Parental and Provenance Effects on Growth of Red Oak Seedlings

by
HOWARD B. KRIEBEL

Ohio Agricultural Research and Development Center
Wooster, Ohio

In 1960, the state agricultural experiment stations of the North Central Region started a cooperative regional project on northern red oak (*Quercus rubra* L.). This research project is a part of cooperative Regional Project NC-51, entitled, "Tree Improvement through Selection and Breeding of Trees of Known Origin." States participating in the red oak project include Ohio, Indiana, Illinois, Kansas, Nebraska, Iowa, Minnesota, Wisconsin, and Michigan.

The primary objective is to identify geographical patterns of genetic variation in tree characters directly or indirectly related to survival, adaptability, growth and timber quality. The relative performance of each population sample is being evaluated in one or more statistically-designed field experiments in each of the nine states.

Seed Collection and Nursery Procedure

Most population samples consisted of open-pollinated progenies from ten female parents. Seed collections were made in all but the extreme southern and extreme northeastern parts of the species range (Figure 1).

Problems of seed size, weight, perishability and rapid nursery growth make provenance tests of red oak difficult to conduct on a large scale. Nearly one and one-half tons of seed were involved. Crop conditions made it necessary for cooperators to postpone collection for 1 or 2 years in some areas. In some cases it was necessary to accept some tree collections one year and the rest of the ten collections the next year. Since practical methods have not been developed for keeping stored acorns from sprouting, all seed was sown as soon as possible after receipt. Thus some progenies in the tests are one or two years older than others. In no case is there a difference of more than one year in age between progenies within a source. In all outplantings, a record of age is being maintained so that differences related to this age variation can be identified.

On the basis of previous research it seems probable that as the trees grow older the effect of this age differential on total growth will become increasingly small in relation to genetic effects related to family and seed origin.

A portion of each seed lot was sown in randomized and replicated nursery beds. The rest of the seed was sown in unreplicated plots in other nursery beds. All sowing was at one nursery at Green Springs, Ohio. The trees were sent to cooperators after one year in the nursery.

Twenty-nine of the population samples shown in Figure 1 yielded enough trees for regionwide trials, and two additional localities are represented in some field tests.

Nursery evaluation provided a basis for later correlation of juvenile and mature characteristics. It had the advantage of making possible rapid measurement of large numbers of trees under a fairly uniform environment, because of the concentration of numerous biotypes in a small area.

Growth measurements were taken in the nursery on the first- and third-years' collections, but not on the smaller number of second-year collections. The height growth data were taken at the end of the first growing season on about 3,100 seedlings of 22 geographic origins, 15 origins in 1961 and 7 origins in 1963. A total of 191 families were sampled.

Covariance analysis showed no effect of seedbed density on plant height.

Measurements of relative time of growth cessation were taken in the nursery in 1961 on the 131 progenies of 16 provenances. Measurements were taken on July 25, by assigning one of the following index numbers to each subplot: 1 = growing; 2 = mixed; 3 = not growing. In 1963, height measurements were taken on all 94 progenies of 11 provenances on 4 dates at 2-week intervals between July 23 and September 3. The dependent variable in the analysis was date of achievement of maximum height, based on a scale of 1 to 4 (1 earliest, 4 latest).

In the statistical treatment, the comparison of groups was based on the hypothesis that the groups were a random sample from an infinite population of similar groups ("Model II"), rather than samples from particular treatments or groups of interest to the experimenter, each with its own population mean which might differ from group to group ("Model I"). In this experiment, the

