GEOGRAPHIC GENETIC VARIATION IN BLACK CHERRY

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Abstract.--Geographic genetic variation for survival, tree growth, and black knot disease susceptibility in a five-year-old black cherry provenance test was examined for relationships with three geographic and eleven climatic variables. Tree growth varied clinally; sources from near the Gulf and Atlantic coasts grew faster than interior sources when planted in central Mississippi. Annual cooling degree days and the amount of precipitation during the summer provided the best explanation of the observed patterns of geographic genetic variation. Seven geographic subregions of closely related provenances with distinct characteristics were identified.

Additional keywords: *Prunus serotina*, provenance test.

A certain amount of risk is involved in any tree improvement program if it is initiated without prior information on geographic genetic variation. The importance of such information has already been recognized in many forest tree species. Some information on geographic variation in black cherry (*Prunus serotina* Ehrh.) is available (Barnett 1977, Cech and Kitzmiller 1968, Cech and Carter 1979, Earnst 1978, Genys and Cech 1975, Wright and Lemmien 1974) but these earlier studies lacked coverage over much of the southern portion of the range. The objective of the present study is to examine and describe the geographic genetic variation of black cherry throughout its range.

MATERIALS AND METHODS

During 1979 and 1980 an extensive collection of open-pollinated seeds from 46 locations across 20 states in the Eastern United States was made by the U. S. Forest Service (Figure 1). The procedures followed for seed collection, seed extraction, and seedling production in the nursery have been described by Pitcher (1984).

In 1982, one-year-old seedlings were outplanted at the Truck Crops Branch Experiment Station of the Mississippi Agricultural and Forestry Experiment Station (MAFES) located near Crystal Springs, Mississippi. Ninety open-pollinated families representing 35 seed sources were planted in a randomized complete block design having four replications and four-tree family row plots. The family plots are not grouped by sources, but rather

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Figure 1. Locations of seed sources in the black cherry range.

are randomly assigned within replications. Spacing among trees is 10 feet by 10 feet, and the planting is surrounded by two border rows.

Survival, dbh, tree height, and black knot disease infection (*Dibotryon morbosum*) were measured five years after the study was planted. These four traits are hereafter called the dependent variables. When a tree was alive and less than 4.5 feet in height, then a value of zero was assigned for dbh. Three geographic characteristics of each provenance--latitude, longitude, and elevation--and eleven climatic traits of each provenance--mean annual temperature (MANTEMP), mean maximum (MAXTEMP) and minimum (MINTEMP) temperatures, mean annual precipitation (MANPREC), the sum of the mean monthly precipitation for June, July and August (SMOPREC), annual heating degree days (ANHTDD) and cooling degree days (ANCLDD), mean number of frost-free days (above 32°F) (MFRFRD), number of days after December 31 to the last 32°F temperature in the spring (MDTOL32), precipitation for the 100 days after the mean date of the last 32°F in the spring (PREC100), and sum of growing degree days above 42°F for the first 100 days after last frost (SGROWDD)--were obtained by the U. S. Forest Service personnel from the National Climatic Center in Asheville, NC. These are referred to as the independent (or predictor) variables in the analyses of this study.

SAS procedures (SAS Institute 1985) were used for all analyses. Analyses of variance, using SAS procedure PROC GLM, were conducted on plot means for each of the dependent variables to test for significance of provenance variation and family-within-provenance variation. Canonical correlation procedure (PROC CANCORR) was used to obtain preliminary information on the relationships between dependent and predictor variables. Principal component analysis was carried out on source means by PROC PRINCOMP to get a weighted combination of the four traits. The standardized first principal component was then used as the dependent variable in stepwise multiple regression analysis (PROC STEPWISE) against the geographic and climatic independent variables for seed origins to identify the best model for explaining patterns of geographic variation. Cluster analysis (Ward's method in PROC CLUSTER) helped to delineate different black cherry regions of closely related provenances, and prediction ratios (PR) provided measures of association among clusters. The prediction ratios were computed from coefficients of determination (R^2) using the formula

$$PR = (1 - R^2).$$

RESULTS AND DISCUSSION

Survival

Fifth-year survival averaged 86 percent for the study, and it ranged from 63 to 100 percent among the provenances (Table 1). Variation among

Table 1. Means and ranges of tree traits in black cherry provenance test.

