GENERAL AND SPECIFIC COMBINING ABILITY FOR FUSIFORM RUST INFECTION IN SLASH PINE

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Abstract.--General and specific combining ability for fusiform rust infection were calculated on a number of five and ten year old slash pine genetic tests. Average family heritability for rust infection at a single location was 0.54 at age five and 0.53 at age ten. General combining ability accounted for 81% of the genetic variation at both ages. Coefficients of genetic prediction between ages five and ten were 96% as large as age ten heritabilities indicating that selection at age five would be as efficient as delaying selection until age ten. Age five family heritabilities calculated for one set of parents classified as resistant at the USDA Forest Service Resistance Screening Center (RSC) averaged 0.33 across three tests with only 52% of the genetic variation attributable to general combining ability. This could be a sampling artifact caused by low infection levels as the susceptible checklots averaged only 31.7% infection. However, it is possible that screening at the RSC changed the population structure. If so, using variance components from control-pollinated genetic tests of unscreened parents to plan subsequent breeding strategies or to predict gains for parents screened at the RSC is inappropriate. Resolution of this question will require more field tests of parents classified as resistant to fusiform rust at the RSC.

Keywords: *Pinus elliottii* Engelm. var. *elliottii, Cronartium quercuum* (Berk.) miyabe ex Shirai f. sp. *fusiforme,* heritability, disease resistance

INTRODUCTION

Fusiform rust *(Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme)* is the most devastating disease on slash pine *(Pinus elliottii* Engelm. var. *elliottii)* in the Western Gulf region of the United States. In Texas alone, 50% of young slash pine trees are infected (Lenhart et al. 1988) and it is likely that many of these individuals will eventually die (Nance et al. 1981) In fact, rust infection is so prevalent and mortality is such an important factor that the level of family infection at age five was determined to be the most reliable predictor of family volume per acre at age 15 (Lowe and van Buijtenen 1991). As a result, disease resistance has been identified as the most important trait for genetic improvement in the Western Gulf Forest Tree Improvement Program (WGFTIP) strategy for this species.

Approximately 1,000 first generation slash pine selections were initially identified by WGFTIP cooperators. Because slash pine is an exotic species in most of the Western Gulf region, the majority of these selections

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were made in plantations of unknown seed source. The selections were rust free, but no other attempt was made to ensure disease resistance. The initial breeding plan required the establishment of control-pollinated genetic tests in which evaluation would be based primarily on volume growth. A number of these tests were planted. However, as results from early open-pollinated genetic tests became available, the importance of improving disease resistance became obvious and a two-step testing strategy was developed. Parents would first be progeny tested at the USDA Forest Service Resistance Screening Center (Anderson and Powers 1985) and only successful candidates would be used in the subsequent long term breeding and testing program (Byram et al. 1991 p. 12). Control-pollinated field tests of progeny from parents classified resistant at the Resistance Screening Center (RSC) are currently being established. This has resulted in two populations of slash pine within the WGFTIP cooperative: 1) a population not screened at the RSC that received very little selection pressure for disease resistance and 2) a population which was screened at the RSC prior to the breeding and establishment of field trials.

Estimates of genetic parameters are important at all stages of a tree improvement program to aid in the development of breeding strategies and the prediction of genetic gains. Because variance components are population parameters, they can be safely applied only to the population from which they are derived. The objectives of this paper are to report heritabilities, the contribution of general combining ability to total genetic variation and the coefficients of genetic prediction between ages five and ten for fusiform rust infection levels in an unscreened population of slash pine. Data from one partial-diallel of parents classified resistant at the RSC are also reported for comparison.

MATERIALS AND METHODS

A summary of the data sets representing the first generation parents used in this study is given in Table 1.A. There were eleven genetic tests evaluated at age five, ten tests evaluated at age ten and nine tests for which comparisons were made between ages five and ten. These plantings represented 51 parents in six series with each series planted in one to three locations. The breeding scheme was a partial-diallel with each parent crossed with an average of 4.4 other parents (a range from a minimum of three crosses per parent to a maximum of ten). Field designs were completely randomized blocks with six to twelve blocks per location and six to ten trees from each cross planted in row plots in each block. Presence or absence of rust was evaluated at each measurement, and the percentage of trees infected in each plot was calculated for analysis. Trees killed by fusiform rust were scored as infected.

For a test to be included in this study, the average fusiform rust infection level of either the plantation or the two unimproved checklots had to be greater than 30%. Plantation averages exceeded 30% in all cases except for tests 387 and 424. In test 387, it was necessary to rely on the performance of the unimproved checklots as an indicator of exposure to fusiform rust at both measurement ages. The age five data for test 424 was deleted from the study because of insufficient rust infection. Analysis of variance was performed on untransformed percentages using GLM (SAS Inst. 1989); only tests with significant differences among crosses at the 0.10 level were analyzed further.

