

Review article

Intraspecific variation of growth and adaptive traits in North American oak species

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Summary — Variation of growth and adaptive traits has been identified in *Quercus rubra* L, which has recognizable geographic patterns in replicated test plantations in the central and western parts of the species range. Traits varying geographically include growth rate, drought resistance, cold resistance, time of flushing and leaf senescence. Patterns may differ in tests in southern regions. In *Quercus falcata* Michx, coastal plain sources are superior to others in both central Mississippi and western South Carolina. In 3 partial-range *Quercus pagoda* Raf tests, local or regional sources out-rank others in growth and adaptability. Both of these species vary widely in cold hardiness. Local trees of *Quercus alba* L are above the average height of all Indiana trees at age 5 yr in southern Indiana, but local trees of *Quercus macrocarpa* Michx in Nebraska are not as fast-growing as trees from seed sources 160 km south. Range-wide patterns remain undefined in both of these species. Among western provenances of *Quercus nigra* L in Louisiana, flushing is latest in trees of the northernmost origins. Only fragmentary information is available on variation of growth and adaptive traits in 7 other oaks, all eastern North American species.

Quercus / oaks / variation / growth / adaptive traits / hardiness

Résumé — Variabilité intraspécifique des caractères d'adaptation et de croissance chez les espèces d'Amérique du Nord. La variabilité des caractères de croissance et d'adaptation a été étudiée chez *Quercus rubra* L; des gradients de variation ont clairement pu être établis chez cette espèce au vu des résultats obtenus dans des plantations installées dans la partie centrale et occidentale de l'aire naturelle. Les caractères, dont la variabilité suit un gradient géographique, sont : le taux de croissance, la résistance à la sécheresse et au froid, la date de débournement et la sénescence des feuilles. Ces gradients peuvent être différents dans les plantations installées dans la partie méridionale de l'aire. En ce qui concerne *Q. falcata* Michx, les origines des plaines côtières sont supérieures aux autres dans la partie centrale du Mississippi, et la partie occidentale de la Caroline du Sud. Dans 3 plantations de *Q. pagoda* Raf ne comprenant qu'un échantillon partiel de provenances, les populations locales étaient nettement supérieures aux autres pour la croissance et les caractères d'adaptation. Les origines locales de *Q. alba* L ont une meilleure croissance que les autres dans le sud de l'Indiana (à 5 ans); alors que chez *Q. macrocarpa* Michx dans le Nebraska, les origines locales sont moins vigoureuses que celles originaires de 160 km au sud. Les gradients de variation au niveau de l'ensemble de l'aire naturelle n'ont pas encore été étudiés pour ces 2 espèces.

En Louisiane, chez *Q nigra* L, le débourrement est plus tardif chez les provenances les plus nordiques. Des données fragmentaires sur la variabilité des caractères de croissance et d'adaptation existent pour 7 autres espèces, toutes issues de l'est des États-Unis.

Quercus / chênes / variabilité / croissance / adaptation / résistance

INTRODUCTION

North America has about 58 species of oaks (genus *Quercus*) of tree size, of which about 20 are considered important in forest management (Fowells, 1965). Many of the North American oaks are distributed over a wide range of latitude and longitude and over several of the plant hardiness zones used as guidelines in horticulture (fig 1, table I). Some are extremely wide-ranging. *Q macrocarpa* Michx, one of the most widely-distributed species, occurs from 28–53 °N latitude and 66–105 °W longitude. Therefore, adaptive traits, and perhaps growth rate as well, could be

expected to vary with seed source in experimental plantations.

In uniform-environment provenance tests of a geographically variable species, extensive provenance sampling covering the entire distribution strengthens the provenance component of variance in relation to stand and family components, whereas range restriction leads to proportionately larger regional and local components (Kriebel, 1965). In several species of *Quercus*, mid-range or confined-latitude sampling indicated that, within the region studied, stand variability was more important than geographic variability, and geographic patterns were not observed (Kriebel, 1965; Houston, 1987; Schnabel and Hamrick, 1990). However, this paper demonstrates that results are very different, at least in *Q rubra*, when samples are more widely dispersed.

