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 38⁰ to 43⁰ 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 iolerance, 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 Familienzugehorigkeit 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 studiec 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 — fcr 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]) Mairitained at Madison, Wis., in cooperation with the University of Wisconsin.

of wood quality in oak than is density for strength evaluations. Hill presented data showing correlations fom 87% to 99% between proportions of vessels and fibers and strength properties for northern red oak.

For applications in pulp and paper, the greater the fiber content of a wood, the greater the pulp yield and paper quality. Simmonds and Hyttinen (1964) showed that the fiber fractions of oak pulps are notably stronger than whole pulps containing 28% fines by weight (mainly parenchymatous tissue). Mottet (1963) showed that increasing amounts of parenchyma reduced tensile, bursting, and tearing strength, as well as folding endurance in tropical hardwoods.

Britt (1966) and Hillis (1972) have reported the importance of fiber length to pulp and paper quality: The longer the fiber, the better the quality.

This paper presents data on the natural variation in tissue-type proportions and in fiber and vessel element lengths in mature wood of northern red oak from across its commercial range. The purpose is to illustrate the range of phenotypic variation, and to promote the inclusion of these quality criteria in breeding programs.

Methods

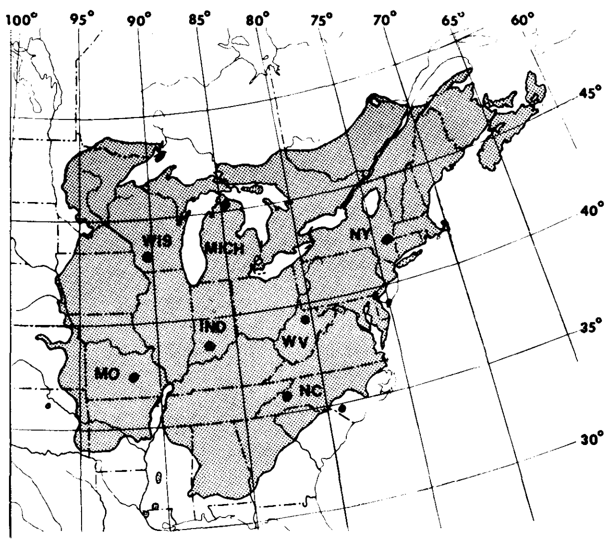
Samples from 240 dominant or codominant, 50- to 100-year-old, northern red oak trees were obtained from seven locations in the commercial range of the species *(Figure 1)*. At each location, trees were selected from several sites *(Table 1)*. Site indices (at age 50) varied from 6 to 26 m, with a median value of 19 m, for the sites examined. Locations ranged from 35.5° north latitude (North Carolina) to 45.5° north latitude (Michigan) and from 74° west longitude (New York) to 91.5° west longitude (Missouri). Elevations varied from 183 to 1524 m; average precipitation, from 73 to 122 cm.

At each location as wide a range of sites as possible was selected. At each site five trees in a .2- to .8-hectare area were measured for total height and diameter at breast height (d.b.h.); two 5-mm increment cores were extracted from each tree at breast height (1.37 m); and site index, aspect, % slope of land, and basal area of the stand were measured.

On a transverse surface of the increment cores (the 38th through 47th annual rings, to insure mature wood) the proportions (volume basis) of vessels, fibers (libriform fibers and tracheids), axial parenchyma, and rays were determined using a Zeiss integrating eyepiece and reflected light (Smith, 1967). Similar measurements were also made on two randomly selected rings from each of the 10-ring segments. Compound (multiseriate) ray proportions were determined using a Dual Linear Traversing Microscope (Smith, 1965).

After the ray proportion measurements were made, the 10-ring segments were cut into thin slices and macerated in Jeffrey's solution (Hiller, 1968). Whole fibers and vessel elements were then measured using a projecting microscope. Ten to twenty fibers and vessel elements were measured per tree.

