GEOGRAPHIC VARIATION IN WHITE OAK ACORN VOLUME

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Abstract.--Geographic variation in white oak acorn volume followed a north-south and northeast-southwest trend with largest acorns from collections in the southwest and smallest from those in north and northeast parts of the species range. Acorn volumes were highly correlated with longitude and potential rate of evaporation of provenance locations.

Additional keywords: Quercus alba, provenance, correlation, potential evaporation.

White oak, Quercus alba L., has an extensive species range that encompasses most of the eastern United States. With such a large distribution, it is possible that white oak has responded to climatic extremes by genetic differentiation. Such differentiation could be reflected in variation of morphological traits traditionally evaluated in early phases of a tree improvement program.

Korstian (1927) showed that large acorns have greater germination, better survival, and produce larger seedlings than small acorns. Similarly, Q. petraea seedling size at age 2 was shown to be positively correlated with acorn size (Jarvis 1963); seedlings from large acorns were three times bigger than those from small acorns. Because large seedlings are usually preferred in regeneration programs, knowledge of the variation pattern of acorn size may be useful for such programs. In this paper we report the results of a study of morphological variation in acorn volume, as a measure of acorn size, throughout the western part of the white oak range.

METHODS

In 1980 white oak acorns were collected by cooperators in the North Central and Southern States. Because 1980 was a poor mast year for this species, acorns were also collected in 1981 (figs. la and lb). The collections consisted of a minimum of 400 acorns from each of 3 to 10 trees per stand. Length (L) and width (W) of 10 random acorns per mother tree were measured with calipers. Acorn volumes (VOL) were determined by means of the equation (Baranski 1975):

$$VOL = pi/6\ W^2\ (L - W/2) + pi/12\ W^3.$$

The data were analyzed using nested analyses of variance (ANOVA), correlation, and regression. Because acorn length, width, and volume were highly correlated with each other (r values for acorn length vs. width and volume were 0.60 and 0.77, respectively, while the value for acorn width vs. volume was 0.95), and because the ANOVAs for all variables were similar, we will confine this report to acorn volume.

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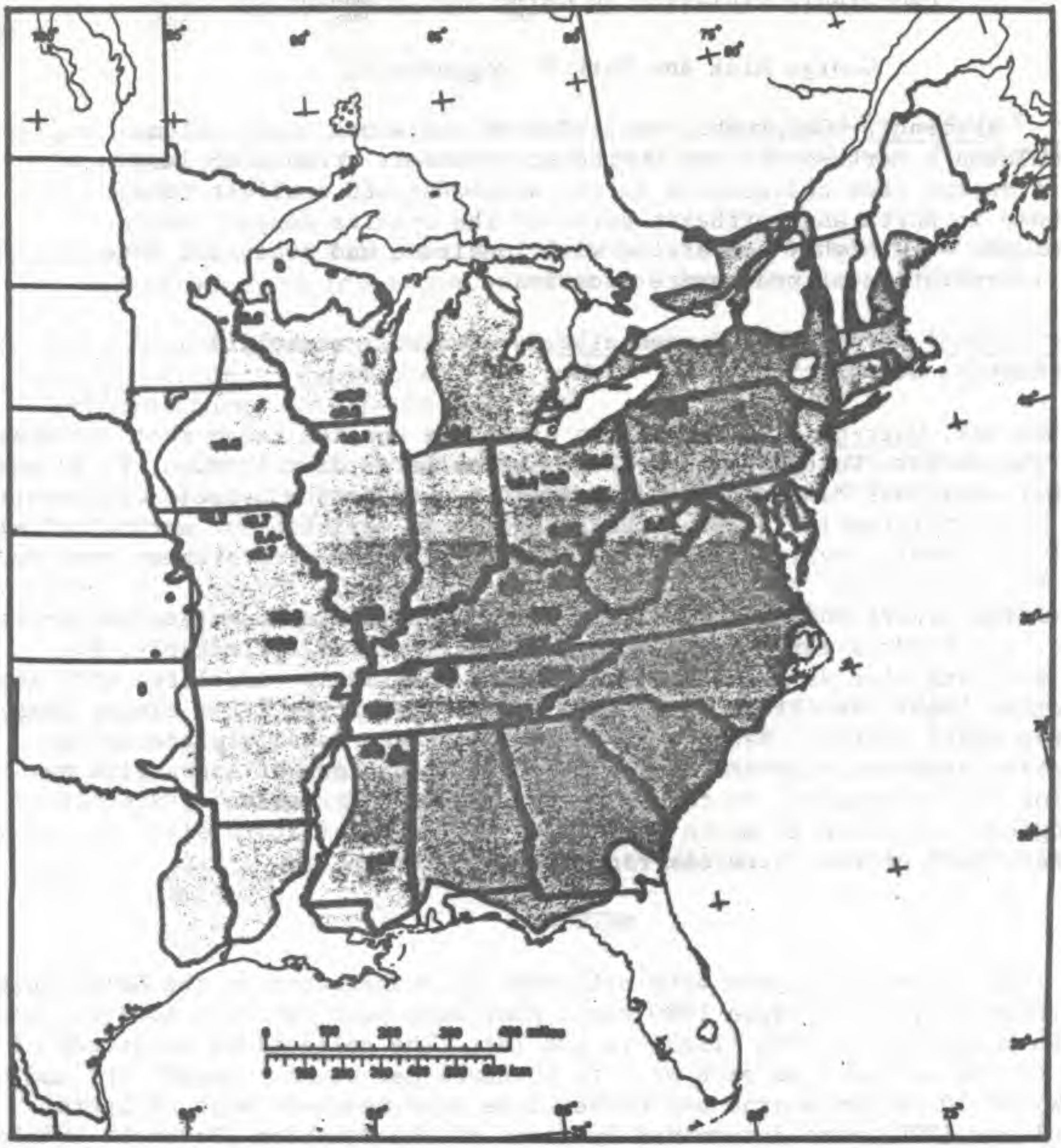