Table I. Plant hardiness zones and approximate extremes of average minimum winter temperature within the natural distribution of 8 North American oaks (US Dep Agric, 1960; Fowells, 1965).

Species	Plant hardiness zones	Range of average annual minimum temperature (°C)
<i>Q macrocarpa</i>	2–9	–43 to –4
<i>Q rubra</i>	2–8	–42 to –7
<i>Q alba</i>	4–9	–34 to –5
<i>Q velutina</i>	4–9	–31 to –6
<i>Q shumardii</i>	5–9	–26 to –3
<i>Q pagoda</i>	6–9	–21 to –4
<i>Q falcata</i>	6–9	–21 to –3
<i>Q nigra</i>	7–9	–18 to –1

Most of the information currently available on intraspecific variation in the North American oaks is based on population samples covering only parts of the species distribution. Far more information is available on *Q rubra* than on any other species. In addition, there have been several provenance experiments on *Q falcata* and the closely-related *Q pagoda*. Reported results from research on *Q alba* and *Q nigra* are not range-wide and are limited to juvenile material. Some information is available on growth and adaptability of *Q macrocarpa* from one provenance test at age 11 years. Apart from these 6 species, there is a little information in the liter-

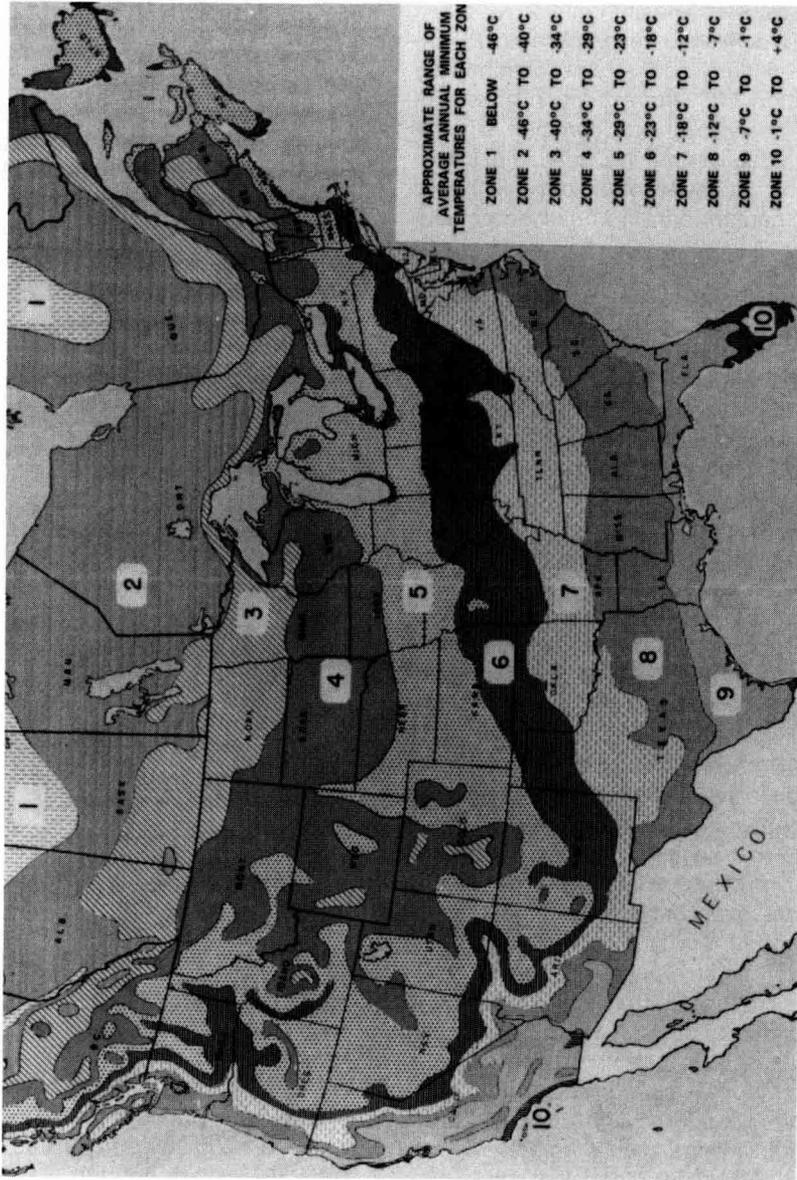


Fig 1. Plant hardiness zones used as guidelines for plant introduction, transfer and breeding in North America (US Dep Agric, 1960).

ature on variation of growth and adaptive traits in North American oaks. Brief discussions on 7 other species are included in this review. The information is taken from: 1) published research; and 2) unpublished data and reports obtained by the author. With the exception of experimental analysis of one commercially important adaptive trait in *Q palustris*, the information on these other oaks is based on fragmentary data from limited population sampling.

NORTHERN RED OAK

About 25 provenance tests of northern red oak (*Quercus rubra* L) of varying size have been established in North America, but some no longer exist and others have not been evaluated. Some are comprehensive, multi-family experiments that are range-wide and replicated in several locations, while others include only a few population samples or are regional in their sampling pattern. The first *Q rubra* provenance tests, which were established by Scott Pauley in Massachusetts in 1951 and 1952, were the most geographically comprehensive tests of this species in North America. They included 80 seed sources that sampled most of the natural distribution. Unfortunately, the plantations were not maintained and the only published report is a study of