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Geographic Variation in Quercus rubra in North Central United States Plantations[1])

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Introduction

Cooperative provenance testing of northern red oak (*Quercus rubra* L.) was initiated in 1962 by the state agricultural experiment stations in the North Central region of the U.S.A. The primary objectives are: (1) to identify genetic variation in important traits and also possible response interactions between geographic origin and planting locality; (2) to make seed source recommendations for the establishment of genetically-improved plantations of red oak in the North Central region.

Methods

Seed was collected from an average of 8 trees per geographic origin (provenance). Collection localities were distributed over most of the species range, except for the southernmost areas (*Fig.* 1). Earlier, trials in Ohio had indicated that extreme southern population samples of Q. *rubra* were not winter-hardy in the North Central region of the U.S.A.

Three successive seed years were required to complete the collections. At the time, long-term storage methods had not been developed for red oak. Therefore, each year's collections were sown in the Ohio Division of Forestry's Green Springs nursery soon after receipt in the autumn. Thus there were three successive years' nursery stock.

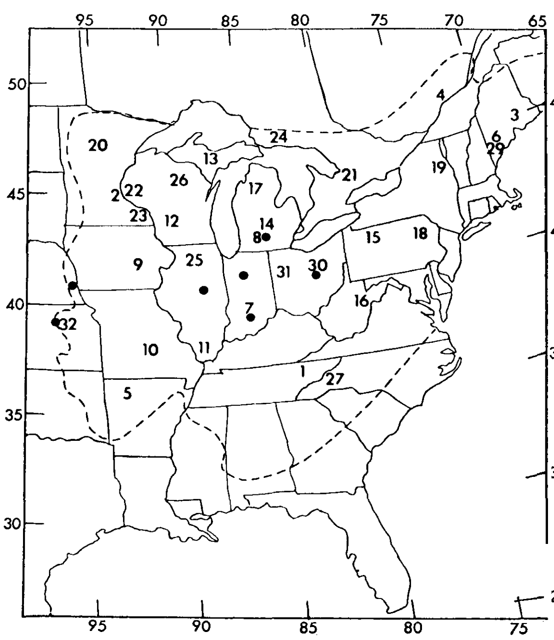

Fig. 1. — Red oak seed collection localities (numbers), experimental plantation localities (dots), and limits of the species distribution (broken line, from LITTLE 1949).

[1]) North Central Regional Project NC-99, Cooperative State Research Service, U.S. Dept. of Agriculture. Approved for publication as OARDC Journal Paper No. 156-76.

[2]) Ohio, Nebraska, Kansas (3), Illinois, Indiana and Michigan state agricultural experiment Stations, respectively, and U.S. Forest Service, Bedford, Indiana.

Seed of 3 of the 10 trees of Arkansas provenance 5 had some characteristics of pin oak *(Quercus palustris* MUENCHH.). Later foliar analysis by S. E. SCHLARBAUM showed that some of the progeny of provenance 5 were hybrids and others *Q. palustris*. Since the pure *Q. rubra* was not kept separate in recording field data, mean values for the provenance may be less representative than other provenance means.

The seed tree identity of each seedlot was maintained in the nursery. Part of each seedlot was planted in 4 replicates. At the end of the first growing season, comparisons were made of parental and provenance effects on growth (KRIEBEL 1965).

Field plantings were made after one year in the nursery, in the springs of 1962, 1963 and 1964. The seedlots were bulked within provenances in all plantings except Ohio. Trees from 31 provenances were field-tested, of which 28 were replicated in more than one test locality. The seven test localities are listed in *Table 1*. Two additional experimental plantations, one in Iowa and one in northern Illinois, could not be maintained. No usable data were obtained from either plantation.

Table 1. — Location of experimental plantations of red oak in the North Central region, survival percentage, and average height at age 13 or 14.

