GENOTYPE-ENVIRONMENT INTERACTIONS IN PROGENY TESTS OF BLACK CHERRY PLUS TREES[1]/

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ABSTRACT--Height growth variation in four progeny
test plantings, containing fifty open-pollinated
black cherry families, was studied after the fifth
and tenth growing seasons. The magnitude of the
family variance components differed among sites,
and in one instance increased with age. Age-age
correlations based on family mean heights were high
and similar at each site, Families from Pennsyl- .
vania generally were taller than those from West
Virginia, but the regional difference was not always
significant.

Genotype-environment interactions were non-
significant at age five, but significant after the
tenth growing season. Using a linear regression
model, the performance of each family was studied
over the range of planting sites, From the
analysis, estimates of phenotypic stability were
calculated for each family, and they are discussed
in terms of selection strategies. Substantial
variation was found among families in mean height
and stability parameters, which could be exploited
by selection in progeny tests to increase genetic
gains on contrasting sites,

INTRODUCTION

The need to ensure the quality of future growing
stock led the U.S. Forest Service to implement an
improvement program for northeastern hardwoods in 1966.

Of all species included in the program, black cherry
(Prunus serotina Ehrh.) was assigned the highest
priority and most of the work thus far has been con-
centrated on its genetic improvement and artificial
regeneration. To date 155 superior phenotypes have been
selected on the Allegheny and Monongahela National For-
ests, and their open-pollinated progenies are periodi-
cally evaluated at numerous locations (Dorn and Miller
1977). General combining ability estimates derived from
these plantings will be used to rogue existing seed
orchards which will furnish planting stock for the
regeneration of cut-over lands on both National Forests.

This paper is a report on the extent and nature of
genotype-environment interactions in a series of black
cherry progeny tests. Estimates of family stability
represent variable responses in height growth to the
environments of planting sites in Pennsylvania and West
Virginia. Because the progeny tests had been estab-
lished within the two regions where seeds had been
collected from plus trees, differences in the adaptation
of families could be expected to occur, The stability
estimates could provide insights for deciding whether
breeding programs should be directed towards the develop-
ment of general or specific adaptation to the environ-
ments of Pennsylvania and West Virginia,

METHODS

In 1970 fifty open-pollinated families were planted
at six locations, three on each National Forest, The
parent trees had been selected primarily on the basis of
their superior growth rate and stem form using the
comparison tree method (Pitcher and Dorn 1967). Thirteen
families were derived from trees selected on the Monon-
gahela National Forest, and the remaining 37 originated
on the Allegheny National Forest. Control families
representing average phenotypes were not included in any
of the plantings.

Using a randomized complete block design with four
replications and four-tree linear plots, the plantings
were established in three- to five-year-old clearcuts
that had supported cherry-maple or northern hardwood
stands. At all locations deer exclosure fences were
erected, and most sites were treated with 2,4,5-T the
year prior to planting, The 1-0 stock was planted using
an earth auger or a planting bar depending upon site con-
ditions. Competition from woody vegetation was con-
trolled periodically at all locations, Data from two
Allegheny plantations were unavailable because of

excessive deer browsing and mortality caused by a late
spring frost. The heights of trees in the four remain-
ing plantations were measured following the fifth and
tenth growing seasons. Due to injuries caused by an
early season snowfall, tenth-year data for plantation
611 were not used.

Initially data sets from each location were analyzed
separately at ages five and ten. The family variance
component was expressed as a percentage of the total varia-
tion at each location. Data sets for each age were then
analyzed with all locations combined, For the age 10 data,
the genotype-environment interaction sum of squares was
partitioned into a component representing the hetero-
geneity of family regressions and a residual component,
using the model of Eberhart and Russell (1966). Linear
regressions were developed by relating family mean
heights at each site to the mean height of each planta-
tion, one in Pennsylvania and two in West Virginia, As
measures of each family's stability, regression coeffi-
cients and sums of squared deviations from regression
were calculated.

RESULTS

In the separate site analyses, significant family
differences in height were found at two of four
locations at age five, and at two of three locations
at age ten (Table 1). Plantation 610 was the only location
where an appreciable change with age occurred in the
magnitude of the family variance component, increasing
from about one percent to 18 percent. At all locations
and ages, the average height of the Allegheny families
exceeded that of the Monongahela families, although this
difference was not always significant, Correlation coeffi-
cients for mean family heights at ages five and ten were
similar and fairly high at all three locations (Table 1).

In the combined analysis of fifth-year height data,
the interaction sum of squares was not partitioned into its
component parts due to its lack of significance (Table 2).
Similarly, because of a lack of significant site variation,
no family stability parameters were derived, Data from
plantation 611 were not included in the combined analysis
of variance because its error was significantly larger than
those of 606, 609 and 610.