cold-hardiness. Nine replicated range-wide tests were planted in the North Central states between 1960 and 1962. Results from 7 of these have been published. The other intensive study was of more than 200 families from Tennessee and adjacent areas; of 10 outplantings, results from 3 are summarized. Additional information was available from 4 other northern red oak studies, 2 in the northeastern and 2 in the southeastern parts of the USA. A summary follows.

Variation in growth rate

Northern red oak (*Quercus rubra* L) varies with geographic origin in rate of height and diameter growth. The geographic pattern was evident in 23-year-old trees in 4 range-wide tests in middle latitudes of the species range from eastern Nebraska to northern Ohio (Kriebel *et al*, 1988), but not at age 14 years in the same tests (Kriebel *et al*, 1976). There was no statistical evidence of a pattern in results from limited-area sampling (Kriebel, 1965; Farmer *et al*, 1981; Houston, 1987; La Farge and Lewis, 1987).

The variation pattern is as follows: height growth means are almost always highest in trees from provenances between latitudes 43 and 46°N in an east-west zone extending from the Mississippi River to western Maine. Trees from outside of this zone are, on the average, slower-growing. In Ohio, Indiana and Michigan experiments, all but one of the provenance samples that exceeded the mean annual increment of its age class by more than 1 standard deviation was of Wisconsin, Michigan, Ontario, New York or Maine origin (Kriebel *et al*, 1988). There were indications of a similar pattern in a test of the same material in eastern Nebraska, where the fastest-growing trees were from Wisconsin and extreme eastern Minnesota (Schlarbaum and Bagley, 1981). These patterns are summarized in table II.

From these evaluations up to age 23 years, we can conclude that at latitudes 40–42°N in the USA significant gains in growth of northern red oak can be achieved by planting trees from seed origins 250–550 km north of the planting locality. In addition, since growth varies with stand and family (Kriebel *et al*, 1988), intra-provenance selection is important for planting in this region.

Table II. Provenances of *Q. rubra* with mean annual height increment at age 21–23 yr (14 in Nebraska) exceeding the test mean by > 1s in replicated range-wide experiments. Provenances are ranked in decreasing order of growth rate. The experiments are at 40–42°N locations in the USA; the database includes the 20 provenances common to all 4 locations (Schlarbaum and Bagley, 1981; Kriebel *et al.*, 1988).