Statistic	Survival (%)	DBH (inches)	Height (feet)	Black Knot (% infected)
Study Mean	86	0.29	5.8	30
Range in Prov. Means	63-100	0.02-1.42	2.9-12.6	7-91

provenances was significant, but the variation among families within provenances was not significant.

Four provenances in the northeast region (#8, #10, #19, and #43) and two in the extreme south (#76 and #80) suffered more mortality than those from the central region. The only exception in the central region was #28 from Texas County in Missouri, which had only 69 percent survival. Although the pattern of geographic variation for survival was not conspicuous in the present study, it appeared similar to the one observed in earlier provenance tests (Genys and Cech 1975, Earnst 1978, Cech and Carter 1979). All of those tests used the same seed sources, and survival was measured at older ages than reported here.

Diameter and Height Growth

Average dbh and tree height were 0.29 inches and 5.8 feet, respectively, after five growing seasons at the Mississippi site (Table 1). Provenance #77 (Columbia, FL) was the fastest growing provenance and was 12.6 feet tall with a dbh of 1.44 inches. Trees from McKeen County in Pennsylvania had the poorest growth, with a fifth-year height of 2.9 feet. Provenance variation was significant for both dbh and height, but family variation within provenances was not. The lack of family variation within provenances may be due to the very small number of families (one or two) that represented nearly half of the provenances.

Diameter and height growth decreased with increasing latitude of the provenance (Figures 2 and 3). Provenances from near the seacoast grew

Figure 2. Geographic variation for tree height at age 5 in black cherry.

Figure 3. Geographic variation for dbh at age 5 in black cherry.

faster than interior provenances at the same latitude. Within the interior, a pattern of poor growth was observed for provenances from near the Mississippi River and from the Blue Ridge and Appalachian Mountains.

One might have anticipated that provenances from milder climates than the central Mississippi planting site (i.e., from south of the site and/or closer to the ocean than the site) would grow faster than provenances from north of the site or from higher elevations, since this has been observed for other hardwood species (Webb 1970). The poor performance of the provenances in the lower Mississippi River valley is unexpected, however, and is opposite to trends observed by Land (1981) for sycamore (*Platanus occidentalis* L.) and by Mukewar and Land (1987) for typical southern red oak (*Quercus falcata* Michx. var. *falcata*). The four poor-performing Mississippi provenances-#62 from Marshall County, #63 from Carroll County, #82 from Amite County, and #84 from Scott County--all come from areas with thin loess soils that are similar to the soils at the planting site. Migration of alleles from farther north by seed movement down the river seems unlikely, since the species does not grow in the alluvial bottomlands of the southern Mississippi River valley. Perhaps an edaphic ecotype occurs on this margin of the species range, as suggested for sweetgum (*Liquidambar styraciflua* L.) by Wells et al. (1979).

Black Knot Disease Infection

Incidence of black knot disease was as high as 91 percent in the seed source from Texas County in Missouri with an overall average of 30 percent (Table 1). The lowest infection of seven percent was recorded in the Mississippi provenances from Carroll and Scott Counties. Provenances from Florida and from most of the northern origins suffered heavy infection, while five out of the six seed sources from Mississippi were least affected. Provenances from the Atlantic and Gulf coastal plains (except those from Mississippi) showed a uniform reaction to the disease, with an overall average of 25 percent infection. These differences among provences for disease susceptibility were highly significant.

Two possible explanations for the pattern of variation in black knot susceptibility are: (1) reduced vigor due to off—site planting may act as a predisposing factor for disease infection, or (2) a different physiological race of the disease organism may be present in the region of the test site, so that only the local provenances have developed resistance to that race. The pattern also supports the proposal of a local edaphic ecotype of black cherry, as suggested for the growth results.

