5	3.5	1.5
Putnam 19	2.5	2.5	4.7	3.2	0.5	0.5	7.9	3.0
Taliaferro 3	2.3	2.7	4.4	3.1	0.5	0.3	3.9	1.6
Troup 4	2.7	3.0	4.7	3.5	0.3	0.3	1.2	0.6
Troup 8	2.4	3.0	4.4	3.3	0.3	0.3	1.5	0.7
Mean	2.5	2.8	4.5	3.3	0.5	0.5	3.1	1.4

Table 4. — Analysis of variance for two traits in Test 2 and Test 3.

Source of variation	Test 2			Test 3		
	Degrees of freedom	Mean squares		Degrees of freedom	Mean squares	
		Height	Galls/tree		Height	Galls/tree
Families	17	10.80*	4.67**	15	10.30	1.50**
Locations + Families x Locations	36	199.70**	6.64**	32	196.45	162.64**
Locations (linear)	1	6,922.28**	192.99**	1	6,033.49**	138.22**
Families x Locations (linear)	17	11.34*	2.64**	15	6.01	1.59**
Pooled deviations	18	4.13**	.07	16	10.18**	.04
Pooled error	153	1.00	.05	135	.88	.04

* Significant at the 5 percent level.

** Significant at the 1 percent level.

Test 2 and 3

Family and location means for height and galls per tree in each test are summarized in *Table 3*. It is apparent that growth rate is faster and incidence of rust infection more severe at the Houston County location than at either the Troup or Greene County locations.

The method of analysis used here indicates which component of the family × location interaction is significant (*Table 4*). The highly significant interaction effects for galls per tree indicate that the regression slopes contribute most to the interactions in each study for this trait, but the highly significant pooled deviations contribute most to the interactions for height in both tests. Family effects were also highly significant for galls per tree in both tests.

Only 3 of the 34 regression coefficients for height were significantly greater or less than unity (*Table 5*), whereas the corresponding value for the number of galls per tree was 22. The variances of the mean squares of deviations from regression (s^2_d) are generally much larger for height than for the number of galls per tree, especially so in Test 3, in which 11 of 16 variances are significant (*Table 5*). The effect of less stability for height than for the number of galls per tree is also apparent in *Table 4*.

Eberhart and Russell (1966) point out that, because the variance s^2_d is a function of the number of environments, an adequate number of environments and replications at each location are necessary to arrive at reliable estimates of s^2_d. Yet they note that good estimates of b can be achieved with just a few environments if they represent the range of expected environmental effects.

Table 5. — Adaptability (b) and stability (s^2_d) estimates for height and galls/tree for two studies at three locations.

Progeny identification	Height		Galls/tree	
	b[1]	s^2_d [2]	b	s^2_d
		TEST 2		
2-SO-65-1	1.17	1.61	.85	.204*
GCIA Coastal Loblolly	1.03	.47	.90	.058
GCIA Piedmont Loblolly	.77*	.75	1.36**	.000
Carroll 6	1.00	2.29	.21**	.051
Chattahoochee 3	.90	.00	2.53**	.178*
Floyd 3	.55**	.00	1.59**	.000
Floyd 27	1.03	35.49**	.69**	.071
Greene 12	1.17	2.66	.74**	.000
Harris 2	.95	5.77*	.74**	.101
Heard 7	1.11	2.48	1.29**	.080
McIntosh 1	1.19	11.41**	1.04	.151
Meriwether 9	1.16	.00	.87	.040
Morgan 10	1.04	3.16	.84	.000
Putnam 7	1.02	.38	.90	.000
Putnam 17	.97	2.54	1.18*	.215*
Putnam 20	1.12	1.20	.55**	.011
Troup 5	1.10	.09	1.00	.053
Troup 10	.72*	.06	.72**	.000
Mean	1.00 ± .10	3.91 ± 1.30	1.00 ± .08	.067 ± .022
		TEST 3		
2-SO-65-1	1.18	13.66**	.98	.096
GCIA Coastal Loblolly	1.08	11.99**	1.06	.178*
GCIA Piedmont Loblolly	.90	6.60**	1.44**	.038
Carroll 7	1.06	6.13**	.90	.000
Chattahoochee 1	.90	1.75	1.27**	.000
Floyd 1	1.00	.00	.63**	.014
Harris 1	1.03	4.14*	.91	.000
Heard 12	.96	72.30**	1.33**	.013
Meriwether 7	.83	.87	.83*	.003
Morgan 7	1.15	5.85**	.70**	.000
Morgan 25	.71	3.69*	.43**	.000
Putnam 13	.97	8.79**	1.11	.000
Putnam 19	1.19	7.24**	2.10**	.003
Taliaferro 3	1.03	1.68	1.29**	.125
Troup 4	1.03	.00	.46**	.000
Troup 8	.99	14.89**	.57**	.013
Mean	1.00 ± .16	9.97 ± 3.53	1.00 ± .07	.030 ± .011

* Significant at the 5 percent level.