Locality	County	State	Survival %	Height, Meters1/	Age
Plattsmouth	Cass	Nebraska	77	5.5**	14
Tuttle Creek	Riley	Kansas	10	3.2**	13
Monticello	Piatt	Illinois	82	3.9**	14
Augusta	Kalamazoo	Michigan	89	6.8*	14
W. Lafayette	Tippecanoe	N. Indiana	59	3.5	13
Georgia Tower	Lawrence	S. Indiana	42	4.1	14
Apple Creek	Wayne	Ohio	54	5.2**	14

[1]) Asterisks indicate significance level of differences among provenance means.

Spacing in the 7 remaining plantations was as follows:

Kansas, Nebraska,	
N. Indiana, Ohio	2.7 × 2.7 m
Illinois	2.4 × 3.0 m
Michigan	1.8 × 3.0 m
S. Indiana	1.8 × 1.8 m

Phenological observations included: relative flushing date, scored in Nebraska in 1975, number of growth flushes, scored in Ohio in 1968, and relative time of autumn leaf coloration, measured in 3 plantations in 1968. A tree was considered "flushed" when 50% of its buds had expanded enough to make the small leaves visible. Leaf coloration observations were made on a single day in the middle of the coloration period in October, rather than by repeated observations after "day 1". The procedure was to score each tree on a scale of 1 to 10. On the scale, 1 = leaves dark green, 6 = leaves fully red (8 in Kansas) and 10 = leaves completely brown, with gradations between. A tree's score was therefore an index value representing the relative degree of chlorophyll degradation on the observation date. The relation of time of autumn leaf coloration to latitude was estimated by analysis of regression of provenance means on latitude. Time of coloration was based on the average of Kansas, Illinois and Ohio provenance means.

Mortality and total height were recorded in all plantations in 1968 or 1969 and again in 1973 or 1974. DBH and crown diameter (averaged for north-south and east-west directions) were measured in some plantations. Seed source differences in height and diameter were evaluated separately for each plantation by analysis of variance, based on plot means. Within plantations, a separate analysis was made for each year's set of provenances. The average height of trees of each provenance in a plantation was converted to its percentage of the plantation mean *(Table 3)*. This

Table 3. — Relative height (expressed as % of plantation mean) of red oak of 31 origins planted at seven localities in the North Central region.[1])

Seed origin data					Relative height when planted in							
No. & State or Prov.	N. Lat.	W. Long.	Elev. m	Year planted	KA	NE	IL	Sou. IN	Nor. IN	MI	OH	Average all sites
20 MN	47.3	94.5	396	1962	88	100	108	84	97	94	88	96
13 MI UP	46.5	87.3	235	1962	89	81	76	80	96	89	101	88
24 ONT	46.2	83.2	190	1962	--	87	75	87	93	96	94	89
22 WI	45.8	92.7	423	1963	95	107	106	--	106	104	102	104
4 QU	45.8	73.8	42	1964	--	--	--	--	--	--	95	95
26 WI	45.6	89.3	488	1962	--	98	104	113	102	99	103	102
2 MN	44.8	93.6	274	1962	92	118	93	88	92	99	87	96
3 ME	44.8	68.5	52	1962	--	97	108	61	91	88	90	92
21 ONT	44.5	80.0	183	1962	--	100	80	101	110	109	114	102
17 MI LP	44.2	85.3	420	1962	--	99	86	136	103	113	102	104
19 NY	44.2	73.3	100	1962	--	104	91	80	109	114	94	101
23 MN	44.1	92.1	297	1963	93	93	91	--	99	106	90	95
12 WI	43.6	90.8	396	1963	75	104	120	--	100	101	103	103
29 ME	43.5	70.8	90	1962	--	97	110	127	103	98	110	106
6 ME	43.5	70.6	90	1962	--	89	95	113	93	93	99	96
14 MI LP	42.8	84.3	265	1964	72	106	99	--	95	--	107	98
8 MI LP	42.3	85.3	259	1964	90	110	118	--	107	--	102	107
25 IL	42.0	89.2	227	1963	--	--	--	--	--	--	93	93
15 PA	41.8	79.2	375	1964	--	105	95	--	107	--	116	106
9 IA	41.7	91.4	314	1963	112	99	101	--	91	98	97	99
18 PA	41.2	76.1	427	1964	91	106	101	--	86	--	94	96
31 OH	40.8	84.2	269	1962	105	109	117	87	109	103	103	106
30 OH	40.7	81.9	293	1964	101	78	84	--	10o	--	89	89
32 KA	39.2	96.5	334	1964	149	112	107	--	100	--	91	108
16 WV	39.2	79.7	700	1964	--	--	--	--	--	--	94	94
7 IN	38.5	86.5	244	1962	--	101	124	123	103	114	111	112
10 MO	37.7	91.5	387	1963	94	99	123	--	103	101	104	105
11 IL	37.5	88.4	165	1962	75	107	118	107	111	99	101	104
1 TE	36.2	84.2	303	1962	112	110	110	119	91	95	100	104
5 AR	35.9	93.2	610	1963	133	97	103	--	102	92	102	102
27 NC	35.6	82.5	884	1964	--	87	95	--	108	--	98	97

