GEOGRAPHIC GENETIC VARIATION
IN SOUTHERN RED OAK

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Abstract.--A five-year-old southern red oak provenance-progeny test planted in central Mississippi exhibits clinal patterns of increasing tree height, diameter, and survival as origin of the acorns moves southward and/or closer to the sea coast. Sources from southeastern Texas and eastern Georgia have grown fastest at the Mississippi site. Narrow-sense heritability estimates for open pollinated families within sources ranged from 0.30 to 0.43 for third-year and fifth-year diameters and heights. Survival did not differ among provenances during the first five years of the study.

Additional keywords: *Quercus falcata* var. *falcata,* provenance test, progeny test, heritability.

The typical variety of southern red oak (*Quercus falcata* Michx. var *falcata*) is one of the most ubiquitous of the upland southern oaks. Its range extends from New York to northern Florida and westward to eastern Texas and Oklahoma (Fowells 1965). Although it is usually not as valuable per tree as its related variety, cherrybark oak (*g*, *falcata* var. *pagodaefolia*), the lumber of equivalent grade from the two varieties is equal in value and is mixed at the sawmill. The combination of (1) high value of oak and (2) frequent occurrence of the typical southern red oak variety makes it an economically important component of the southern forests.

Provenance and progeny studies have been conducted for northern red oak (*Quercus rubra* L.) (Kriebel 1965, Taft 1965, Webb 1970) and cherrybark oak (Randall 1973). However, no information is available about geographic genetic variation in typical southern red oak or about genetic variation among trees within provenances of the species. The purposes of the study reported here are to (1) describe patterns of geographic genetic variation in the southern population of the species (2) identify the fastest growing sources for central Mississippi, (3) compare the relative magnitudes of genetic variation within provenances as versus genetic variation among provenances, and (4) provide estimates of heritabilities for height and diameter growth of trees within provenances.

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MATERIALS AND METHODS

Open-pollinated acorns from 112 southern red oak trees representing 43 stands in 23 provenances (Figure 1) were collected in 1979 and kept sepa-