At age ten both family and site effects on height
were significant, as was their interaction (Table 3).
Environmental influences among and within sites were
greater than family effects. Partitioning of the inter-

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Table 1, Plantation heights, family variance components
        and correlation coefficients for family mean
        heights at ages five and ten.

Plantation	Mean Height Age 5	Age 10	Family Var, Comp. Age 5	Age 10	Corr. Coeff.
	(meters)		(percent)		
606 Allegheny	1.43	3.22	2,75 ns	0.38 ns	.77**
609 Monongahela	1.64	4,12	13.95 **	15.99 **	.77 **
610 Monongahela	1.63	3.75	0.65 ns	18,27 **	.76 **
611 Monongahela	1.59	-	14.93 **	-	

**
    Significant at the .01 level.

Table 2. Combined analysis of variance for the variation
         in height growth at age five,

Source of Variation	df	Mean Square	EMS
Site	2	2.81 ns	$\sigma_e^2 + f\sigma_{b(s)}^2 + b\sigma2_{sf} + bf\sigma_s$
Block within site	9	0.69 **	$\sigma_e^2 + f\sigma_{b(s)}^2$
Family	49	0.24 *	$\sigma_e^2 + b\sigma_{sf}^2 + bs\sigma_f^2$
Site X Family	98	0.16 ns	$\sigma_e^2 + b\sigma_{sf}^2$
Error	435	0.14	σ_e^2

   * Significant at the .05 level.
** Significant at the .01 level.

Table 3. Combined analysis of variance for the variation
         in height growth at age ten.

Source of Variation	df	Mean Square	EMS
Site	2	40.75 *	$\sigma^2_e + f\sigma^2_{b(s)} + b\sigma^2_{sf} + bf\sigma^2_s$
Block within site	9	7,93 **	$\sigma^2_e + f\sigma^2_{b(s)}$
Family	49	2.32 *	$\sigma^2_e + b\sigma^2_{sf} + bs\sigma^2_f$
Site X Family	98		$\sigma^2_e + b\sigma^2_{sf}$
Heterogeneity	49	1.76 *	
Residual	49	1,07 ns	
Error	432	1,1	

Significant at the .05 level,
Significant at the .01 level.

action sum of squares revealed that the variation among
family regression coefficients was significant at the
five percent level. Stability statistics (regression co-
efficients, sums of squared deviations, and coefficients of
determination) are listed by family in Table 4. There
was substantial variation among families in mean height
growth (2.91 to 4.44 meters) and stability parameters
(e,g., slopes of -1.42 to 2.98), Because the analysis
was based on variation at only three sites, only those
regressions with coefficients of determination greater than
,994 can be judged significant at the five percent level.
However, as 62 percent of the interaction sum of squares
was attributable to the heterogeneity of regressions, the
calculated regression statistics should be reasonably
effective characterizations of those families having high
coefficients of determination (Shukla 1972).

When genotype-environment interactions are analyzed
as linear functions of plantation means, a slope value
of 1,00 represents the average regression. If a stable
family is one whose performance remains relatively
constant from site to site, then a slope near zero and

Table 4. Heights of open-pollinated black cherry
           families and their phenotypic stability
           parameters at age ten,

Family	Mean Height	b_i	d_i	r_i^2
	(meters)			
B 2	4.30	2.62	0,896	.760
B 4	4.35	0,67	0.074	.715
B 5	4.24	−0.32	0.259	.144
B 9	4.01	0.32	0.031	.581
B 11	3.47	2.39	0,073	.970
B 16	4,23	0.79	0.617	.300
B 18	4.11	1,56	0,290	.776
B 19	3.76	1.30	0,093	.883
B 21	3,26	−0,85	0,003	.990
B 23	3.39	−0.73	0.834	.210
M 7	3.53	2.64	0.016	.995
M 8	3.70	−0.31	0.001	.982
M 11	3.21	0.06	0.027	.050
M 12	3.66	−1.42	1.015	.452
M 13	4.12	1,26	0.058	.919
M 14	3.33	0.37	0.001	.982
M 15	3.97	1,03	0.019	.958
M 17	3.72	1.60	0,140	.883
M 18	4.20	2.11	0.288	.865
M 23	4.44	0.28	0.115	.221
M 24	3.85	2.59	0.049	.983
NE 1	4.16	1.25	0.217	.751
NE 8	3.75	0,54	0.178	.402
R 8	3.38	−0.04	0.529	.001
R 13	3,66	−0.75	0.016	.933
R 14	3.56	0.99	0.000	.999
R 15	3.83	0,85	0.848	.260
R 16	3.45	−0,40	0.418	.135
R 18	2.97	0.24	0,024	.493
R 21	3,60	1.42	2.066	.289
R 22	3.84	2,14	0,201	.904
S 3	3,90	0.84	0.015	.951
S 8	3,62	2,98	0.389	.905
S 12	4,10	1.94	0.109	.935
S 19	3.61	1.60	0,030	.972
TV 2	4.40	0.42	0,086	.459
TV 3	4,10	−0.30	0,443	.076
MO 2	4,18	2.59	0.443	,862
MO 8	4.21	2,09	0,009	.995
MO 20	3.23	1,09	0.001	.997
MO 24	3,02	0,76	0.450	,346
MO 25	3,07	1,79	0,091	,936
MO 26	2,84	1,05	0,011	,977
MO 30	2,91	1,03	0.487	,475