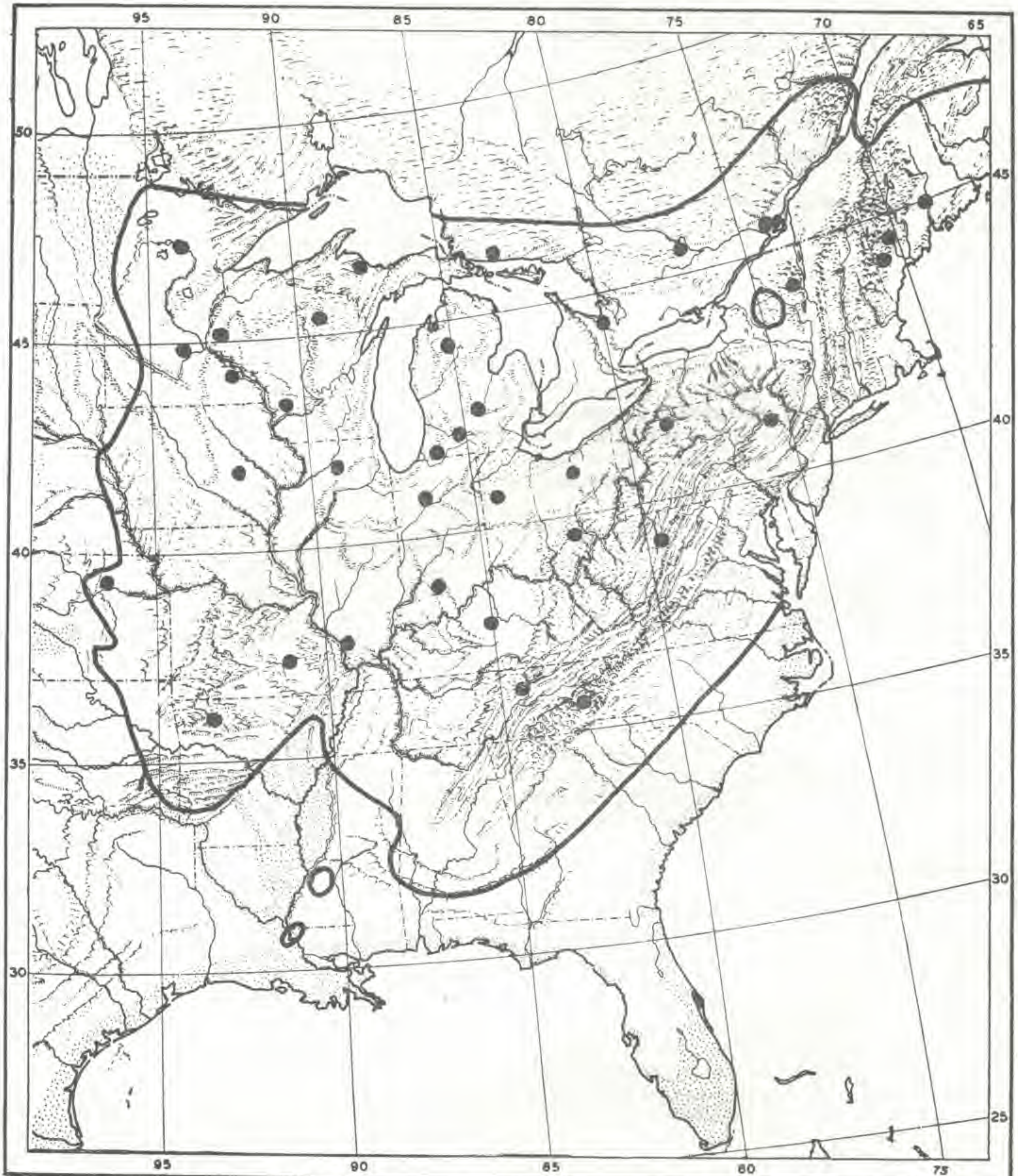

Figure 1. Sampling points within the botanical range of *Quercus rubra* L. (Little 1949). Base map adapted from D. E. Lee, "Base Map for American History," courtesy Houghton Mifflin Co.

differences among the groups (provenances and families) contain a source of variability additional to that within groups, and the parameters to be estimated are these "components of variance" (Bliss and Calhoun, 1954, pp. 96-97).

Expectations of mean squares were determined by the methods outlined by Schultz (1955).

Variation in Seed Weight

Average seed weights are presented in Figure 2 for all population samples which had sound acorns in sufficient quantity for sampling.

Northern acorns were light in weight and had the small size, narrow shape and deep cupule characteristic of the previously-recognized form *Quercus borealis* Michx. f. Other collections had heavier acorns of the large, broad, shallow-cupped type formerly called *Q. borealis maxima* (Marsh.) Ashe. (Rehder 1949). These two forms are no longer recognized as separate taxa because of intergradations and apparent failure to breed true, and the name *Quercus rubra* now applies to both forms (Harlow and Harrar 1950, Little 1953).