Data analysis included calculation of means, ranges, standard deviations, standard errors of the location means ($S_{\bar{x}}$), coefficients of variation, regressions with site factors ($y = a + bx$), and nested analyses of variance for variance components among all sources.



M 143 993

Figure 1. — Northern red oak trees were obtained from seven locations within the commercial range of the species. M 143 993.

Table 1. — Locations of sampling areas and related data.

State	County	North latitude	West longitude	Site index range	Age range	D.bh range	Total height range	Elevation range	Average growing season	Average annual precipitation
		°	°	m	yr	cm	m	m	days	cm
Missouri	Dent Iron	37.75	91.50	8.2–22.9	51–72	13–38	7.9–25.9	244–396	182	109
North Carolina	Buncombe Haywood	35.50	80.50	11.6–26.2	72–92	23–57	12.2–35.4	701–1524	194	98
West Virginia	Tucker	39.10	79.75	13.1–26.5	65–97	23–57	14.6–32.6	549–701	145	122
Indiana	Jackson Lawrence Monroe	38.90	86.00	17.4–23.8	59–73	20–55	18.3–32.3	213–259	181	111
New York	Orange	41.40	74.00	6.1–21.6	59–74	19–47	5.8–26.8	274–427	194	105
Michigan	Cheboygan	45.50	84.90	11.3–21.3	53–72	20–39	12.2–23.8	183–213	128	73
Wisconsin	Grant	43.00	91.00	11.3–21.9	60–95	21–49	11.6–26.8	244–305	155	82

Source of variation	Degrees of freedom	Variance components of mean squares
Location	6	$\sigma_E^2 + 2\sigma_T^2 + 10\sigma_S^2 + 68.4028\sigma_L^2$
Sites within locations	41	$\sigma_E^2 + 2\sigma_T^2 + 10\sigma_S^2$
Trees within sites	192	$\sigma_E^2 + 2\sigma_T^2$
Cores within trees	240	σ_E^2

Results and Discussion

Statistics for sampling sites, locations, and the species as a whole are given in *Table 2*. Data are based on values, per tree, from individual rings for tissue proportions, and on ten-ring segments, per tree, for fiber and vessel element lengths.

Across the range of locations and sites sampled, northern red oak averages about 20% vessels, 41% fibers, 23% axial parenchyma, and 16% rays. Average vessel element length is 0.45 mm and average fiber length is 1.35 mm.

The relative variability of tissue proportions and fiber and vessel element lengths is probably best evaluated by comparison of the coefficients of variation (C.V.), which are unitless and compensate for means of different size: $C.V. = \frac{S}{\bar{x}}$ where: S = standard deviation $\bar{x}$ = mean.

The most variable of the tissue proportions based on C.V. is proportion of vessels which exceeds the other tissue proportions by as much as 10%. The coefficients are 30% (vessels), 20% (fibers), 22% (axial parenchyma), and 22% (rays). Vessel element and fiber length have coefficients of 29% and 27%, respectively.

Data ranges for both tissue proportions and cell lengths found in the literature (Myer, 1922; Bergman, 1949; Hill, 1954; Panshin and de Zeeuw, 1970; Dässler *et al.*, 1973; and Manwiller, 1974) are generally within the ranges shown in *Table 2*. However, mean values from the literature are not consistent, due to smaller sample size or other conditions of study. A more complete review of tissue proportions for other species may be found in Maeglin (1974).

To facilitate determination of the major sources of variation for each tissue proportion and cell length, and to aid

Table 2. — Means and variation of tissue proportions and fiber and vessel lengths for northern red oak in the United States by locations.