Table 4, continued

Family	Mean Height	b_i	d2	r2
	(meters)			
MO 31	4.03	1,83	0.138	,909
MO 32	3,47	1,53	0.342	,739
MO 43	3.28	1,69	0,192	.860
MO 45	2.91	0,56	0.336	,277
MO 46	3.44	0.93	0.503	.414
MO 47	3,45	1,55	0.028	.973

Families preceeded by MO are from the Monongahela National Forest. All others are from the Allegheny.

a small sum of squared deviations from regression will reflect this stability. Some authors (Eberhart and Russell 1966) have found low regression coefficients to be associated with low overall yields, and have, for practical reasons, redefined stability as the slope of the average regression. No relationship between the slope and the average height was evident in the black cherry data.

DISCUSSION

In this study, genetic effects could not be separated into within- and among-provenance variation, as genotypes represented the progeny of 50 superior trees selected in as many stands. Provenance variation may be Important however, as past studies of black cherry progenies have shown that the differences in height growth between provenances are larger than those occurring among families within provenances (Wright and Lemmien 1974, Barnett 1977).

Carter et al. (1982) have also found large provenance differences at various test locations, but relative to the effect of provenance by location interactions, these differences were of less importance when averaged over all locations, Similarly, in our study, genotype-environment interactions were significant after the tenth growing season. Although the method used to investigate these interactions does not define the variation in the response to actual site variables, its use is appropriate when the role of individual geno-types in the total interaction variance is to be

characterized in terms of stability parameters. These
parameters should facilitate the selection of geno-
types which have the desired response to the planta-
tion environments of the Allegheny and Monongahela
National Forests. These estimates pertain only to con-
trasts among the three environments, but even with this
limited sampling substantial family differences are
evident in their responses to different sites.

So far there is no unequivocal answer as to whether
genotypes from each region are better adapted to their
native environments than to others. The Monongahela
families as a group appeared to exhibit greater respon-
siveness to the better growing conditions in the two
West Virginia plantations. Although statistical signif-
icance was lacking (due to the limited number of sites
sampled), the regression coefficient for all Monongahela
families combined was larger than for the Allegheny
families (1.4 versus 0.9). Conversely, the Allegheny
families tended to be taller at all locations. A
similar trend was reported by Carter et al. (1982), who
found that northern seed sources of black cherry grew
relatively taller in northern plantations than in West
Virginia plantations.

When family genotypes are to be selected for both
height growth and phenotypic stability the desired level
for each criterion will have to be determined by the
goal of any breeding program. If the intent is to
develop a variety with broad adaptation to a range of
sites on both National Forests then genotypes character-
ized by above average growth and a regression coefficient
near zero will be most suitable. Families B4, B9, M23,
and TV2 would fit into this category. If, however,
specific adaptation to a set of more favorable environ-
ments is to be developed, then genotypes having large
regression coefficients and at least average growth
would be selected, Most of the Monongahela families and
several Allegheny families (B2, B11, M18, R22, and S8)
meet these criteria, as they were more responsive than
most to the Monongahela sites.

Because all genotypes in the Forest Service program
have been established in several series of progeny
trials, the opportunity exists to compare a more compre-
hensive set of stability estimates over the range of
environments in which they are growing. Such broadly
based estimates would be more reliable in characterizing
families, and would be more definitive in determining
adaptation to Monongahela versus Allegheny environments.

Based on recent findings, plus-tree selection in the wild may not be an effective means of improving either the height or diameter growth of black cherry (Pitcher 1982). However, the amount of variation in height growth in progeny tests is ample to justify an improvement program based on family selection practices, Such a program should incorporate estimates of the level of family stability, as genotype by environment inter-actions have been important in all black cherry experi-ments designed to detect them. Although no evidence has been found that separate varieties are required for the two National Forests, family selection based on means and stability parameters could increase genetic gains at individual sites.

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