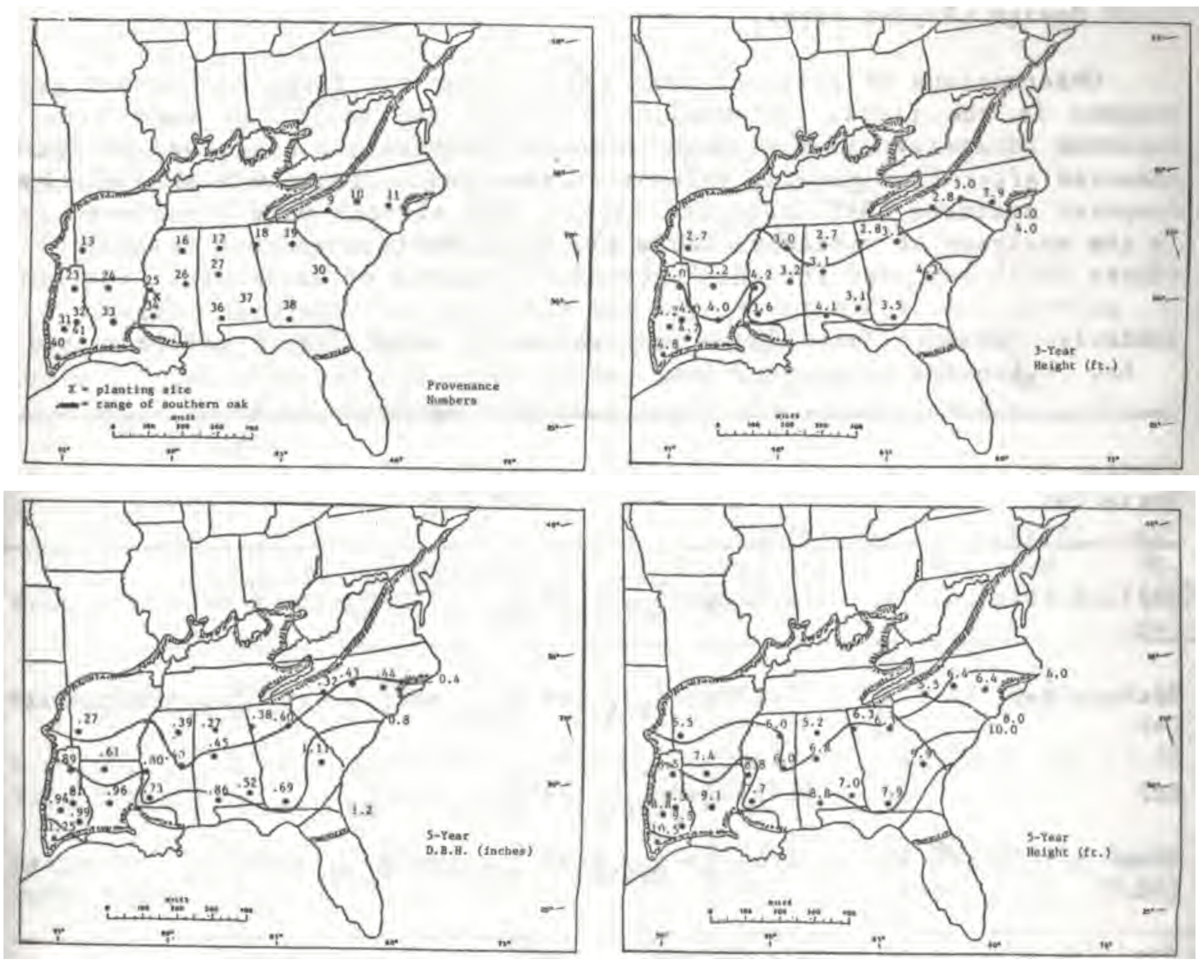

Figure 1. Maps of the natural range of southern red oak with locations of provenances and patterns of geographic genetic differences for third-year height, fifth-year DBH, and fifth-year height.

rately identified by mother tree. Provenances ranged in latitude from 29.7°N (Harris County, Texas) to 35.4°N (Montgomery County, North Carolina), and in longitude from 78.3°W (Sampson County, North Carolina) to 95.4°W (Harris and Trinity Counties, Texas).

Seedlings were raised during 1980-81 at the USDA Forest Service nursery in Starkville, Mississippi. In February 1982 the 2-0 seedlings were outplanted at the MAFES (Mississippi Agricultural and Forestry Experiment Station) Truck Crops Branch Experiment Station near Crystal Springs, Mississippi. Spacing among trees is 10 x 10 feet and the planting is surrounded by two border rows. The experimental design is a randomized complete block with five replications and three-tree family row plots. The row plots of families from the same provenance were planted adjacent to each other within a replication, so that analysis of variance will treat the study as a split plot design. Seed sources are the whole units and families within sources are the subunits. The design is called a compact family block design (Snyder 1966).

Observations of survival were taken after the first and second growing seasons in the field. Groundline diameter and height of each tree were recorded after the third growing season. Survival, d.b.h., and height were measured after five growing seasons in the field. Data were analyzed by SAS computer software (SAS Institute 1985). All effects were considered random in the analyses of variance (Table 1), and a Satterthwaite-F (pseudo-F) test (Hicks 1973) was used for the "provenance" source of variation. Patterns of

Table 1. Format of analysis of variance used for a southern red oak provenance-progeny test.

Sources of Variation	D.F.	E.M.S.[a]
Replications (=R)	4	$(1/h)\sigma^2_W+\sigma^2_{RF(SP)}+f\sigma^2_{RS(P)}+fS\sigma^2_{RP}+fSP\sigma^2_R$
Provenances (=P)	22	$(1/h)\sigma^2_W+\sigma^2_{RF(SP)}+f\sigma^2_{RS(P)}+r\sigma^2_{F(SP)}+rf\sigma^2_{S(P)}+fs\sigma^2_{RP}+fsr\sigma^2_P$
RxP	88	$(1/h)\sigma^2_W+\sigma^2_{RF(SP)}+f\sigma^2_{RS(P)}+fs\sigma^2_{RP}$
Stand w/i Prov (=S/P)	20	$(1/h)\sigma^2_W+\sigma^2_{RF(SP)}+f\sigma^2_{RS(P)}+r\sigma^2_{F(SP)}+rf\sigma^2_{S(P)}$
Families w/i Stand w/i Prov (=F/S/P)	69	$(1/h)\sigma^2_W+\sigma^2_{RF(SP)}+r\sigma^2_{F(SP)}$
RxS/P	80	$(1/h)\sigma^2_W+\sigma^2_{RF(SP)}+f\sigma^2_{RS(P)}$
RxF/S/P	276	$(1/h)\sigma^2_W+\sigma^2_{RF(SP)}$
Among Trees w/i Plots	1120	σ^2_W
Total	1679	