	Missouri	North Carolina	West Virginia	Indiana	New York	Michigan	Wisconsin	All locations
PERCENT VESSELS[1]								
Ave.—%	22.7	18.8	16.6	20.1	19.8	19.8	19.0	19.5
Rng. of individ.—%	5.7-56.0	6.1-40.2	5.1-46.2	6.1-50.3	6.2-39.5	7.9-39.2	6.4-43.5	5.1-56.0
Rng. of site means—%	17.4-26.5	14.4-23.3	13.7-19.7	18.4-21.6	17.4-23.0	15.5-23.4	15.3-22.8	13.7-26.5
Std. dev.—%	6.57	5.94	5.30	6.41	5.15	5.09	5.20	5.95
$S_{\bar{x}}$—%	.73	.77	.59	.83	.62	.66	.62	.27
Coeff. of var.—%	29	32	32	32	26	26	27	30
PERCENT FIBERS[1]								
Ave.—%	35.7	47.4	44.7	41.7	40.7	40.1	40.0	41.3
Rng. of individ.—%	14.6-56.0	20.0-65.5	19.5-63.9	10.6-66.7	19.2-61.9	18.4-66.7	13.0-62.2	10.6-66.7
Rng. of site means—%	27.7-40.4	40.4-52.2	35.1-52.4	36.6-47.2	35.2-45.1	35.4-47.5	31.6-49.7	27.7-52.4
Std. dev.—%	8.10	6.74	8.32	8.02	6.50	7.36	7.98	8.36
$S_{\bar{x}}$—%	.91	.87	.93	1.04	.78	.95	.95	.38
Coeff. of var.—%	23	14	19	19	16	18	20	20
PERCENT AXIAL PARENCHYMA[1]								
Ave.—%	25.1	18.0	23.1	23.2	23.9	24.0	24.6	23.4
Rng. of indiv.—%	11.3-43.5	8.5-30.9	11.8-38.5	12.6-38.1	14.0-39.3	12.4-40.1	13.2-40.3	8.5-43.5
Rng. of site means—%	20.6-28.2	16.9-20.2	19.0-28.6	19.6-26.1	22.1-26.4	21.4-27.7	20.6-28.2	16.9-28.6
Std. dev.—%	5.36	3.25	5.04	4.31	3.76	4.49	5.17	5.03
$S_{\bar{x}}$—%	.60	.42	.56	.56	.45	.58	.62	.23
Coeff. of var.—%	21	18	21	19	16	19	21	22
PERCENT RAYS[1]								
Ave.—%	16.6	15.9	15.1	15.3	15.6	16.2	16.6	15.9
Rng. of indiv.—%	5.6-28.3	4.1-25.1	6.4-26.9	7.2-27.8	6.9-26.2	6.4-29.7	7.3-28.1	4.1-29.7
Rng. of site means—%	14.7-20.0	13.4-18.3	12.7-18.7	13.2-17.8	12.4-18.8	14.5-17.5	14.5-18.2	12.4-20.0
Std. dev.—%	4.29	2.87	3.75	3.35	3.20	2.92	2.89	3.43
$S_{\bar{x}}$—%	.48	.37	.42	.43	.38	.38	.34	.16
Coeff. of var.—%	26	18	25	22	20	18	17	22
VESSEL LENGTH[2]								
Ave.—mm	.41	.45	.45	.44	.47	.47	.51	.45
Rng. of individ.—mm	.127-.816	.143-.762	.159-.842	.195-.730	.143-.862	.192-.883	.198-.835	.127-.883
Rng. of site means-mm	.38-.45	.42-.47	.44-.47	.41-.49	.40-.53	.42-.53	.47-.53	.38-.53
Std. dev.—mm	.120	.129	.123	.114	.138	.131	.132	.130
$S_{\bar{x}}$—mm	.004	.007	.006	.007	.007	.008	.007	.002
Coeff. of var.—%	29	29	27	26	29	28	26	29
FIBER LENGTH[2]								
Ave.—mm	1.34	1.40	1.37	1.31	1.30	1.34	1.41	1.35
Rng. of individ.—mm	.41-2.46	.49-2.35	.62-2.33	.54-2.40	.55-2.08	.65-2.47	.78-2.58	.41-2.58
Rng. of site means-mm	1.22-1.45	1.30-1.55	1.29-1.44	1.19-1.46	1.22-1.37	1.28-1.40	1.29-1.49	1.19-1.55
Std. dev.—mm	.392	.378	.364	.355	.318	.339	.317	.360
$S_{\bar{x}}$—mm	.014	.022	.018	.020	.017	.020	.017	.007
Coeff. of var.—%	29	27	26	27	24	25	22	27

[1]) Based on individual ring measurements.