Variance components for seed weight were calculated from the analysis of variance, using the following model for expected mean squares:

Source of variation	Expected mean squares
Provenance (p)	$\sigma^2_{f(p)} + f\sigma^2_p$
Female parent (f)	$\sigma^2_{f(p)}$

In both years there was a large variation in seed weight attributable to female parent, although in the 1961 analysis the provenance effect was the larger one. The 1963 analysis does not include seeds of the "northern" type, and Table 1 shows that in this material only about one fourth of the measured variance **in** seed weight can be attributed to sampling locality. The remaining three fourths of the variation is associated with differences between seed parents.

The Relation between Seed Weight and First-Year Height Growth

It has been known for a long time that there is a correlation in oaks between seed size or weight and rate of juvenile plant development. Bauer (1880) was the first to report this relationship. Johnsson (1952) found highly significant regressions between mean heights of 12-year-old families of European oaks and seed weight. He also studied this relationship over a 7-year period in five families. The correlation at the age of 1 year was +0.944, but by the seventh year it had declined to +0.466.

Table 1. Components of variance in seed weight analysis

Year	Source of variation	D.F.	Mean square	Variance component
1961	Provenances	15	5232.4	595.2
	Female parents	115	393.4	393.4
	Total	130		
1963	Provenances	6	2134.3	163.1
	Female parents	63	503.8	503.2
	Total	69		

Korstian (1927) studied the effects of red oak acorn weight on size of seedlings at the end of one growing season by dividing acorns into three weight classes. He found a positive relationship between weight class and seedling height.

In this study we used family means as Johnsson did, but ran a separate regression analysis on each population sample, because our particular interest was the seed-seedling relationship within the population sample. A pooling of all the widely-scattered provenance collections introduces other effects on plant height such as differential photoperiodic response. A pooled regression was in fact computed and found to be nonsignificant.

Under these conditions of seed sampling, namely (a) limiting the scope of a single regression analysis to the population sample and (b) using means of random seed samples unstratified by weight, seed weight did not have much effect on seedling size, except in two cases.

Two other regressions were significant at a probability level of < .05, but the number of regressions shown in Table 2 favors chance occurrence of such a relationship.

Table 2. Regression of first-year tree height on seed weight

Growth year	Provenance	Linear regression equation	t_b[1]
1961	Norris, Tenn.	Y = 11.54 + .0269X	2.562*
	Excelsior, Minn.	Y = 5.64 + .0382X	2.122
	Bradley, Me.	Y = 8.87 + .0292X	1.460
	N. Gorham, Me.	Y = 10.31 − .0004X	0.010
	Paoli, Ind.	Y = 14.95 + .0068X	0.439
	Grand Tower, Ill.	Y = 6.98 + .0516X	2.400
	Marquette, Mich.	Y = 13.30 − .0264X	0.530
	Cadillac, Mich.	Y = 10.57 + .0067X	0.148
	Wadhams, N. Y.	Y = 10.62 + .0360X	0.891
	Cass Lake, Minn.	Y = 3.59 + .0404X	6.215***
	Wasaga Beach, Ont.	Y = 8.55 + .0345X	1.397
	Sowerby, Ont.	Y = 9.19 + .0413X	1.811
	Rhinelander, Wis.	Y = 5.59 + .0335X	1.324
	E. Waterboro, Me.	Y = 8.27 + .0319X	0.717
	Lima, Ohio	Y = 10.72 + .0197X	2.141
1963	Augusta, Mich.	Y = 5.62 + .0034X	0.386
	Okemos, Mich.	Y = 5.55 + .0163X	1.244
	Irvine, Pa.	Y = 4.80 + .0185X	1.294
	Dallas, Pa.	Y = .84 + .0576X	3.236*
	Asheville, N. C.	Y = 5.06 + .0240X	1.387
	Wooster, Ohio	Y = 3.54 + .0258X	2.081
	Manhattan, Kans.	Y = .47 + .0534X	5.621***

[1] t_b = significance of the regression coefficient = b/s_b

Figures 3 and 4 show the regressions for the two population samples which had a highly significant seed weight-plant height relationship. Of these two, the Kansas collections were of the large, broad, heavy-acorn type, while the Minnesota collections consisted entirely of the small, narrow, light-weight acorn type.