<i>Test location</i>			
<i>Ohio</i>	<i>Indiana</i>	<i>Michigan</i>	<i>Nebraska</i>
S Maine	W Wisconsin	N Michigan	E Minnesota
S Ontario	S Wisconsin	S Ontario	W Wisconsin
N Michigan	S Ontario	W Ohio	
W Wisconsin		N New York	
		W Wisconsin	

We do not know whether the same superiority of northern over southern origin trees of *Q. rubra* applies to plantations in other regions. Fragmentary but inconclusive data suggest that it might not apply in regions farther south. In a replicate of the above experiments that was planted in Kansas, tree diameter was inversely correlated with seed source latitude, *ie*, the southern provenances had the faster-growing trees. However, data were taken at age 11 years, and the plantation had low survival percentages of all seed source samples (Deneke, 1975). A similar trend was noted in a progeny test in eastern Tennessee that included families from Tennessee, Virginia and Kentucky. The shortest 10 families in mean height at age 20 years were from the more northern origins (Schlarbaum, 1991). Since all the seed sources were in a narrow latitudinal range relative to the species distribution, results are not comparable with those of the range-wide tests.

Variation in adaptive traits

Northern red oak varies geographically in drought resistance. Trees from prove-

nances in low rainfall regions west of the Mississippi River, near the range limits, are more drought-resistant than those of other origins. These differences were observed in a provenance test in Kansas, at the southwestern limits of *Q. rubra*, where mean summer temperature is highest and mean annual precipitation is lowest within the species range. Trees originating from this region, including Iowa, Kansas and Missouri, had higher survival rates than those from any other provenance (Deneke, 1975).

Cold hardiness of northern red oak depends upon geographic origin. Twigs collected from 16- to 18-year-old trees of 38 origins growing in Massachusetts (Pauley and Johnson, 1955) were subjected to controlled freezing experiments. Cold hardiness was strongly related to estimated mean annual minimum temperature of the origin and to latitude of origin. In all cases, however, cold hardiness was greater than that required by the climate of the origin, suggesting that twig hardiness in established trees is not an important factor in natural selection under contemporary climatic conditions (Flint, 1972).

Data of bud-break or leaf flushing of northern red oak depends upon seed source; in the north central region of the

USA, flushing begins in trees of northwestern origin, then proceeds '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 (Kriebel *et al*, 1976). This trend is not significantly correlated with latitude and it is only weakly correlated with longitude (Schlarbaum and Bagley, 1981). In eastern Tennessee, the pattern of flushing is very different: the general trend begins in trees of southern origins and ends in trees of northern origins (Gall and Taft, 1973; Schlarbaum, 1991).

Data of bud-break advances with increase in seed source elevation; in western North Carolina, the time spread between the lowest and highest elevation source was 11 days, regardless of plantation elevation (McGee, 1974).

Unlike the flushing date, the time of leaf senescence in *Q. rubra* is very strongly correlated with the latitude of the seed source, progressing clinally from north to south (Deneke, 1975; Kriebel *et al*, 1976; Schlarbaum and Bagley, 1981).

SOUTHERN RED OAK

Two principal studies have been conducted on geographic variation in southern red oak (*Quercus falcata* Michx). One comprises two 43-origin, range-wide provenance tests in the Piedmont region of western South Carolina (Schoenike *et al*, 1982). The other is a central Mississippi test of 112 trees from 43 stands in 23 provenances, including most of the natural distribution with the exception of Florida and areas north of 36°N (Mukewar and Land, 1987). In addition, a few families of 4 provenances were tested at the Michaux Quercetum in southeastern Pennsylvania (San-

tamour *et al*, 1980), with partial replication in northern Ohio (author's records).