Figure la.--Location of white oak acorn collections and average acorn volume in cubic centimeters. Acorns from Minnesota, Wisconsin, and Pennsylvania were collected in 1980; all others were collected in 1981. Shaded area includes natural white oak range.

In an effort to clarify the relation between acorn volume and longitude, annual evapotranspiration rates were generated for each acorn provenance using Thornthwaite and Mather's (1957) computer program. The program requires inputs of monthly temperatures, precipitation, latitude, and longitude. Long-term temperature and precipitation averages were obtained from weather stations closest to acorn collection sites from National Oceanic and Atmospheric Administration (NOAA) 1980 Annual Summaries of Climatological Data. Annual rates of potential evaporation (expressed as positive numbers), precipitation, potential moisture deficit, actual evaporation, and actual soil moisture deficit generated by this program were then correlated with acorn volumes. (The soil water-holding capacity was assumed to be 300 mm at all locations).

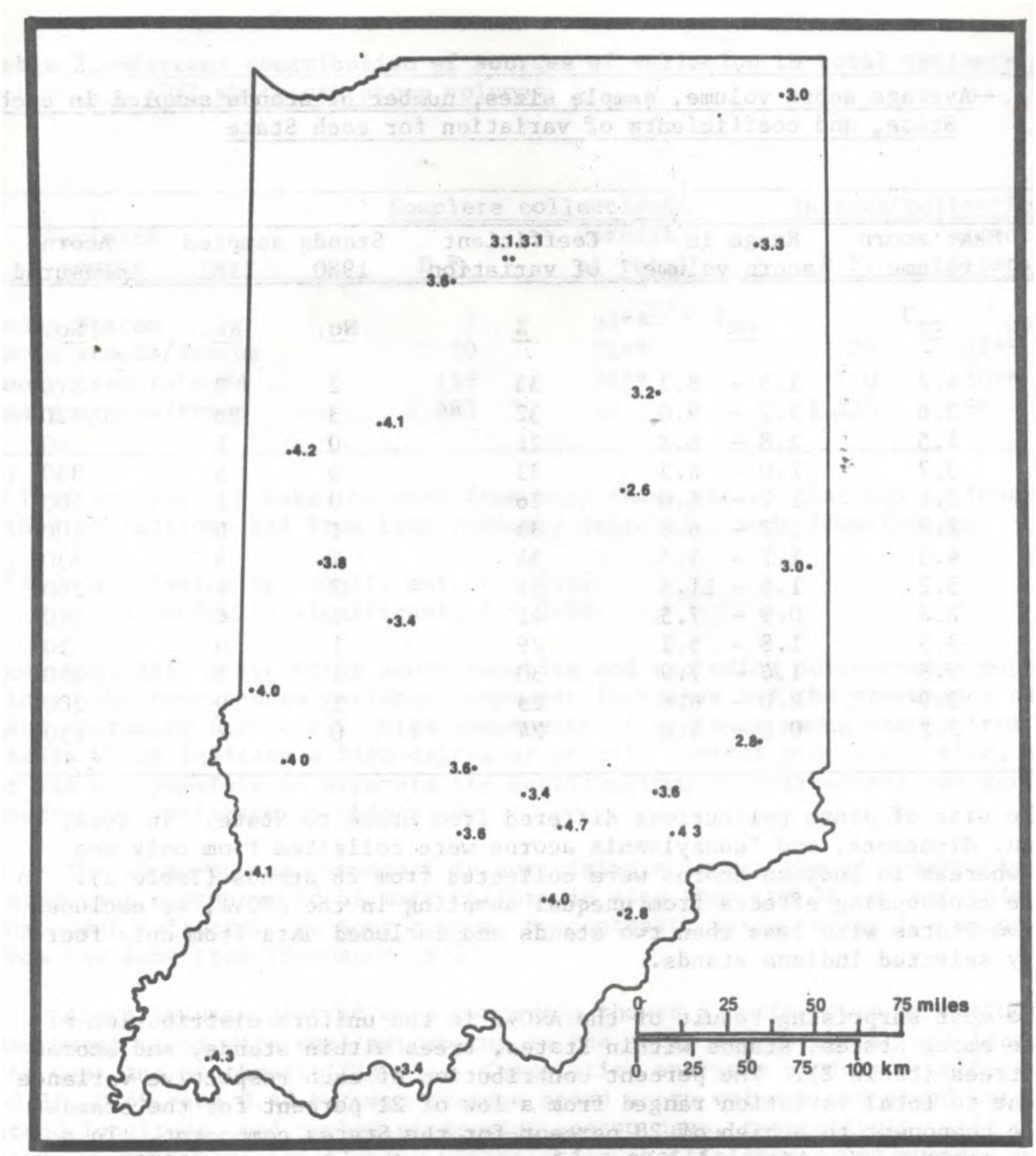

Figure lb.--Location of white oak acorn collections from Indiana and average acorn volume in cubic centimeters. All Indiana acorns were collected in 1981.

Variation in acorn size between years could not be analyzed because collections from common mother trees were not available for both years. However, 1980 and 1981 measurements on several acorns of two southern Illinois trees indicated that year-to-year variation was minor. Nevertheless, we confined the ANOVAs to 1981 data.