Relative Influence of Female Parent and Provenance on First-Year Height Growth

Means of the height growth measurements are listed by provenance and grouped by growing season in Table 3.

Height growth was analyzed from what could be considered a nested design, i.e., provenances, mother trees

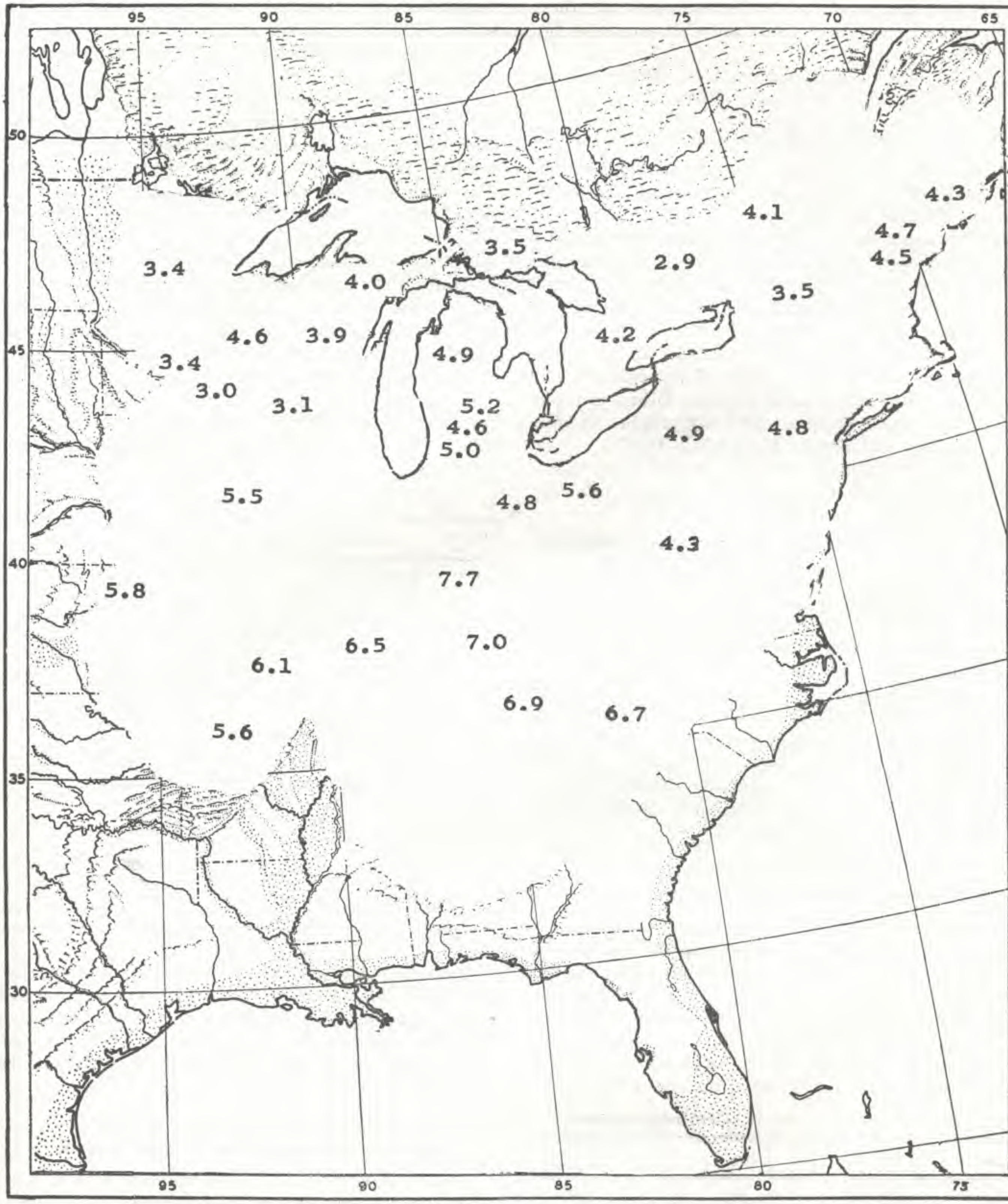

Figure 2. Mean seed weights in grams of red oak population samples (base map credit as for Figure 1).