Variation in growth rate

Seed source had a strong effect on tree height in South Carolina at age 10 years. Southern red oaks that surpassed the local source were from the lower coastal plain of North and South Carolina, southern Mississippi, southeastern and north-central Louisiana, southeastern Arkansas and southeastern Missouri. Those growing more slowly were from Piedmont and mountainous regions of Virginia and North Carolina, Tennessee, Florida, eastern Texas, Alabama, southern Missouri and southern New Jersey. These provenances are near the periphery of the species range. No clinal trends were found, nor were there any meaningful correlations with latitude, longitude, mean annual temperature or length of growing season.

In central Mississippi, provenance effects at age 5 years accounted for about 70% of total variation, and families within stands 20%. There was very little difference among stands within provenances. Southern red oaks from seed sources in southeastern Texas and eastern Georgia were significantly faster-growing than those from the other 21 provenances.

Farther north, in southeastern Pennsylvania, the comparison was made between 2 seed sources of southern red oak that are northern for the species and 2 sources in the southern part of the species range. Progenies from seeds collected in the nearby region of Maryland and Virginia outgrew those of Alabama and Arkansas origins.

Variation in adaptive traits

Survival of southern red oak in South Carolina and Mississippi is not source-related.

In southeastern Pennsylvania, it is; trees from Mississippi suffer heavy mortality from winter temperatures. Trees of Arkansas sources are less affected, but of the 4 provenances tested, only Virginia and Maryland trees had high survival rates (Santamour *et al*, 1980). In Ohio, where winters are more severe, trees of the Virginia seedlot that were hardy in Pennsylvania all died within the first few years after planting. Other sources were not tested (author's records).

CHERRYBARK OAK

Harlow *et al* (1991) now follow Jensen (1989) in classifying cherrybark oak as *Quercus pagoda* Raf rather than as a form of southern red oak (*Quercus falcata* var *pagodaefolia* Ell). The 2 oaks were considered by Ware (1967) and Jensen to be sister species that are incompletely reproductively isolated. In support of species separation, Jensen stated that, "differences between them can be detected consistently in geographically widespread locales, indicating that recognition of these taxa as species is in keeping with the generally accepted species concept in oaks." *Q falcata* characteristically occupies a xeric habitat, whereas *Q pagoda* occurs in mesic habitats.

Variation in growth rate

Cherrybark oak has been described as the most rapidly growing southern oak (Randall, 1972). As in *Q falcata*, the growth rate of *Q pagoda* is very dependent upon seed source. In a western Tennessee test that included 36 phenotypic selections at age 10 years, trees from Mississippi and Arkansas seed sources grew poorly compared with those from the Tennessee sources (Overton, 1981). By age 14 years,

the tallest of the Tennessee families had a mean height of ≈ 11 m, 2–6 m above the means of southern and western trees (University of Tennessee, unpublished data).

In a more recently initiated study near the Mississippi River in extreme northwestern Kentucky (including provenances from Louisiana, Mississippi, Alabama, Tennessee, Kentucky and Virginia), the trees from Tennessee and Mississippi were outgrowing those from other sources at age 5 years. Some were 6 m in height (Rousseau RT, unpublished data).

Farther north, in Indiana, cherrybark oaks from the northern extremity of the species range in southern Indiana were significantly taller than all others at age 7 years. The test included 9 seed sources in 6 states (M Coggeshall, unpublished analysis and these proceedings).

Variation in adaptive traits

Cherrybark oak is highly variable in cold hardiness. In western Tennessee, families of local origin averaged 92% survival at age 10 years, while those from Mississippi and Arkansas averaged 66% (Overton, 1981). In southern Indiana, Coggeshall's records show that only trees from extreme southwestern Indiana, the northernmost point in the species range, remained completely healthy after a 10-day period with a low temperature of -31°C . There was a high negative correlation between degree of winter injury and seed source latitude.