Geographic Genetic Variation

The canonical correlation procedure indicated that the growth traits are highly correlated with all the climatic variables measuring temperature and precipitation, except the sum of growing degree days (SGROWDD) and precipitation for the 100 days after last 32°F in the spring (PREC100) (Table 2). Growth—trait correlations with latitude are large and negative,

Table 2. Correlations between dependent and predictor variables in black cherry provenance test.

	Dependent Variables			
Predictor Variables	Survival	dbh	Height	Black Knot
MANTEMP	0.03	0.75	0.81	-0.22
MAXTEMP	0.06	0.74	0.80	-0.18
MINTEMP	0.00	0.74	0.80	-0.25
MANPREC	0.04	0.51	0.58	-0.11
SMOPREC	-0.36	0.75	0.76	-0.03
ANHTDD	-0.04	-0.74	-0.80	0.20
ANCLDD	0.03	0.74	0.80	-0.27
MFRFRD	-0.03	0.74	0.80	-0.27
MDTOL32	-0.01	-0.71	-0.77	0.27
PREC100	0.33	0.13	0.21	-0.12
SGROWDD	0.21	0.18	0.18	0.10
Latitude	-0.06	-0.75	-0.81	0.18
Longitude	0.45	-0.12	-0.04	-0.09
Elevation	-0.07	-0.64	-0.69	0.31

while the correlations with elevation are moderate and negative. There is no relationship, however, between the growth traits and longitude. Survival and black knot disease have very poor or no relationship with any of the fourteen predictor variables. Tree height and mean annual temperature are the most important dependent and independent variables, since they ranked highest for the standardized canonical coefficients in the first canonical correlation. This first canonical correlation was 0.97 and accounted for 94 percent of the combined variation.

The standardized first principal component, a weighted combination of the four dependent variables, expresses 99 percent of the combined variables' variation among provenances. The pattern of variation of this derived variable is similar to the ones observed for the growth traits. When it is used as a single dependent variable in stepwise regression, latitude and mean annual temperatures of provenance are equally good as single predictors in explaining geographic genetic variation. However, the best model containing two predictor variables (annual cooling degree days and the sum of monthly precipitation during the summer) is much better than either of these single-predictor models and the best three-variable model (latitude, the sum of monthly precipitation during the summer, and elevation) is slightly better than the two-variable model. The predictive capabilities of these two larger models are 83 and 85 percent, respectively.

Since mean annual temperature or annual cooling degree days are closely related to latitude and elevation (correlations vary between -0.76 and-0.97), temperature at the seed origin may be the primary natural selection force influencing geographic genetic variation in the species. Precipitation during summer months is the next most important predictor in the models, indicating that degree of water stress during the growing season is also an influential factor. The provenances with slower growth variation from the lower Mississippi River valley and from the Appalachian highlands are, in fact, from areas of low precipitation during summer months (Figure 4b). The Appalachian highlands are also cooler than the adjacent provenances on the same latitude (Figure 4a). Therefore, the geographic patterns observed for growth traits may be explained as adaptations to temperature and summer precipitation, rather than by edaphic ecotypes or migration of alleles down the river systems.

Cluster Analysis

Cluster analysis based on fifth-year survival, growth, and black knot susceptibility when planted in central Mississippi identified two main groupings of provenances in the black cherry range: a southern group for the southeastern and southern coastal plains (approximately) and a northern group for the piedmont, mountains, and interior highlands (Figures 5 and 6). The only deviation of these groupings from the stated physiographic divisions is in the Mississippi River valley, where the northern group "Its across a northern extension of the coastal plain.

Further subdivision of each main group indicated three clusters of similar provenances in the south and four clusters in the north (Figure 5 and 6). The three southern clusters are geographically mutually exclusive