Percentage data were transformed using the inverse sine transformation (Steel and Torrie 1960 p. 158) before any additional analyses were conducted. General combining ability (GCA) and specific combining ability (SCA) were calculated on a single location basis using the computer program DIALL (Schaffer and Usanis 1969). Negative values and terms that were not significant at the 0.25 level on the basis of an F test were set to zero. DIALL was also used to calculate cross-products for the age-age comparisons.

Table 1. The number of parents, crosses and blocks in each field trial used in this study. Plantation rust infection levels are shown for ages five and ten.

A) Parents not screened at the RSC.

Test	Number of Parents	Crosses	Blocks	Average Rust Infection(%) Age 5	Age 10
Series A					
351	11	20	10	43.1	44.0
352	11	20	10	31.1	38.0
387	11	23	12	26.7[1]	24.2[1]
Series B					
423	8	23	6	40.7	42.7
424	8	25	6	--[2]	38.0
Series C					
437	6	12	12	49.4	48.2
477	6	12	12	49.9	41.3
Series D					
438	8	19	12	75.3	74.2
439	8	19	12	51.4	55.4
464	8	19	12	62.9	69.2
Unrelated Tests					
259	11	29	12	45.5	--[3]
561	7	13	12	40.7	--[3]

B) Parents screened at the RSC.[3]

	Number of Parents	Crosses	Blocks	Average Age 5 Rust Infection(%) Test	Checklot
522	9	22	12	18.7	21.9
523	9	19	12	33.7	28.7
541	9	19	12	27.7	44.4

[1] The average infection of the susceptible checklots were 36.2% at age five and 32.1 % at age ten.
[2] Insufficient rust at age five (<30%).
[3] Age ten evaluations not yet available.

Negative cross-products were accepted. Family heritabilities were calculated according to van Buijtenen (1976) using the following formulae:

$$h^2_{fam} = \frac{\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_E / r}$$

where σ^2_{GCA} is the variance for general combining ability, σ^2_{SCA} is the variance for specific combining ability, σ^2_E is the error variance and r is the harmonic mean for the number of plots/family.

Coefficients of genetic predictions (CGP) were computed for infection levels between ages five and ten within individual locations (Baradat 1976). CGPs are generalized heritabilities indicating the fraction of the breeding value for one trait that can be manipulated by phenotypic selection on a second trait. The ratio of the CGP to the heritability can be used as an

indicator of early selection efficiency. CGPs are calculated as:

$$CGP = \frac{Cov(A_1, A_2)}{\sigma_{p1} * \sigma_{p2}}$$

where $Cov(A_1,A_2)$ is the additive covariance between traits A_1 and A_2, and σ_{p1} and σ_{p2} are the phenotypic standard deviations for each trait.

Three field tests of a group of parents classified as resistant at the RSC are included for comparison (Table 1.B). Overall rust infection levels were lower in this series. Test 522, with an average rust infection of 18.7% and a checklot infection rate of 21.9%, did not meet the criteria outlined above to ensure an adequate challenge by rust. It is reported here because of the limited amount of field data available for parents screened at the RSC; however, the results should be viewed with caution.

RESULTS AND DISCUSSION

Family heritabilities, their standard errors and the fraction of genetic variation attributed to GCA are summarized in Table 2. For the unscreened population, single location estimates of family heritability averaged 0.54 at age five with a range from 0.31 to 0.73. At age ten, family heritabilities averaged 0.53 with a range from 0.16 to 0.79. These values were extremely similar despite the fact that the age ten data included one test with insufficient rust infection to be included in the age five data (test 424) and lacked two other locations that have not yet reached age ten (tests 259 and 561). These figures compare favorably to the individual heritabilities calculated by Dieters as reported by Hodge et al. (1995). As one would expect, estimates of individual tree heritabilities were lower; however, estimates based on a large number of progeny tests did not vary greatly by test age. Evaluations at ages five, eight and eleven were 0.156, 0.148 and 0.146 respectively. Single location heritabilities have an upward bias because the genotype by environment interaction is ignored and the true heritabilities are expected to be lower.

Series D tests appeared to have substantially higher average rust infection levels (Table 1), lower heritability estimates and lower percentages of GCA than the tests in the other series (Table 2). This could be the result of environmental sampling. If the tests were planted in high rust infection years and locations, any inherit resistance may have been overwhelmed and genetic variation masked. However, it is likely that these parents are susceptible and have less GCA for disease resistance. Tests of open-pollinated seed from these parents at the RSC resulted in the elimination of five of the eight parents from any further use in the breeding population. Furthermore, test 437 from series C was planted adjacent to test 438 from series D in the same year and had a much lower average rust infection in the same environment (50% vs 75%). This was despite the fact that the checklot common to both tests had a similar infection level (60% vs. 66%).