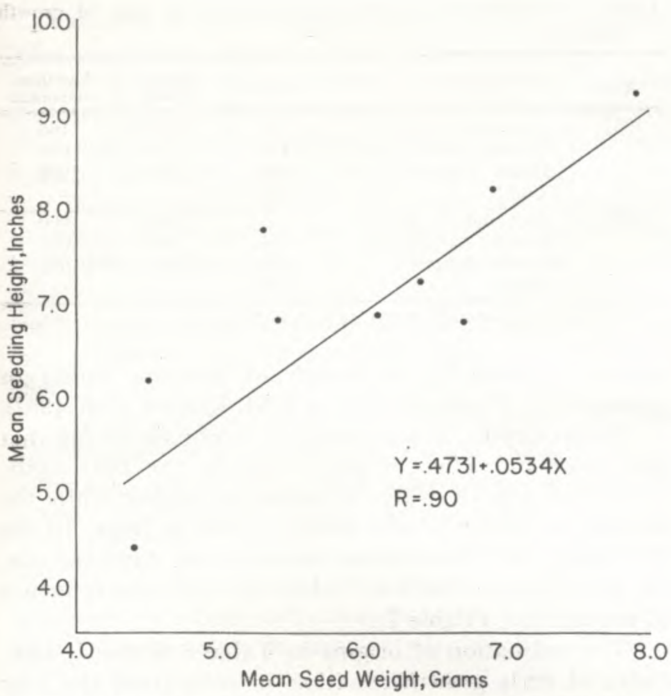

Figure 3. Regression of one-year-old seedling height on seed weight, for trees of Manhattan, Kansas origin

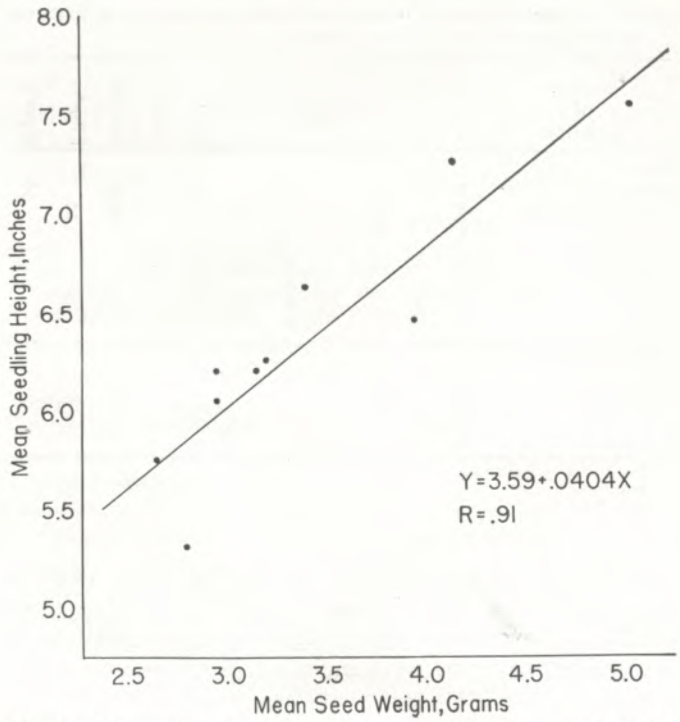

Figure 4. Regression of one-year-old seedling height on seed weight, for trees of Cass Lake, Minnesota origin

within provenances, and individual observations within mother trees within provenances. In the 1961 analysis of 16 provenances, numbers were unequal and block effects were not estimated. The model is:

Source	Expected mean squares
Provenances	$\sigma^2_i + i\sigma^2_{f(p)} + 8.13\ i\sigma^2_p$
Female parents	$\sigma^2_i + i\sigma^2_{f(p)}$
Individuals	σ^2_i

Variances and variance components of this analysis are given in Table 4.