RESULTS AND DISCUSSION

Mean acorn volumes ranged from a low of 2.2 cm^3 for acorns from West Virginia to a high of 5.2 cm^3 for those from Missouri (table 1), considerably higher than acorn volumes reported by Baranski (1975). Coefficients of variation ranged from 21 to 41 percent.

Table 1.--Average acorn volume, sample sizes, number of stands sampled in each State, and coefficients of variation for each State

State	Mean acorn volume	Range in acorn volume	Coefficient of variation	Stands sampled 1980	Stands sampled 1981	Acorns measured
	cm^3	cm^3	%	No.	No.	No.
IL	4.2	1.5 - 8.3	33	2	3	370
IN	3.6	1.2 - 9.0	32	3	26	1,320
IA	4.5	2.8 - 6.8	21	0	1	40
KY	3.7	1.0 - 8.3	33	0	5	330
MI	3.1	1.7 - 6.0	26	0	1	100
MN	2.8	1.2 - 6.8	33	1	0	100
MS	4.3	1.7 - 9.5	34	1	3	330
MO	5.2	1.5 - 11.5	36	2	4	260
OH	2.8	0.9 - 7.5	41	1	4	340
PA	3.5	1.8 - 5.1	29	1	0	10
TN	3.9	1.4 - 7.9	30	1	3	350
WI	3.9	2.0 - 6.6	23	2	0	200
WV	2.2	0.8 - 4.6	24	0	2	150

The size of acorn collections differed from State to State. In Iowa, Michigan, Minnesota, and Pennsylvania acorns were collected from only one stand, whereas in Indiana acorns were collected from 26 stands (Table 1). To minimize confounding effects from unequal sampling in the ANOVA, we excluded data from States with less than two stands and included data from only four randomly selected Indiana stands.