** Significant at the 1 percent level.

[1]) For b, significance refers to whether b is significantly greater than or less than unity.

[2]) For s^2_d, significance refers to the significance of deviations from regressions for each family.

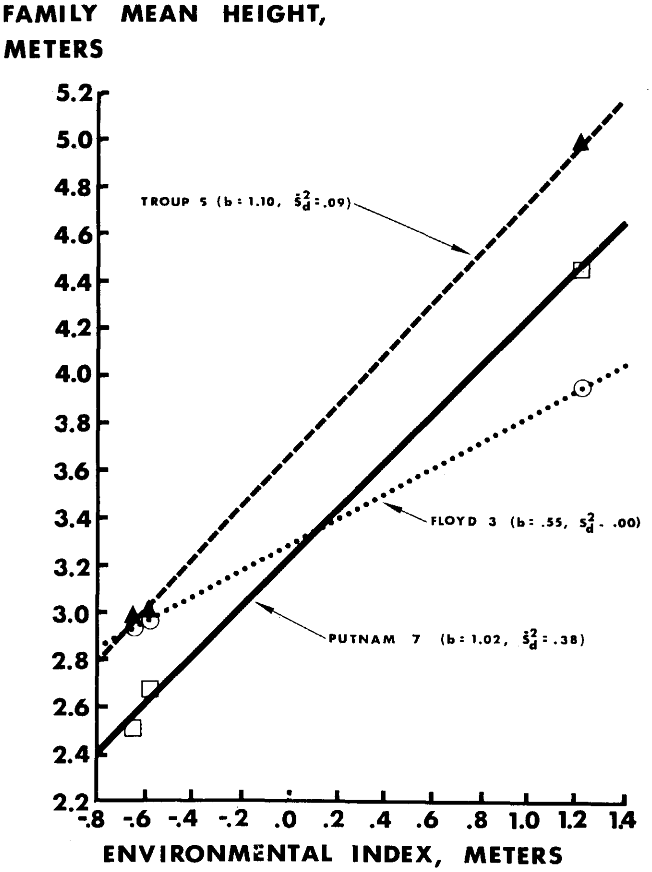

Figure 1. — Three sample regressions of family mean height on the environmental index.

The reliability of the regression coefficient b is indicated by the high correlations (height, r = 1.000**; galls/tree, r = 0.997*) between the b's in Tests 2 and 3 for the three controls common to both tests. In contrast, the correlations (height, r = 0.492; galls/tree, r = 0.180) between the stability parameters s^2_d for the three controls in both tests were not significant.

It would appear from these correlations that the estimates of the b's in this study are reasonably reliable, but that the estimates of s^2_d for each family are not reliable. Therefore, these correlations seem to confirm Eberhart and Russell's claim concerning the number of environments needed to give reliable estimates of b and s^2_d. However, it must be stated that the limitation of these tests to three locations leaves many questions unanswered.

In contrast to the weak stability parameters, most families are adaptive to a wide range of site conditions. This would be an acceptable result if we could determine which families are best over the range of environments tested. However, significant differences among families for height are absent when tested at all three locations in Test 3 (*Table 4*). Since genotype × environment interactions include variations among regressions and among average deviations from regression, the principal source of variation resulting in failure to detect differences among families is the large, significant value for the average deviations from regression in Test 3 (*Table 4*). It would appear, therefore, that a larger number of locations might have permitted detection of