[1]) Plantations 13—14 years old.

made it possible to compare provenance means of trees differing in location or in age at time of measurement. The converted average heights were then ranked from highest to lowest and correlations were run between all pairs of plantation rankings.

Seedling-sapling height growth correlations were run on 15 provenance means, using the nursery means at age 1 and the all-plantation means at ages 8 and 14. Correlations between total height, stem diameter and crown diameter were calculated from individual tree observations in Ohio.

Phenological Variation

Time of flushing

Distinct regional groupings of provenances were apparent in time of flushing *(Fig. 2)*. Trees from provenances in Minnesota, Wisconsin, the Upper Peninsula of Michigan and Northern Ontario were the first to leaf out, followed by trees from the northeast, including southern Ontario, New York and Maine, and from the Central States, Arkansas, and Tennessee. Late-flushing trees were mainly from a narrow latitudinal belt from southern Michigan across northeastern Ohio to northeastern Pennsylvania. Two population samples seemed distinct from adjacent groups: (1) trees from the northern lower Peninsula of Michigan (provenance no. 17) which were much later in flushing than trees of origins farther east and west at the same latitude; (2) trees from western North Carolina (provenance no. 27) which leafed out much later than any other trees in the southern part of the species range.

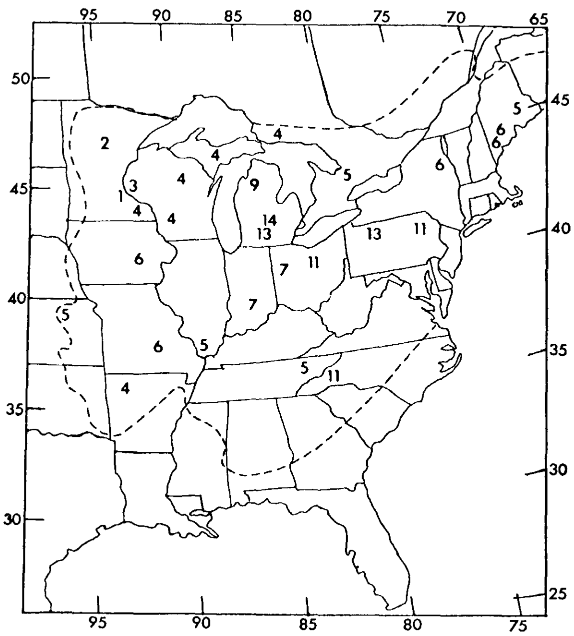

Fig. 2. — Average flushing date of red oak in relation to provenance, from 1 = April 26 to 14 = May 9. Recorded in Nebraska in 1975 by S. E. SCHLARBAUM.

The early flushing of trees of south-central origin, compared with trees of mid-latitude origin, agrees with results obtained by GALL and TAFT (1973). Two of their 6 origins of red oak were the same Tennessee and eastern Ohio origins included in these experiments. In Tennessee, the average flushing date of the local trees was 10 days earlier than that of the eastern Ohio trees. In Nebraska, the Tennessee trees flushed 6 days earlier than Ohio trees *(Fig. 2)*. GALL and TAFT also found that trees of other south-central sources flushed early compared to those from eastern Ohio, as we did, although the sources were not the same.