The most surprising result of the ANOVA is the uniform distribution of variance among States, stands within States, trees within stands, and acorns within trees (table 2). The percent contribution of each respective variance component to total variation ranged from a low of 21 percent for the stands variance component to a high of 28 percent for the States component. In a previous analysis of white oak acorn volume variation, Baranski (1975) found that almost half of total variance was associated with regional populations and the other half with individual trees; none of the variation was associated with an among-stand-level component. The difference between these analyses is due to differences in the geographic distribution of samples. Baranski's (1975) sampling covered the whole white oak range, whereas the data reported here are primarily from the northwestern, western, and southern parts of the species range. The increased variation in acorn size from Baranski's sampling the complete range apparently obscured any stand variation that may have been present. In a more intensive survey of acorn size variation in the southern Appalachians, Baranski found that a stand component accounted for between 12 and 19 percent total variance, more in agreement with the present analysis.

Another ANOVA was applied to the data from the 27 Indiana stands (table 2). In this analysis, the among-tree variance component was about 50 percent, while the among-stand component was only 12 percent. These results are supported by Kriebel (1964) in a northern red oak (Q. rubra) study in which he found that by

Table 2.--Percent contribution of sources of variation to total variance of 1981 white oak acorn volumes

Variance source	Complete collection[a/] D.F.	Complete collection[a/] Percent of total	Indiana collection D.F.	Indiana collection Percent of total
Among States	7	28**[b/]		
Among stands/States	20	21**	25	12*[b/]
Among trees/stands	159	26**	100	50**
Among acorns/trees	1,683	26	1,134	38

[a/] This analysis is based on data from only those States that had at least two stand collections and from four randomly selected stands from Indiana.

[b/] ** = statistically significant, $P < 0.01$.
 * = statistically significant, $P < 0.05$.

geographically restricting acorn sampling and excluding northernmost populations, the mother-tree variance component increases and the provenance component decreases (table 2). High components of variance among acorns from trees/stands would indicate a high degree of genetic control over acorn size, although it was not possible to separate the contributions of environment and genetic sources of variation in this study.

The among-acorns component is surprisingly large; casual observation indicated that acorns would be more uniform in size than the 38 percent this component reflects. In Acer rubrum, by contrast, variance was low among seed from the same tree (Townsend 1972).

Acorn volumes plotted on a range map showed a north-south or northeast-southwest trend with smallest acorns in the north and northeast and largest in the west and southwest (fig. 1). Correlation analysis produced coefficients of -0.31, 0.69, and 0.48 between average stand acorn volumes and stand latitude, stand longitude, and number of growing season days, respectively. All correlations were highly significant. Correlation coefficients using average volumes for individual trees instead of those for stands as dependent variables produced only slightly lower coefficients. In general, this is the same pattern observed by Baranski (1975) except that his acorn volumes were much more highly correlated with growing season ($r = 0.69$) than those in this study. Acorn volumes were also found to be significantly correlated with provenance potential and actual rates of evaporation with r values of 0.54 as well as with soil moisture deficit ($r = -0.31$). No correlation was found between acorn volume and annual precipitation.

Using average acorn volumes per stand, a multiple regression equation was developed to generate a contour plot of variation in acorn volume as a function of latitude and longitude (fig. 2); the multiple regression equation accounted for 56 percent of variation in acorn volume (1980 and 1981 data were used to produce this equation). The resulting contour plot reflects the general northeast-southwest geographic trend in white oak acorn volume. However, these