WHITE OAK

White oak (*Quercus alba* L) grows throughout the eastern United States, with the exceptions of northern Maine and the Florida peninsula. It also occurs in parts of southern Ontario and Quebec. Although it is one of the most common and commercially im-

portant oaks in the eastern United States, there is no range-wide provenance test of the species. The most geographically dispersed set of population samples is in the Michaux Quercetum test in southwestern Pennsylvania, which includes small numbers of trees of 18 families from 9 provenances (Santamour *et al*, 1980). Eight of these provenances are replicated in Wooster, Ohio. There are 2 tests established by Coggeshall in southern Indiana containing 63 and 70 families from throughout Indiana. Results from an unpublished evaluation of 5-year-old in the Indiana tests sent to the author by Coggeshall are included in this review.

Variation in growth rate

No geographic pattern of variation in growth rate was evident among 24-year-old white oaks of 9 provenances in Pennsylvania. The sampling dispersion was from Massachusetts and Virginia in the east to Wisconsin and Arkansas in the west (Santamour *et al*, 1980). Results were the same in the Ohio replicate at age 11 years (author's data). This absence of a pattern is not surprising, considering the small number of provenances and the variation among seedlots. In southern Indiana, where 5 latitudinal transects were made, including 2 stands per transect, family differences were about 2.5 times stand differences. Stand, transect and stand-within-transect differences were not significant at either test location. Growth of trees from local stands exceeded the test mean at both test sites. These early Indiana results suggested that, in that region, some gain in growth of white oak may be obtained by using seed sources (or stands) from a latitude of up to 2 °N of the planting site, but that extreme northern Indiana seed should be avoided for planting in southern Indiana.

There was no evidence from any of these limited-sample *Q. alba* experiments that survival rate was related to the geographic origin of the seed.

BUR OAK

Bur oak (*Quercus macrocarpa* Michx) has a very wide north-south natural distribution (table 1), extending from Manitoba nearly to the Gulf of Mexico. It also has a wide longitudinal range, extending from New Brunswick far into the prairies. Bur oak is extremely drought-resistant (Fowells, 1965). Provenance variation has been studied in eastern Nebraska and on a smaller scale in eastern Pennsylvania and Ohio.

Variation in growth rate

In eastern Nebraska, a test of 50 seed sources sampled the species range, but population sampling was mainly concentrated in Kansas and Nebraska. Height at age 11 years was maximum in trees originating 160 km south of the plantation at 40 °N. There was no observed continuous geographic pattern of growth rate (Dicke and Bagley, 1980). In eastern Pennsylvania, only 2 seedlots each from Kansas, South Dakota and Minnesota were tested. Height growth tended to increase with decreasing latitude of seed origin; Kansas trees averaged about 1.5 times the height of Minnesota trees (Santamour *et al*, 1980).

Variation in adaptive traits

Date of leaf fall was not related to the latitude of the seed origin in Nebraska. In southeastern Pennsylvania, survival rate of bur oak by age 25 years was 4 times high-

er among Kansas trees than among Minnesota trees. Since the test site has a milder winter climate and higher precipitation than either the Kansas or Minnesota collections, the differential survival does not appear to reflect differences in either cold hardiness or drought resistance. Bur oaks from these 2 sources had a high survival rate in northern Ohio.

WATER OAK

Water oak (*Quercus nigra* L) is a southern, mild-climate species. At its northernmost limits, mean minimum winter temperature is -18 to -12°C (US Dep Agric, 1960). Most information on geographic variation is available from one 5-year-old provenance test in central western Louisiana and from southeastern Pennsylvania.

Variation in growth rate

In Louisiana, 68 water oak families were taken from 12 sampling points in the western part of the species distribution, consisting of 3 north-south transects, one along the Mississippi River and the others 160 km east and west of it. At age 5 years, there was no distinct geographic pattern. Trees from the middle Mississippi River and middle eastern Mississippi sources were consistently high in both diameter and height growth, but trees of southwestern Louisiana origin, which averaged 4.2 m at age 5 years, were superior overall in rate of height growth independent of diameter (Adams, 1989).