Table 3. Mean tree height by provenance, measured at the end of the first growing season

Growth year	Provenance	Mean 1st-yr. height in inches
1961	Paoli, Ind.	16.1
	Norris, Tenn.	15.3
	Grand Tower, Ill.	13.9
	Jasper, Ark.	13.3
	Wadhams, N. Y.	13.3
	Lima, Ohio	12.6
	Sowerby, Ont.	12.2
	Wasaga Beach, Ont.	11.6
	Bradley, Me.	11.5
	Marquette, Mich.	11.2
	Cadillac, Mich.	11.1
	E. Waterboro, Me.	11.1
	N. Gorham, Me.	10.3
	Excelsior, Minn.	8.2
	Rhinelander, Wis.	8.2
	Cass Lake, Minn.	6.4
1963	Asheville, N. C.	8.3
	Okemos, Mich.	7.2
	Irvine, Pa.	6.5
	Dallas, Pa.	6.4
	Wooster, Ohio	6.4
	Augusta, Mich.	5.9

Another analysis was made of height growth of trees from six provenances of the third year's collections. All six provenances had ten seed tree collections. The measurements were taken at 2-week intervals between July 23 and September 17. The object of the periodic measurements was to record genetic differences, if any, in time of shoot growth cessation. This will be discussed in the next section.

The fifth series of measurements (September 17) was the same as the fourth, indicating no further height growth between September 3 and September 17. The fifth series was therefore omitted from the analysis.

The model for the expectations of mean squares is shown in Table 5, and the analysis in Table 6.

The two analyses gave quite different results. The first (Table 4) shows large differences between provenances but not much variation related to female parent. The variation among individual observations is large. The second analysis (Table 6) indicates a larger mother-tree effect, although the results are of limited significance because of the large block interaction.

Evaluation requires consideration of the distribution of the population samples, which were more widely dis-

Table 4. Components of variance in a first-year height growth analysis (1961 growing season)

Source of variation	D.F.	Mean square	Variance component
Provenances (p)	15	3228.1	95.5
Female parents (f)	116	122.7	5.0
Individual observations within p/f	392	102.9	102.9
Total	523		

Table 5. Expectations of mean squares in an analysis of first-year height growth. 1963 growing season.

Source of variation	σ^2fdb(p)	bσ^2fd(p)	bσ^2fb(p)	dbσ^2f(p)	fσ^2dpb	fσ^2dpb	fbσ^2dp	fpbσ^2d	fdσ^2pb	fdbσ^2p	fdpσ^2b
Total											
Blocks (b)	X		X		X		X		X		X
Provenances (p)	X	X	X	X	X	X			X	X	
p x b	X		X		X				X		
Dates (d)	X	X			X	X	X	X			
d x b	X				X		X				
d x p	X	X			X	X					
d x p x b	X				X						
Female parents (f) in p	X	X	X	X							
f x b in p	X		X								
f x d in p	X	X									
f x d x b in p	X										

f = female parent
p = provenance
d = date
b = block

persed over the species range in the first study than in the second one. The 16-source analysis included some northern provenances with rather uniformly small trees. No northern origins were included in the 6-source analysis.

It is clear that if one were interested in slow growth, the most logical approach would be to select primarily on the basis of geographic origin. If fast growth is desired, however, selection of individual seed parents will be important. Some consideration should be given to geographic origin, even after rejection of the most northern origins.

These early conclusions generally agree with the results of a study of single-tree progenies of red oak by Schreiner and Santamour (1961), and appear to be supported by recent unpublished measurements of 10-year-old families of red oak at Wooster.

Variation in Time of Growth Cessation

As in growth rate analysis, the importance of geographic origin in time of growth cessation depends on how wide a latitudinal distribution is included in the analysis. The general pattern of onset of dormancy in field tests of other hardwood tree species under conditions of adequate winter chilling is a progression from northern to southern genotypes. Sometimes there is a significant relationship to length of growing season or photoperiod (Pauley and Perry 1954, Kriebel 1956, 1957).