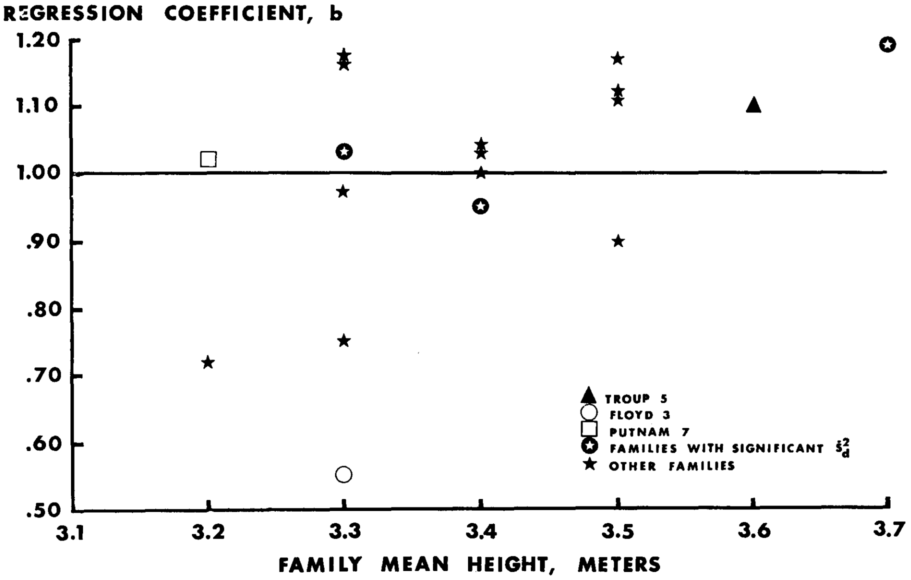

Figure 2. — The relationships of the family regression coefficient and the family mean height for three loblolly pine families.

significant differences among families for heights in Test 3 as well as in Test 2.

To illustrate the application of regression analysis as an indicator of adaptability and the response of different families in height growth to changing environments, three families are represented in *Figures 1* and *2*. The slope of Floyd 3 is significantly less steep than unity and the slopes of Troup 5 and Putnam 7. Hence, Floyd 3 is poorly adapted, since its yield did not change in proportion to the environmental index. By contrast, Troup 5 and Putnam 7, with regression slopes approximately equal to 1.0, had the same adaptability to good and poor sites so that their relative performances for height tended to be the same at all sites. In this case Troup 5, with an average height of 3.6 meters, would be considered well adapted to all three sites, whereas Putnam 7, with a mean height of 3.2 meters, would be considered poorly adapted to all three sites, if the difference between the two families were statistically significant. In contrast, Floyd 3 grew as well as or better than the other two families at the poorest sites. Hence for this comparison, we have a genotype × environment interaction.

When we have this kind of interaction, we must forecast the site index before we plant. Unless we can accurately and inexpensively predict site quality, it is only useful to select families which are well adapted to a wide range of sites, such as Troup 4.

The redeeming feature of the data in Tests 2 and 3 is that most of the families are broadly adaptable for height. This result agrees with Owino's (1977 a) study of 11 family sets of loblolly pine tested at nine locations in the Southern United States. Apparently loblolly pine families in general tend to be adaptable in height growth and are capable of responding to increases in site quality.

The concepts of adaptability and stability also lend themselves to an evaluation of the number of galls per tree as a measure of resistance to fusiform rust.

Three families from Test 2 are used to demonstrate the application of regression analysis in analyzing their relative susceptibilities to rust in high and low rust-hazard environments (*Figures 3* and *4*).

For this trait, b > 1.0 is evidence of susceptibility at high-hazard sites, and b < 1.0 is evidence of resistance at those sites. Hence, Floyd 3 (b = 1.59) is more susceptible