A matter of practical importance for tree breeders is the fraction of the total genetic variation attributable to GCA. For the unscreened population, GCA was 81% of the total genetic variation at both ages (Table 2.A). Correlation coefficients among parental GCA estimates were compared across locations in all possible pairwise combinations (Table 3). These correlation coefficients were always large and positive. Relatively large family heritabilities, a high fraction of GCA to total genetic variation and moderate to high correlations between parental values all support the current breeding strategy. This strategy emphasizes the selection of parents with good general combining ability and assumes that there will be little important genotype by environment interaction.

Table 2. Family heritabilities, standard errors, GCA/GCA+SCA at ages five and ten for rust infection levels. Coefficients of genetic prediction between ages five and ten.

A) Parents not screened at the RSC.

	Age 5			Age 10			
Test	h^2	S.E.	GCA (GCA+SCA)	h^2	S.E	GCA (GCA+SCA)	CGP (Age 5/10)
Series A							
351	0.63	0.30	1.00	0.64	0.31	1.00	0.63
352	0.57	0.29	1.00	0.54	0.26	1.00	0.48
387	0.31	0.17	1.00	0.16	0.24	1.00	0.30
Series B							
423	0.53	0.30	1.00	0.58	0.32	0.86	0.56
424[1]	----	----	----	0.44	0.26	0.70	----
Series C							
437	0.73	0.44	0.84	0.79	0.46	0.91	0.76
477	0.53	0.38	1.00	0.73	0.44	1.00	0.49
Series D							
438	0.41	0.27	0.47	0.37	0.26	0.41	0.38
439	0.41	0.27	0.46	0.48	0.29	0.54	0.44
464	0.46	0.29	0.52	0.58	0.32	0.65	0.52
Unrelated Tests[2]							
259	0.67	0.30	0.74	----	----	----	----
561	0.64	0.38	0.86	----	----	----	----
Ave:	0.54		0.81	0.53		0.81	0.51

B) Parents screened at the RSC.[2]

522	0.47	0.27	0.80[3]
523	0.53	0.31	0.76
541	0.00	0.16	0.00[4]
Ave:	0.33		0.52

[1] Test 424 was not used at age five because the average infection levels for the plantation and susceptible checklots were only 23.2% and 15.3%, respectively.
[2] Tests 259, 561, 522, 523 and 541 have not yet reached age ten.
[3] Insufficient rust infection to ensure that the entries were adequately challenged (test average = 18.7%, susceptible checklots = 21.9%).
[4] General combining ability was not significant at the 0.25 level although families were significantly different at the 0.10 level on GLM.

Coefficients of genetic prediction (CGP) between ages five and ten were very similar in magnitude to the age ten heritabilities (Table 2.A). The nine data sets for which comparisons could be made had an average CGP of 0.51 with a range from 0.30 to 0.76. Test 387 had a larger CGP between ages five and ten than the heritability at age 10. This may be the result of the low precision of the age ten heritability estimate which had a standard error larger than the estimate. Selection on age five data would be expected to be more productive than direct selection at age ten in this test. The average CGP was 96% as large as the age ten heritability. Therefore, selection at age five can be expected to be as efficient as direct selection at age ten when infection levels are above 30% and statistically significant.

Table 3. Pearson correlation coefficients between parental GCA estimates for all possible pair-wise comparisons of tests.

Tests	Correlation Coefficients	Probability>|R|
Age 5		
351-352	0.79	0.004
351-387	0.57	0.069
352-387	0.61	0.047
437-477	0.83	0.039
438-439	0.76	0.029
438-464	0.96	0.001
439-464	0.85	0.008
Age 10		
351-352	0.72	0.012
351-387	0.66	0.026
352-387	0.56	0.076
423-424	0.85	0.007
437-477	0.93	0.007
438-439	0.85	0.007
438-464	0.96	0.001
439-464	0.87	0.004

The five-year-old results from a series of nine parents classified as resistant at the RSC are reported in Table 2.B. One location had less rust infection than desirable for the evaluation of resistance. In test 522, the average family infection levels ranged from 7 to 32% with a plantation mean of 18.7%. In this series of tests, heritability averaged 0.33 with a range from 0.0 to 0.53. Test 541 had no significant GCA effects. A number of explanations are possible for the apparent differences between the genetic parameters for the screened and unscreened populations. This data represents only one set of parents and may be biased due to sampling. Rust infection levels are low and may be inadequate to allow reliable expression of genetic effects. Another possibility is that screening at the RSC altered the population structure; therefore variance components will be different in this new population. Investigation of these hypothesis will require additional field data from genetic tests of parents screened at the RSC.

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