[2] Based on ten-ring segments.

Table 3. — Estimated components of variance for northern red oak tissue proportions and cell lengths.

	Property					
Components estimated[2]	% Vessel	% Fiber	% Axial parenchyma	% Rays	Vessel length	Fiber length
Location (σ_L^2)	1.00134	8.36962	4.11465	0.00000[3]	0.00090	0.00084
Site (σ_S^2)	3.95511	16.98168	4.74847	2.73154	0.00057	0.00249
Tree (σ_T^2)	5.85924	12.70175	5.19757	2.23347	0.00000[3]	0.00597
Core (σ_C^2)	12.79217	31.03446	11.88912	6.13245	0.00347	0.01941

[1] Assuming all factors be random effects.

[2] σ_L^2 = Locations; σ_S^2 = Sites-within-locations; σ_T^2 = Trees-within-sites; σ_C^2 = Cores-within-trees

[3] Actual negative value, assumed to be zero.

in future design efficiency, the components of variance were determined and are shown in *Table 3*.

In all instances the cores-within-tree error term provided the largest component of variance, ranging from 70% of total variance for vessel length to 45% of total variance for percent fiber. For tissue proportions location accounts for a relatively small amount of total component variance (from 0—16%); sites-within-location and trees-within-site account for a moderate and about equal proportion of the total cell lengths; location accounts for 18% of vessel length but only 3% of fiber length. Sites-within-location accounts for 12% of vessel length and 9% of fiber length. However, for trees-within-site there was a zero variance component for vessel length and 21% for fiber length.

The tissue proportions that have the greatest effect on wood properties are vessel and fiber. The data suggest that future sampling for vessel proportions would be most efficiently conducted by concentrating on few locations and sites but taking more trees and cores. For fiber proportions though, more cores from a moderate number of trees on more sites would appear in order.

The most efficient concentration of effort for cell lengths would appear to be in more locations and cores for vessel length, and more trees and cores for fiber length. These apparent directions for efficient sampling would, of course, be dependent on cost accounting.

Effect of Site

To estimate the genetic improvement potential of a desired tree characteristic, the effect of environmental factors on the characteristic must first be known.

To estimate environmental influence, regressions of tissue proportions and cell lengths on site index and other site factors were calculated. The following tabulation shows correlation coefficients (r) with site index for all data combined.

Tissue proportions	r
Vessels	—0.50**
Fibers	+ .65**
Axial parenchyma	— .36*
Rays	— .56*
Cell lengths	
Vessels	+ .09NS
Fibers	+ .43**

* = 0.05, ** P = 0.01, NS = Not significant; n = 47.

The addition of other factors in multiple regression did not improve the relationhip significantly.

The regressions explain, at best, only 42% of fiber proportion variability and less than 1% of vessel element length. This fairly small amount of explained variability due to site index and other site factors suggests that there may be some genetic control over these wood quality factors. A more complete discussion of the site-tissue proportion relationships, along with information on relationships with ring width, is found in Maeglin (1974).

Conclusions

Variation in tissue type proportions and fiber and vessel lengths has been shown. Only a relatively small amount of the variability is explained by site index or other site factors. Material from provenance tests should be examined to determine heritabilities of these properties. Values for genetic gain can then be calculated.

Commercial quality can be enhanced if the proportion of fibers is increased while vessel and axial parenchyma proportions are reduced and rays remain fairly constant. Efforts to lengthen both fibers and vessel elements should also be made if significant genetic gains are predicted.