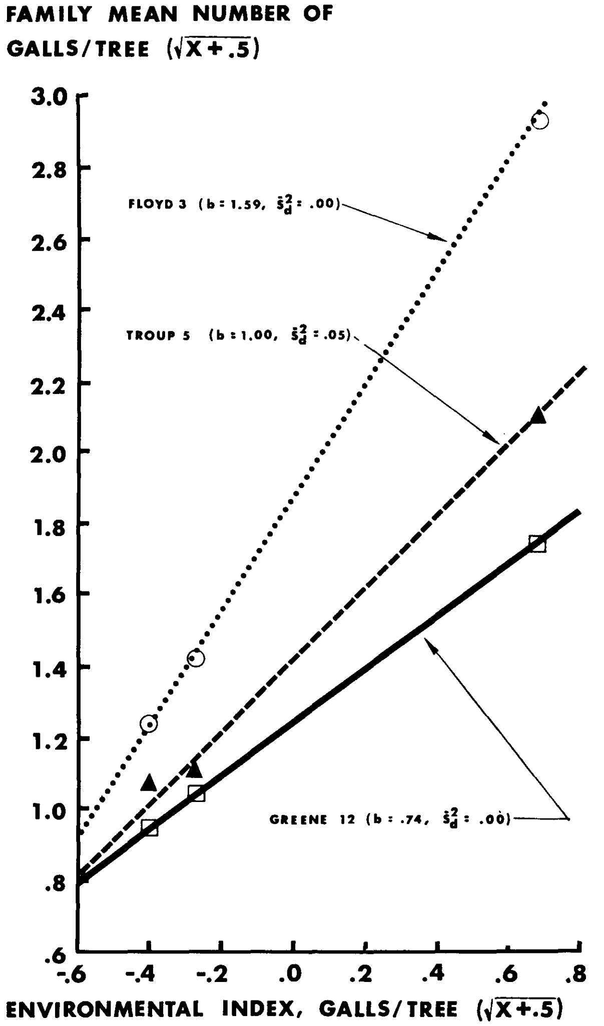

Figure 3. — Three sample regressions of family mean number of galls per tree on the environmental index.

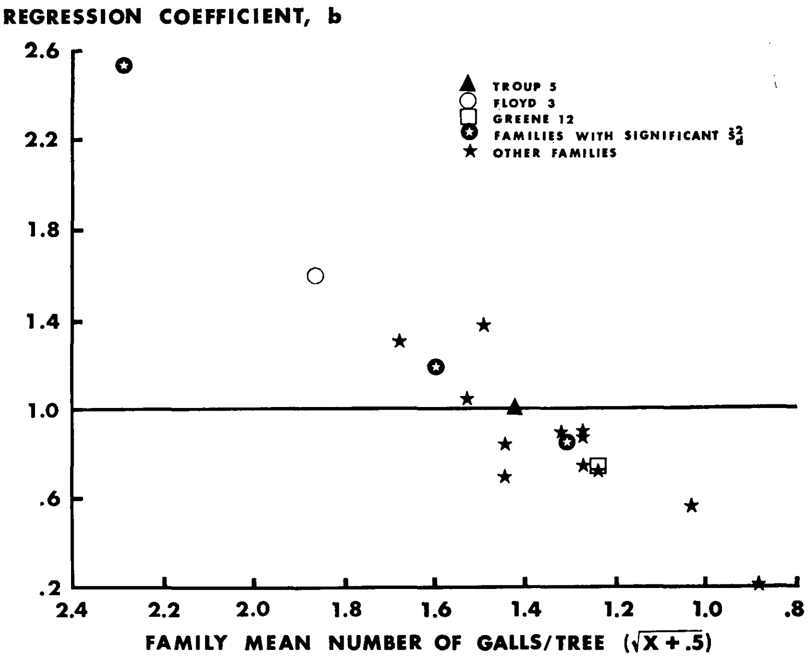

Figure 4. — The relationships of the family regression coefficient and family mean number of galls per tree for three loblolly pine families.

(less adaptable) on the high-hazard sites than either Troup 5 (b = 1.00) or Greene 12 (b = .74). Troup 5 is well adapted to the different levels of rust infection at all sites.

The low mean infection level (*Table 3*) and good adaptability of Greene 12 constitute a very desirable combination of traits. On the high-hazard sites Greene 12 clearly suffers less infection than do the other families. In fact, Greene 12 is significantly less susceptible to rust infection than Floyd 3 at all three locations, based on the Student-Newman-Keuls test.

Greene 12 is not an exception, but instead it typifies the very close relationship between the number of galls per tree and the regression of the family mean number of galls per tree on the environmental index. In Test 2 the correlation between the family mean and b is r = .962** and in Test 3, r = 936**. For height, the corresponding correlations are r = .497* and r = 363. Hence, since the adaptability and family mean galls per tree are not independent, selection for one trait will select for the other. However, even if families like Greene 12 with low slopes have infection levels above the average at the low rust-hazard sites, the level of infection is so low that it probably does not matter.

Another way of assessing the effect of genotype × environment interactions is to compare the genetic gains achieved by selection of the best families for each trait at each location with those achieved by the best families averaged over all locations (*Table 6*). In *Table 6* the two best families for each trait were selected by means of the independent culling level method. That is, the two tallest families which have the fewest galls per tree were chosen, and families having the fewest galls per tree were selected if they were above a certain minimum height. In *Table 6* it can be seen that the results are mixed: in two cases the greatest gain is obtained by selecting the best families at each location, and in the other two cases the best gains occur when the best families are selected on the basis of their average performance at all locations. Except for galls per tree in Test 2, the differences are small.