[a] h = harmonic mean number of trees per plot.

geographic genetic variation were illustrated with isogenic lines drawn on a range map of the species in the southern United States, and Students t-test was used to determine significant differences of provenance means from the overall study mean. Narrow-sense heritability estimates on an individual-tree basis were determined from family variation within stands within provenances by the equation

$$h_N^2 = \frac{4\sigma^2_{F(SP)}}{\sigma^2_w + \sigma^2_{RF(SP)} + \sigma^2_{F(SP)}},$$

where the variance components were determined by equating actual mean squares with the expected mean squares in Table 1.

RESULTS AND DISCUSSION

Overall survival for the study was 93 percent after five growing seasons in the field (Table 2), so that no significant differences were

Table 2. Southern red oak study means, coefficients of variation, and ranges in provenance means for survival, stem diameter, and height.

Statistic	Percent Survival 1st Yr.	Percent Survival 2nd Yr.	Percent Survival 5th Yr.	Third Year Groundline Dia. (in.)	Third Year Ht. (ft.)	Fifth Year DBH (in.)	Fifth Year Ht. (ft.)
Study Mean	95	94	93	0.95	3.51	0.63	7.42
C.V. for Plot Means	13.50	15.96	16.38	23.17	18.08	41.66	18.33
Range in Prov. Means	89-100	87-97	80-87	0.65-1.41	2.69-4.84	0.27-1.25	5.21-10.56

detected among sources, stands, or families for this trait. Mean height for the study doubled from 3.5 feet at age three (three growing seasons in the field) to 7.4 feet at age five, and the error variance increased by about the same amount as indicated by essentially no change in the coefficient of variation. By age five the average tree had a DBH of nearly two-thirds of an inch, but values varied widely as illustrated by the large coefficient of variation and wide range in source means.

Genetic variation among the 112 families in the study was significant for both diameter and height at both age three and age five (Table 3). Provenance effects accounted for approximately 70 percent of this variation, and family differences within stands within provenances made up another 20 percent. However, variation among local stands within provenances was only significant for root collar diameter at age three, and it accounted for only

Table 3. Variance component estimates and narrow-sense heritabilities for third-year and fifth-year diameters and heights in the southern red oak study.

Trait	h^2_N	Variance Components and Results of F-tests[a/] (1) Provenance Estimate (% Total)	(2) Stand w/i Prov. Estimate (% Total)	(3) Family w/i Stand Estimate (% Total)	Total Family Variance (1+2+3)
Root Collar Age 3	0.30	0.0301** (70)	0.0043** (10)	0.0088** (20)	0.0432
Height Age 3	0.40	0.3350** (67)	0.0612 ns (12)	0.1043** (21)	0.5005
D.B.H. Age 5	0.40	0.0700** (73)	0.0085 ns (9)	0.0170** (18)	0.0955
Height Age 5	0.43	1.9635** (72)	0.2462 ns (9)	0.5161** (19)	2.7258

a/** = significant at 99% level of probability;
* = significant at 95% level of probability;
ns = nonsignificant.

ten percent of the family variability. A similar lack of genetic differences among local stands has been reported by Land (1981) for sycamore (*Platanus occidentalis* L.). Migration probably predominates over local natural selection forces (but not regional natural selection) in forming patterns of genetic variation in these species' natural populations.