Table 6. Components of variance from a first-year height growth analysis of trees of 6 provenances (1963 growing season)

Source of variation	D.F.	Mean square	Variance component
Blocks (b)	2	13998.3	48.7
Provenances (p)	5	6583.9	31.9
p x b	10	2039.7	93.5
(Dates)	(3)	(12794.7)	(68.5)
(d x b)	(6)	(379.6)	(4.6)
(d x p)	(15)	(190.5)	(2.0)
(d x p x b)	(30)	(104.1)	(7.7)
Female parents (f) in p	54	1035.3	52.2
f x b in p	108	384.2	89.3
f x d in p	162	52.2	8.4
f x d x b in p	324	26.9	26.9
Total	719		

Table 7. Components of variance in analysis of time of growth cessation

Year	Source of variation	D.F.	Mean square	Variance component
1961	Provenances (p)	15	5.857	.166
	Female parents (f)	116	.449	.053
	Other sources[1]	260	.236	.236
	Total	391		
1963	Provenances (p)	5	1.169	.000
	Female parents (f)	54	.762	.049
	Other sources[1]	120	.672	.672
	Total	179		

[1]Individual subplot observations within f within p.

Consequently, in our studies it is not surprising that the provenance effect is fairly large in the 1961 study, which had a fairly wide dispersion of origins, while the mother-tree effect is only about a third as large. In the 1963 study, with few origins, mostly of the same latitude, the provenance effect is nil, while there is some influence of mother tree (Table 7).

The ordination of origins in Table 8 is clearly indicative of early growth cessation in trees from the four provenances in the northwestern part of the species range. Trees from Marquette, Michigan probably differ from these because of selective effects of the milder lakeshore climate in the sampling locality. The more southern (late-growing) origins can not be ranked accurately from Table 8, because measurements were not repeated late in the summer and early in the fall as in 1963. Later observations of all 30 provenances in field plots should give a good basis for a description of the overall clinal pattern.

Summary

A nursery evaluation was made of growth of one-year-old red oak seedlings (*Quercus rubra* L.) to provide a basis for later juvenile-adult correlations. Family effects were analyzed within population samples, as well as comparisons between samples from different parts of the botanical range.

Table 8. Mean relative time of growth cessation; 16 provenances, 1961 growing season

Source No.	Locality	Relative time of growth cessation (earliest to latest)
2	Excelsior, Minn.	3.0
26	Rhinelander, Wis.	3.0
20	Cass Lake, Minn.	3.0
17	Cadillac, Mich.	2.9
31	Lima, Ohio	2.6
11	N. Gorham, Me.	2.6
6	Grand Tower, Ill.	2.5
5	Jasper, Ark.	2.4
1	Norris, Tenn.	2.3
7	Paoli, Ind.	2.0
24	Sowerby, Ont.	2.0
13	Marquette, Mich.	2.0
21	Wasaga Beach, Ont.	2.0
3	Bradley, Me.	1.9
19	Wadhams, N. Y.	1.9
29	E. Waterboro, Me.	1.6

Variation in seed weight over the botanical range reflected the geographical distribution patterns of the two acorn types which provided much of the basis for the previously-recognized subspecific division. These are: (1) a small, ovoid or ellipsoid acorn and deep cupule from northern parts of the species range, and (2) a larger and broader acorn and shallow cupule from the rest of the range. When samples were analyzed together covering both these regions, the effect of provenance on seed weight was larger than the effect of female parent. Under conditions of more restricted mid-range sampling, however, parental effect was about three times the provenance effect.

A close relationship between seed weight and seedling height was found in only two of the provenance collections. Other factors had more of an influence on height growth in the rest of the collections.

The provenance effect on growth rate was very noticeable when a widely-scattered series of provenances was analyzed, including collections from the northern limits of the species range. In this analysis the effect of female parent was proportionately very small. On the other hand, when sampling was confined to a few geographic origins not so widely distributed in latitude and excluding extreme northern localities, the influence of mother tree on early growth was somewhat larger than the provenance effect. Similar relationships between these two variance components were obtained from two analyses of variation in time of growth cessation.

The study indicates that there is a strong effect of geographic origin on seedling growth rate in red oak when the analysis includes seed from a wide geographic distribution, particularly when it includes samples from the most northern part of the botanical range. With more restricted sampling, with correspondingly reduced photoperiodic effects, individual inheritance appears to be the most important source of variation in juvenile growth rate.

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