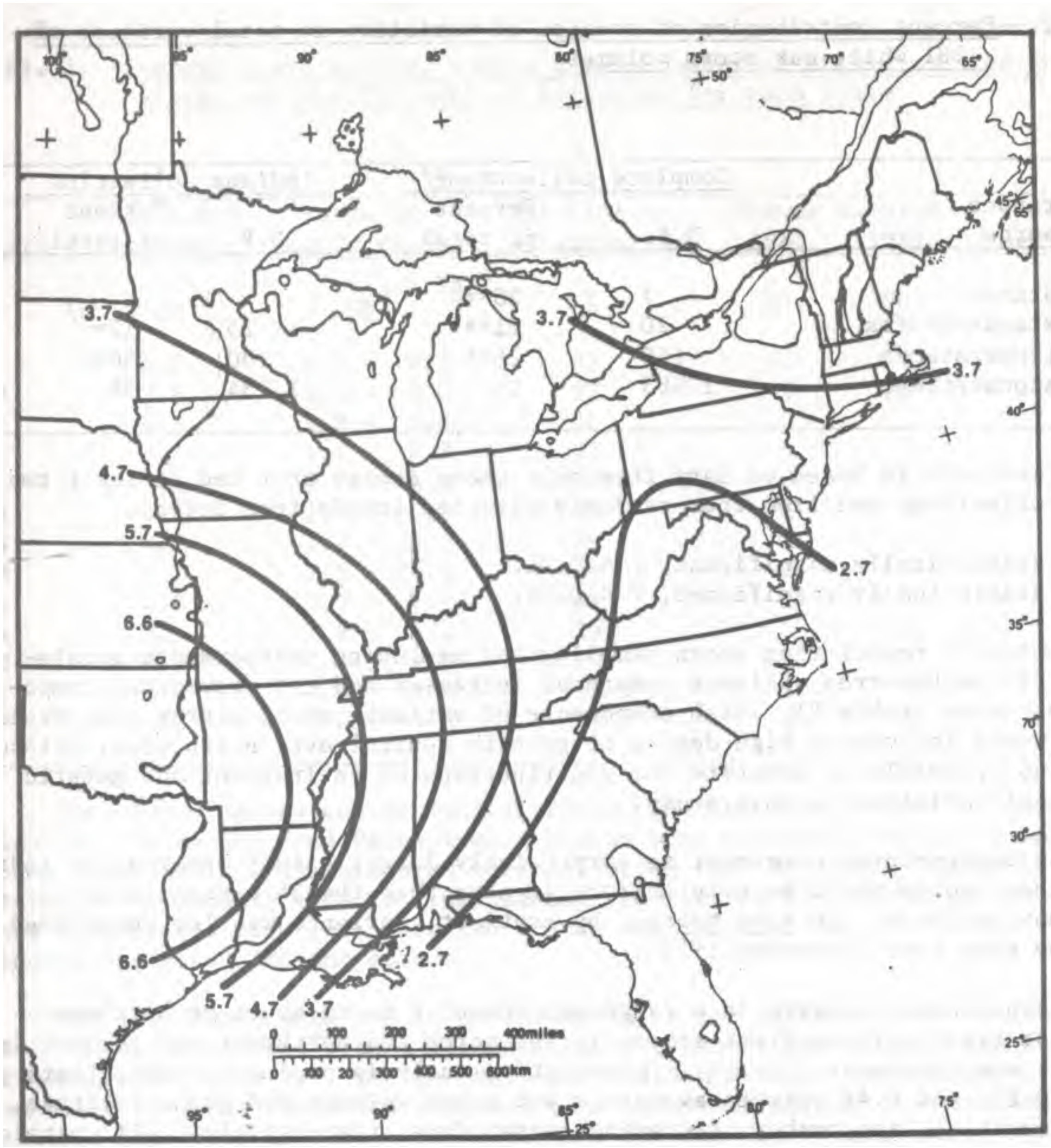

Figure 2.--Variation in acorn volume as a function of latitude and longitude (Volume = $103577 + 23299 \text{ lat} - 551 \text{ lat}^2 + 5 \text{ lat}^3 - 12315 \text{ long} + 184 \text{ long}^2 - 0.7 \text{ long}^3 - 42977 \text{ lat/long} - 77 \text{ lat} \times \text{long}$). Contour lines represent acorn volumes in cubic centimeters.

contours represent broad geographic trends in average acorn size so substantial variation in acorn size (a minimum of 44 percent) would be expected within a given contour interval.

Such seed size patterns along northeast-southwest transects have also been reported for Pinus rigida (Ledig and Fryer 1974) and A. rubrum (Townsend 1972). Although the specific causes for these patterns have not been established, moisture relations have been implicated. For example, Thorbjornsen (1961) reported a strong relation between seed coat thickness and provenance precipitation-evaporation ratio along an east-west cline for P. taeda. Although in white oak the basis for this pattern is not clear, the high correlation between provenance evaporation rate and acorn size implies that soil moisture availability may be a selection criterion for acorn size if the provenance actual evaporation rate is considered an indirect indicator of soil water availability. Seedlings in areas with high soil moisture availability may have greater access to dissolved mineral nutrients and therefore do not need the stored nutrients from large cotyledons of large acorns. On the other hand, seedlings in dry areas depend on the stored nutrients from large cotyledons and therefore may be exposed to a selection pressure favoring large acorns.

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