The significant genetic variation among families within stands within provenances indicates that genetic gains in growth can be accomplished from selection of individual trees within stands to serve as parents for a seed orchard. the amount of gain is dependent upon the size of the narrow-sense heritability. In a provenance-progeny test the narrow-sense heritability must be based on the additive genetic variance among trees from the same breeding population (families within stands within provenances), since crosses among different provenances may not give a purely additive response. Narrow-sense heritability estimates in the present study are near 0.40 (Table 3), which are quite high. These estimates may be inflated from genotype-by-site interactions, since the study was grown on only one site, or by the incorrect assumption that all individuals of a family are half sibs. Squillace (1974) has shown for open-pollinated families that a better approximation of additive genetic variation is three times the family variance component, rather than four times the component. With this adjustment and some reduction for genotype—by—site interactions, the heritabilities might be halved to give values near 0.20. These values are close to those found for other species and can still provide genetic gains from mass selection.

The significant variation among provenances indicates that additional genetic gains at the central Mississippi site can be obtained by using acorns collected from the best geographic origins. Ranked provenance means show that progenies obtained from southeast Texas (#40 from Harris County and #41 from Jasper County) and eastern Georgia (#30 from Bulloch and Candler Counties) grow significantly faster than the study average at the Crystal Springs site (Table 4). Other provenances that fall in the superior

Table 4. Ranked provenance means for third—year and fifth—year diameters and tree heights in the southern red oak provenance—progeny test. Only those provenances that are significantly greater (57. probability level) than the study mean are given.

Third Year						Fifth Year					
Root Collar Diam. (in.)			Height (ft.)			DBH (in.)			Height (ft.)		
Source	Rank	Mean	Source	Rank	Mean[a]	Source	Rank	Mean	Source	Rank	Mean
40	1	1.41	40	1	4.84	40	1	1.25	40	1	10.50
			41	2	4.68	30	2	1.11	30	2	9.94
			30	3	4.32	41	3	0.99	41	3	9.50
			25	4	4.24	33	4	0.96			
			31	5	4.20						
Study Mean = 0.95			Study Mean = 3.51			Study Mean = 0.63			Study Mean = 7.42		
CD = 0.23[b]			CD = 0.66			CD = 0.27			CD = 1.41		

[a] Lines connect means that are not significantly different at the 5% probability level according to the Student-Neuman-Keuls test.

[b] CD = critical difference = SEM x "t" (having error df at 5%), where SEM = $\sqrt{2 \times (\text{error SS/DF})/(\text{No. of Reps})}$

group for at least one of the growth traits include #33 from Rapides Parish in Louisiana, #31 from Trinity and Polk Counties in Texas, and #25 from Warren County in Mississippi. The sources #40, #41, and #30 all come from within 50 to 75 miles of the coast and probably represent adaptation to a milder climate with a longer growing season than found for the other sources. However, sources #31 and #33 are only 100 miles from the Texas-Louisiana coast and are south of the planting site, so that they are also probably adapted to a long growing season. Source #25 is slightly north of the planting site, but the trees come from near the Mississippi River. A possibility for its superior performance is discussed below.

A better picture of patterns and possible causes of geographic genetic variation in southern red oak is obtained by mapping the provenance locations and means and then drawing isogenic lines (Figure 1). The lines indicate that when trees are planted in central Mississippi, there is a clinal increase in growth as geographic origin of the acorns moves south in latitude or towards the coast at the same latitude. Trees from milder oceanographic climates grow more per year than trees from colder continental climates when planted at that site. The one abnormality in this trend is an apparent bulge in isogenic lines up the Mississippi River. One would have anticipated that the bulge would be in the opposite direction due to migration (seed movement) down the river. That type of response and hypothesis was given by Wells et al. (1979) for sweetgum (*Liquidambar styraciflua* L.) in Mississippi. Perhaps the reason for the faster growth of "Mississippi River neighborhood sources" than other sources at the same latitude is hybridization with cherrybark oak. This possibility has not yet been investigated.

CONCLUSIONS

The geographic area of acorn collection had no effect on survival of southern red oak for the first five years after planting in central Mississippi. Provenance differences and family-within-stand-within-provenance differences for stem diameter and height growth were highly significant, however, and indicated a great amount of genetic diversity within the species' natural population. Provenances from southeast Texas and eastern Georgia proved to be the fastest growing sources when planted in central Mississippi. It is believed that these sources have evolved in milder climates and have a longer growing season than other sources in the study. Hybridization with cherrybark oak is proposed as a possible reason for the good performance of sources from near the Mississippi River.

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