Acknowledgement

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Abstract

Northern red oak trees from throughout the commercial range of the species in the U.S. were sampled for tissue proportions and fiber and vessel lengths. Mean tissue proportions for the species are 20% vessels, 41% fibers, 23% axial parenchyma, and 16% rays. Mean vessel length is 0.45 mm and mean fiber length is 1.35 mm.

Variability, as measured by coefficient of variation, ranged from 20% for fiber proportion to 30% for vessel proportion. Axial and ray parenchyma have coefficients of variation of 22%. Vessel element length varied by 29% and fiber length by 27%.

Only 42% of the expressed variability was explained by site index or site factors, at best.

Values of component variance are given to aid in determining efficiency in future sampling, such as in provenance tests.

It is suggested that wood from northern red oak provenance tests should be examined to estimate how much of the observed variation in these wood quality parameters is genetic, and to calculate genetic gains. If significant gains are predicted, efforts should be made to lengthen fibers and increase fiber proportions by genetic means.

Key words: Northern red oak (*Quercus rubra* L.), tissue-type proportions, fiber length, vessel element length, genetic improvement, natural variation.

Zusammenfassung

Titel: Die natürliche Variation der Gewebeanteile sowie der Länge von Gefäßzellen und Fasern im Holz älterer Bäume der nördlichen Roteiche *(Quercus rubra* L.).

Gefäßzellen, Fasern, axiales Parenchym und Markstrahlen wurden untersucht in 10 markfernen Jahrringen (38. bis 47. Jahrring) an 50- bis 100jährigen Bäumen von unterschiedlichen Standorten. Bei mittleren Werten für die auf Holzquerschnitten ermittelten Anteile von 20% Gefäßzellen, 41% Fasern, 23% Parenchym und 16% Markstrahlen betrug die Variabilität in gleicher Reihenfolge 30%, 20%, 22% und 22%. Die Länge der Gefäßzellen betrug im Mittel 0,45 mm bei einer Variabilität von 29% und die der Fasern 1,35 mm und 27%.

Von der Variabilität in den einzelnen Merkmalen konnte nur ein relativ geringer Anteil auf die unterschiedlichen Wuchsbedingungen verschiedenartiger Standorte zurückgeführt werden.

Zur Klärung von Möglichkeiten einer Verbesserung der Holzqualität durch Züchtung auf einen höheren Faseranteil und auf längere Fasern werden Provenienzversuche zur Einschätzung von Heritabilitäten und genetischem Gewinn empfohlen.

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Early Growth Results in a Diallel Progeny Test of Eucalyptus grandis (Hill) Maiden

I. A. Field Study

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Introduction

Eucalypt plantations constitute a considerable proportion of the world's exotic hardwood forests. Adaptability, phenomenal growth rate under suitable conditions, and an expanding world market for hardwood fibres are the major reasons for the exceptional interest that many *Eucalyptus* species enjoy outside their native range.

Proper management and silvicultural techniques, combined with applied breeding programmes are resulting in greatly increased output from forest lands. However, reports on genetic work on eucalypts are scarce, and it is only in recent years that they received substantial attention in this field.

Considerable variation between and within species has been reported (Green, 1971; Dadswell, 1972; Brown *et al.*, 1972; Davidson, 1973); and low heritability estimates were obtained for tree height, diameter, straightness, and branching habit of open-pollinated *E. regnans* families (Eldridge, 1971). Controlled pollination experiments by Hodgson (1975) and Eldridge (1970) on *E. grandis* and *E. regnans* respectively demonstrated the incidence of selfing and subsequent inbreeding depression in these species.

More than 350 000 hectares have been planted to *Eucalyptus grandis* in the Republic of South Africa, and this species is generally the most important in a number of subtropical countries.

In the present work control-pollinated seed from a diallel crossing scheme was used to raise full-sib families in a greenhouse in North Carolina and in a field test in south-central Florida, U.S.A. The major objectives of the study were:

1. To gain information on the mode in inheritance of quantitative traits in *E. grandis* by investigating:
   a. the magnitude of additive and non-additive variances.
   b. maternal and reciprocal effects.