Since there are no clear-cut differences in the genetic gains obtained by means of their evaluation at each location and those obtained when the evaluations are based on the average performances at all locations, the latter method would seem to be the most efficient one for selecting the best families in Tests 2 and 3. As a further refinement of the selection procedure, height and galls per tree may be combined with the adaptability and stability parameters for each trait to select the best families. These traits are combined on a paired basis, which we might term an „independent culling level of paired traits."

The families selected for any two of the four traits (except for the pair b + s^2_d) are listed in *Table 7*. Those considered acceptable for all four traits are shown above the line. To be selected, a family had to be: (1) average or better for height and galls per tree, (2) within two standard errors of b = 1,00 for height, (3) b < 0.92 in Test 2 and b < 0.93 in Test 3 for galls per tree, (4) $s^2_d < 2.61$ in Test 2 and $s^2_d < 6.44$ in Test 3 for height, and (5) $s^2_d < .045$ in Test 2 and $s^2_d < .019$ in Test 3 for galls per tree. Finally, they had to meet these standards in four of the five pairs

Table 6. — The gains achieved when the two best families for each trait at each location are compared with the gains achieved for the two best families averaged over all locations.

Method	Height	Galls/tree
	Meters	*Number*
	TEST 2	
Best at each location	0.12	-1.23
Average of all locations	.15	-.25
Difference	-.03	-.98
	TEST 3	
Best at each location	0.18	-.60
Average of all locations	.10	-.80
Difference	+.08	+.20
Average difference	+.025	-.39

Table 7. — Best families selected on the basis of height, fusiform rust resistance, adaptability (b), and stability (s^2_d).

Height and galls/tree	Height and b for height	Height and s^2_d for height	Galls/tree and b for galls/tree	Galls/tree and s^2_d for galls/tree
Troup 4	Troup 4	Troup 4	Troup 4	Troup 4
Carroll 6	Carroll 6	Carroll 6	Carroll 6	Morgan 7 [2]
Putnam 20	Putnam 20	Putnam 20	Putnam 20	Carroll 7 [2]
Troup 5	Troup 5	Troup 5	Morgan 7 [2]	Greene 12 [2]
	Heard 7 [1]		Greene 12 [2]	Troup 10 [2]
	McIntosh 1 [1]		Troup 8 [2]	Morgan 25 [2]
			Troup 10 [2]	
			Morgan 25 [2]	

[1] Families with poor rust resistance.

[2] Families with poor height growth.

of traits listed in *Table 6*. Ideally, the standards would be much higher than this, but in practice it is usually necessary to compromise in order to select an acceptable number of families which satisfy minimum standards for two or more traits.

Conclusions

Despite the fact that the analysis of variance indicates some significant genotype × environment interactions, the adaptability and stability parameters suggest that the best families are those that maintain a stable superiority in growth rate and resistance to rust over wide ranges of site quality and rust hazard. Genetic gain does not seem to be diminished appreciably when the best families are selected on the basis of average performance at all locations, even when there are strong interactions for a few families.

Of the three studies, only Test 2 shows significant differences among families for height. Although all show some form of significant genotype × environment interactions for height, Tests 2 and 3 are designed to break down this source of variation into two components, adaptability (b) and stability (s^2_d). These data suggest that stability, *i.e.*, the scatter of points about the slope, is the main source of interaction for height. This kind of instability, or nonlinearity, means that it is not possible to select certain families for certain physiographic provinces or levels of site quality. Such families must be selected for the whole range of sites for planting, if they are to be selected at all. Actually, ages 5 and 6 years are early for detection of differences among families for height in progeny tests. In our experience these differences become more pronounced at ages 10 or 15.

In contrast to height, resistance to fusiform rust shows highly significant differences among families (females in Test 1). This is so despite significant genotype × environment interactions. In fact, the regression of galls per tree on the environmental index is an excellent criterion for selection. For this trait, a very low value of b is desirable; that is, there is a high correlation between b and galls per tree. The reason for this becomes understandable when we realize that, on low rust-hazard sites, differences do not matter, since the general infection rate is so low. In fact, in low rust-hazard plantations, significant differences among families are usually not detectable. The important test of resistance is the degree to which families resist infection on high rust-hazard sites: families whose susceptibilities remain low in high rust-hazard environments have low b values. Hence, despite the apparently high interactions, differences among families for rust are strong and can be evaluated on the basis of performance at all locations. Further, in contrast to height, the slopes of most families tend to be very stable and predictable for galls per tree. That is, the values for s^2_d remain very low relative to those for height. However, this should be confirmed by testing larger numbers of environments.

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