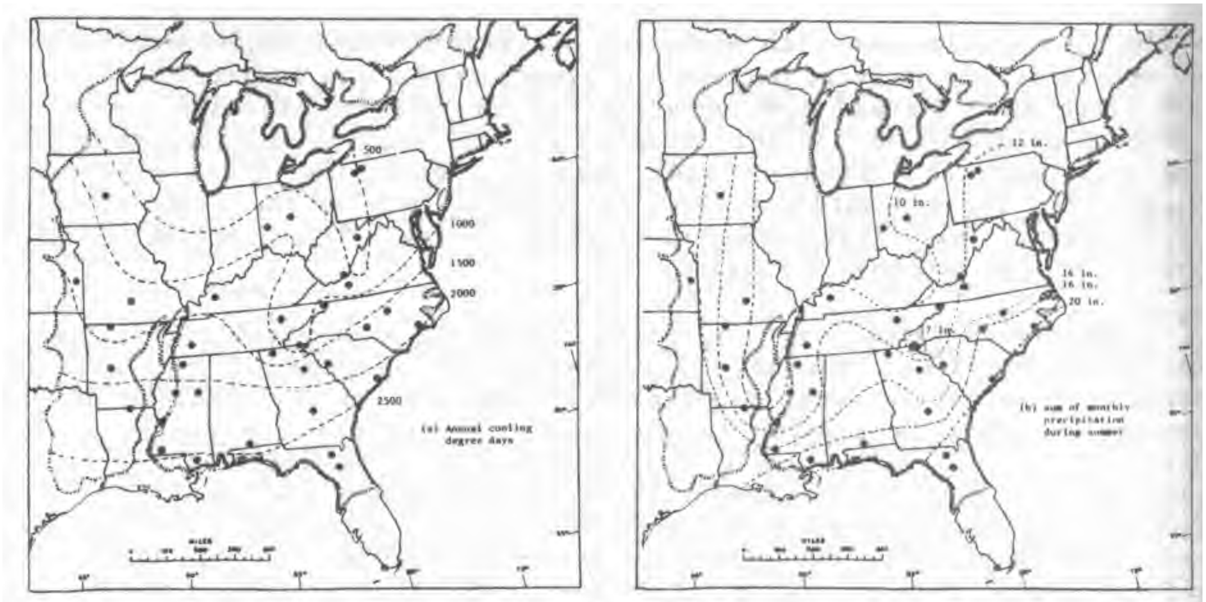

Figure 4. Geographic patterns of two climatic measures of temperature and moisture that influence provenance variation in black cherry.

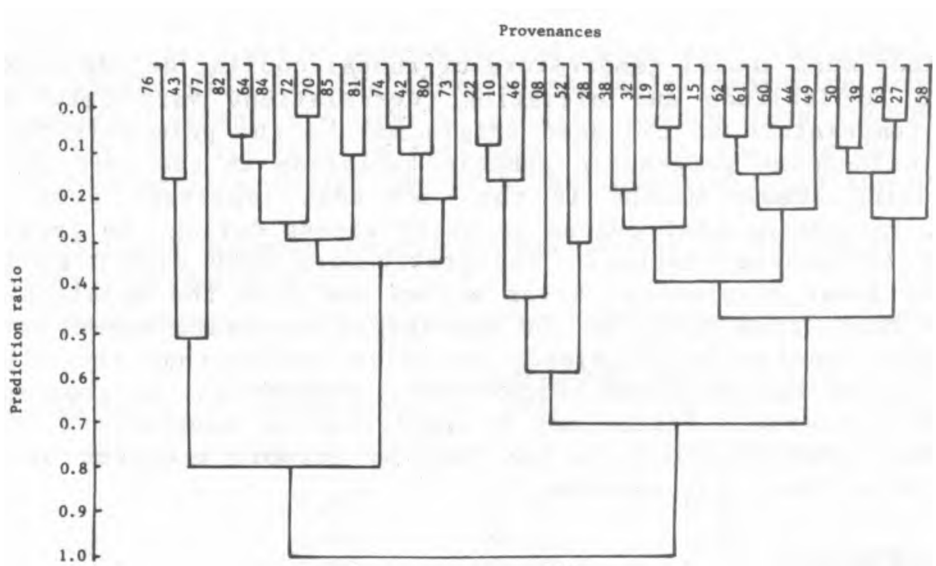

Figure 5. Output of cluster-analysis in the form of a dendrogram for black cherry provenances.