Number of growth flushes

The number of flushes of growth at ages 6 to 8 varied from 1 to 3 among individual trees and from 1.6 to 2.2 among provenance means *(Table 2)*. Differences among provenances, though small, were significant. At this early age, large trees tended to have more growth flushes than small trees. The coefficient of correlation (r) between height and number of growth flushes, based on provenance means, was +.52 (significant at the 1% level). The provenance with the greatest vigor (no. 7, southern Indiana) also had the greatest number of growth flushes.

Table 2. — Red oak provenance variation in number of growth flushes and relative time of autumn leaf coloration.

No. & State or Prov.	Average No. of growth flushes	Average degree of leaf coloration2/
20 MN	1.9	9.0
26 WI	1.9	8.2
13 MI UP	1.8	7.9
2 MN	2.0	7.6
22 WI	1.9	7.6
24 ON	2.0	7.6
3 ME	1.9	7.2
21 ON	1.9	7.1
29 ME	1.9	7.1
4 QU	1.8	7.0
23 MN	1.8	7.0
19 NY	1.9	6.8
12 WI	1.8	6.7
9 IA	2.0	6.6
17 MI LP	1.9	6.5
6 ME	2.0	6.5
30 OH	1.6	6.5
32 KA	1.8	6.5
31 OH	1.9	6.4
25 IL	1.8	6.4
14 MI LP	1.8	6.3
18 PA	1.9	6.0
8 MI LP	1.8	5.8
27 NC	1.9	5.2
15 PA	1.7	5.1
11 IL	2.1	4.9
16 WV	1.8	4.7
7 IN	2.2	4.6
10 MO	2.0	4.5
1 TE	2.1	4.4
5 AR	2.0	4.3

[1]) Up = Upper Peninsula, LP = Lower Peninsula.
[2]) Trees scored 1 = green to 10 = brown.

In Ohio and Michigan, and possibly elsewhere in the North Central region, multiple flushing seems to be associated with juvenility. Mature trees are only single-flush. Though the number of growth flushes in young trees might be related to such traits as resistance to injury by insects attacking new leaves or shoots, there is no basis for selection at this time, nor is there adequate variability for selection based on source means.

Time of autumn leaf coloration

Trees varied in foliage color from completely green through red to completely brown on a single observation date in 3 of the 4 plantations scored. Provenance differences were significant at a 1% or lower level in all 4 plantations (Kansas, Illinois, Michigan, Ohio). Color uniformity was high within provenances. In Ohio, for example, the average coefficient of variation within a provenance was only 2.5% of the mean.

Time of leaf coloration was closely related to the latitude of the seed origin *(Fig. 3)*. The north-to-south trend in relation to origin is evident in the combined ranking for 3 plantations *(Table 2)*.

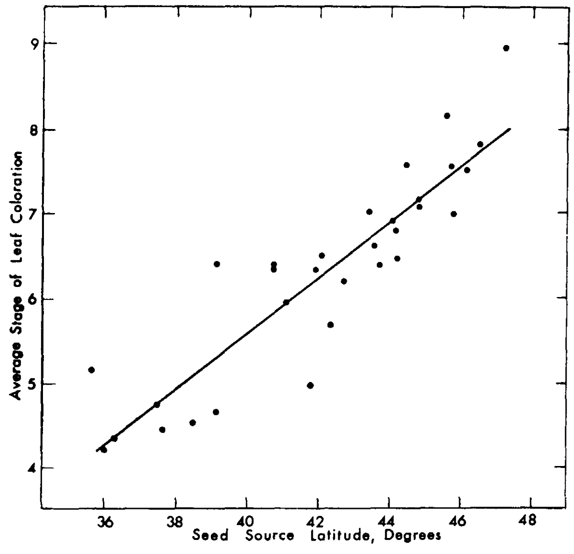

Fig. 3. — Regression of relative time of fall leaf coloration on seed source latitude; averages of Kansas, Illinois and Ohio provenance means ($p < .001$, $r = .90$).