and are roughly defined as (1) northern Florida, (2) the southeastern Atlantic and lower Gulf coastal plains, and (3) the central Gulf coastal plain. Two of the northern clusters are mutually exclusive of each other and approximate (1) a central interior and (2) a northern interior region. The other two northern clusters are geographically dispersed throughout the central interior and northern interior regions. One of these dispersed groups is represented by five high elevation provenances (#8, #10, #22, #46, and #52 in Figure 6) in the eastern part of the Appalachian Highlands and one high elevation provenance (#28) in the Ozark Plateau. The other

Figure 6. Clusters of closely related provenances of black cherry.

dispersed group contains two high elevation provenances from the Valley and Ridge physiographic area of the Appalachian Mountains (#39 and #50), one high elevation provenance from eastern Kansas (#27), and two low elevation provenances from the northern extension of the coastal plain along the Mississippi River (#58 and #63).

Each of the seven clusters represents a unique combination of survival, growth, and black knot disease susceptibility (Table 3). Among the three clusters of the southern region, survival increases while growth rate and disease susceptibility decrease from cluster #1 through cluster #3. Differences in the amount of precipitation during the summer are more conspicuous than the differences in annual cooling degree days and elevation. Survival and disease susceptibility are usually higher for the northern clusters than for the southern ones, and average growth of these northern clusters closely follow the differences in annual cooling degree days. Exceptions are found in northern clusters #6 and #7, which are geographically dispersed. Cluster #6 has unusually low survival when planted in central Mississippi, while cluster #7 exhibits a very low incidence of black knot.

The dispersed cluster #7 provides an example of why cluster analysis should be used only with other supporting multivariate analyses in biosystematic studies of a species. Since it clusters provenances by similarities in dependent traits, it tells nothing about the factors influencing those similarities. Cluster #7 has slow-growing provenances with low disease incidence, so that it is different from the fast-growing southern clusters and from the disease-susceptible northern clusters. However, the factors contributing to the slow growth are different for the Mississippi River valley sources than for the Appalachian sources, as discussed earlier. Thus, the five sources within cluster #7 are probably genetically diverse. These biosystematic studies require careful examination of data by several

Table 3. Cluster means for black cherry provenances.

Cluster Names	Dependent Variables: Survival (%)	dbh (inches)	Height (feet)	Black Knot (% infected)	Independent Variables: Annual Cooling Degree Days	Summer Precipi-tation (inches)	Ele-vation (feet)
SOUTHERN REGION							
1. Northern Florida	70	0.96	10.1	44	2484	20.8	107
2. Southeastern Atlantic & Lower Gulf Coastal Plains	81	0.56	7.9	24	2073	16.5	353
3. Central Gulf Coastal Plain	90	0.42	6.9	16	2172	13.1	414
NORTHERN REGION							
4. Central Interior	96	0.23	5.6	37	1531	13.5	1142
5. Northern Interior	93	0.04	3.9	45	898	11.3	1078
6. Appalachian & Ozark Highlands	75	0.08	4.0	53	859	12.1	1910
7. High & Low Elevation Group	94	0.18	4.9	15	1431	12.2	1216

analyses procedures, including canonical correlations, principal components, stepwise regression, and cluster analyses, to help identify taxonomic groups and causal factors. The proposed groups must then be verified by biochemical and cytogenetic investigations.

CONCLUSIONS

Provenance variance is significant for survival, tree height, dbh, and black knot disease susceptibility in black cherry when planted in central Mississippi. Seed sources from near the Gulf and Atlantic sea coasts grow faster than those from interior regions. Seed sources from Mississippi and from some of the high elevations in the central and northern regions have above-average resistance to black knot disease. Annual cooling degree days and the sum of monthly precipitation during the summer are the best two variables for explaining the observed geographic genetic variation in the species. Seven groupings (or clusters) of provenances in the study reported here can be identified, based on similarities in survival, growth, and disease resistance. The five of these which are geographically mutually exclusive may be tentatively defined as "provenances", but must be verified by biochemical and cytogenetic investigations. Abnormally slow growth from sources in the lower Mississippi River valley is apparently an adaptation to high water deficits during the summer rather than an edaphic ecotype or a reflection of migration of alleles down the river system.

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