Survival and Growth

Survival

Survival percentage varied widely among the plantations *(Table 1)*. Provenance differences in survival rate were statistically significant in the Kansas plantation but not elsewhere. In Kansas, trees of Kansas, Iowa and Missouri origin had significantly higher survival rates at the 1% level than did trees of other origins (DENEKE 1975). Of the three high-survival sources, Kansas ranked highest.

The results in Kansas showed that there is genetic variation in drought tolerance in red oak. The plantation was situated at the western limits of the species distribution, in a region where prevalent summer temperature and precipitation conditions are near the respective high and low for native red oak localities. Under these conditions, red oaks indigenous to the warmest and driest parts of the species range were most capable of survival.

There was no evident geographic variation in cold hardiness as found by FLINT (1972) in twig experiments, and as would have been expected had extreme southern provenances been included in the experiment.

Height growth

Seed source had a significant effect on height growth in five of the seven plantations when the trees were 13—14 years of age *(Table 1)*.

There was a slight region-wide consistency in provenance performance. Approximately 75% of the time, seedlots which were above (or below) average at one planting site were above (or below) average at other planting sites as well, i.e. had a similar position in the "average all sites" column *(Table 3)*. Among the seedlots which grew well at most planting sites were 7-IN, 32-KA and 8-MI.

The extent to which results at one plantation agreed with those at other plantations can also be shown by means of the between-plantation correlations given in *Table 4*, from which the high-mortality Kansas plantation was omitted. There were some moderately strong correlations among the plantations located in Indiana, Michigan and Ohio.

Some weak geographic trends were noticeable *(Table 3)*. Trees of origins 32-KA, 5-AR, 10-MO, 11-IL, and 7-IN from the southwestern portion of the range grew at above average rates, trees of the three Minnesota origins grew 95—96% of average, trees from the three Wisconsin origins grew 102—104% of average, and trees from origins less than 150 km from the northern limits of the species grew 88—96% of average. On the other hand, seedlots 8-MI and 14-MI from nearby localities in Michigan grew at very different rates, as did seedlots 6-ME and 29-ME from nearby localities in Maine. Since these seedlots were 10-tree samples, stand differences in growth rate evidently occurred in these two widely-separate parts of the species range. In addition, nursery experiments showed that there were significant differences among the offspring of different trees within the same stand. Variance component analysis indicated that these family differences were more important than provenance differences (KRIEBEL 1965).

Table 4. — Between-plantation correlations in height (expressed as r, the correlation coefficient), with significance levels.

	NE	IL	IN (sou.)	IN (nor.)	MI
IL	.48*				
IN (sou.)	.16	.53*			
IN (nor.)	.24	.21	.24		
MI	.32	.02	.36	.61**	
OH	-.05	.23	.58*	.56**	.35

Age-age correlations

Correlations of nursery and all-plantation provenance means at ages 1, 8 and 14 were:

Age comparison	Correlation coefficient (r)	Significance level
1 vs 8	.61	5% level
1 vs 14	.42	not significant
8 vs 14	.67	1% level

The low level of the correlations is due partly to the fact that the age 1 and age 8 or 14 data are for different sites, and partly to the animal damage which was prevalent in the early years of some plantations.

Even the age 8 vs 14 correlation is lower than that found in several species. It makes juvenile selection for growth rate impractical. For example, selection of the five tallest provenances at age 8 would eliminate two which would be included in the five tallest at age 14.

Stem and crown diameter

Diameter differed significantly among trees of different seed sources. At age 14, DBH averaged 7.6 cm and seed source means varied from 6.0 to 8.1 cm. Seed source differences in crown diameter were also significant. The stands had not yet closed when the measurements were taken.

Height, diameter and crown diameter were strongly correlated ($r = .85$) to .90), indicating that all were a function of growth rate genes.

Conclusions

There is a geographic pattern in flushing date of red oak. In the North Central region, the earliest-flushing trees are those of northwestern origin. The flushing trend is then "eastward" through trees of northern origin to trees of northeastern origin, and also "southward" to trees of central and southern provenance, ending in trees of mid-latitude origins from southern Michigan to Pennsylvania.

The time of autumn leaf coloration is strongly correlated with seed source latitude. Early coloration is associated with high latitude and late coloration with low latitude.

The number of growth flushes in young trees varies with seed source. The differences among provenance means are small and there is no apparent geographic pattern of variation.

There is geographic variation in capacity to survive summer heat and drought conditions. Trees native to regions where such conditions often occur, e.g. Kansas, are most capable of survival.

Growth rate varies with geographic region of origin, but the regional effect is small except for the slow growth of trees of extreme northern provenances in areas farther south. Growth rate also varies with stand or local population and with progeny, and is apparently influenced most by these factors.

The average growth rate of young trees of a particular provenance is not very closely related to their later rate of growth. The correlation between height at age 8 and at age 14, though higher than the nursery-field correlations, is not strong enough to justify provenance selection for growth rate in the early sapling stage.

The apparent importance of local variation in growth rate of red oak indicates that further improvement effort in the North Central region should concentrate on phenotypic selection without particular regard to geographic origin. For planting in the 38° to 43° latitudinal belt in the region, native trees for progeny testing may be selected anywhere west of the Appalachians, except in the extreme north as described and south of the southernmost of our provenances.

Summary

Geographic variation in red oak is described up to age 14 in 7 replicated experiments in the North Central region of the U.S.A. Time of flushing and of autumn leaf coloration are under strong genetic control and have well-defined geographic patterns of variation. Drought-hardiness is highest in trees from regions subject to summer drought. Growth rate varies with seed source but genetic control appears to be more related to stand and family than to geographic origin within the species distribution.

Key words: red oak, flushing, leaf senescence, drought tolerance, growth rate.

Zusammenfassung

Es wird über Ergebnisse aus 7 Provenienzversuchen mit Roteiche berichtet, die in den nördlichen Zentralstaaten der USA bis zum Alter 14 beobachtet wurden. Hierbei traten in der Blattentfaltung und in der herbstlichen Blattverfärbung ausgeprägte Variationsmuster auf, die auf starke genetische Kontrolle schließen lassen. Herkünfte aus Trockengebieten der natürlichen Verbreitung zeigten die höchste Trockenresistenz. Im Wachstumsvermögen ergaben sich Provenienzunterschiede, die jedoch durch standortbedingte sowie aus der Familienzugehörigkeit resultierende Unterschiede überdeckt wurden.

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Natural variation of tissue proportions and vessel and fiber length in mature northern red oak

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Introduction

Northern red oak (*Quercus rubra* L.), one of the widest ranging and most valuable oaks in the United States, has been gaining in utilization for both solid wood and fiber products. The increased utilization brings with it the need for additional information on wood quality.

In recent years northern red oak has been included in genetic studies and breeding programs (Kriebel and Thielges, 1969; USDA Forest Service, 1974). As these programs progress, the need for the inclusion of wood quality factors also becomes more important.

In softwoods, density is the prime indicator of wood quality (solid wood strength and pulp yield potential). The good relationship of density to quality in softwoods is due to simple anatomical structure consisting mainly of tracheids and rays. Wood density in softwoods is affected primarily by cell wall thickness and the proportions of early and latewood.

In hardwoods, however, density is not as good an indicator of quality. The wood itself is complex, variously composed of vessels, fibers and tracheids, axial parenchyma, and rays. Variations in cell size, wall thickness, and tissue-type proportions are added indicators of why density is not such a good measure of wood quality in hardwoods. In oak, two measures of wood quality that are important in product quality — for both solid wood and fiber uses — are tissue-type proportions and fiber and vessel lengths.

Hill (1954) and Khurshudyan (1958) have both shown that the proportions of vessels and fibers are better indicators

[1]) Maintained at Madison, Wis., in cooperation with the University of Wisconsin.