Variation in adaptive traits

Q nigra trees of northern Arkansas origin flushed 7-10 days later in Louisiana than

trees of more northern origin. A late frost damaged foliage of local and southern provenance material, but there was no injury to the Arkansas trees (Adams, 1989). In southeastern Pennsylvania, near the northern range limits, survival of trees of Virginia provenance was highest, averaging 76%. Survival of Maryland and Mississippi trees was lower (Santamour *et al*, 1980). Only 3 trees from one source (Virginia) were tested in northern Ohio, a colder climate than southeastern Pennsylvania. Records show that all 3 were growing at age 11 years.

OTHER NORTH AMERICAN OAKS

With the exception of one study of *Quercus palustris* Muenchh, information on variation of growth and adaptive traits in other oaks is based on the testing of open-pollinated progenies at the Michaux Quercetum, Longwood Gardens, PA. Seed samples from various North American oaks were collected from a small number of trees in each of 2-9 geographically dispersed localities. Trees from each seedlot were divided into 2 row-plot replicates; the total number of trees planted per seedlot varied from 11 to 42. Analysis of juvenile material indicated that there was genetic variation in growth and phenology, but no geographic patterns could be identified (Gabriel, 1958; Santamour and Schreiner, 1961; Schreiner and Santamour, 1961). An assessment of growth and survival of all oak collections in the Quercetum was made at age 25 years (Santamour *et al*, 1980). Three-tree plots of many of the Quercetum collections were planted by Kriebel at Wooster, Ohio and measured at age 11 years. The data were not published and a large part of the test was subsequently lost due to road construction. Given the limitations of these experiments, the results nevertheless report the perfor-

mance of source-documented trees and provide some useful information on growth and climatic adaptability in relation to provenance.

Pin oak

Experiments with pin oak (*Quercus palustris* Muenchh) on 19 natural and 2 cultivated populations well-distributed throughout the natural distribution were designed and carried out to evaluate the severity of iron chlorosis in solution culture and soil environments. There were significant differences in resistance among the progenies of different pin oak parents, but the rankings varied considerably among experimental environments. There was some indication of a geographic pattern; population samples from northcentral and northwestern parts of the species range (Indiana, Illinois, Missouri) were consistently among the most resistant populations. One population from northern Illinois was a particularly promising candidate for testing and selection (Berrang and Steiner, 1980).

Shumard oak

In Pennsylvania, the growth rate of Shumard oak (*Quercus shumardii* Buckl) was higher in trees of Mississippi provenance than in trees from Illinois, Tennessee and Florida sources. Juvenile trees of all sources except Illinois had an extended growing season and were killed back by early fall frosts. However, at age 25 years, the 70% survival rate of Shumard oaks of Mississippi origin was nearly as high as that of Illinois trees and growth rate was higher, up to 17.1 m. In the colder climate of northern Ohio, the Mississippi and Florida collections were not winter-hardy. Trees of Illinois origin were 17% taller on

the average than trees from the Tennessee provenance.

Black oak

There are 11 seedlots of 6 provenances of black oak (*Quercus velutina* Lam), in the 25-year data from Pennsylvania. Seed origins include Alabama, Tennessee, North Carolina, Virginia, Illinois and Michigan. The Ohio collections originally included 8 *Q. velutina* seedlots from the same provenances and Connecticut. In southeastern Pennsylvania, seedlot differences in 25-year height growth within provenances were small. Although black oaks of Tennessee and Illinois origins were slightly faster-growing than others, averaging 16.3 m, North Carolina trees had the highest survival rate. In northern Ohio, the mean height of one Michigan family was 30% greater than the mean of 2 Tennessee families. Black oaks of Alabama origin were not winter-hardy in Ohio and there was dieback of Virginia and North Carolina trees.

Scarlet oak

The Michaux Quercetum plantings include 4 provenances of scarlet oak (*Quercus coccinea* Muenchh) in Pennsylvania and 3 in Ohio. In Pennsylvania, trees from Tennessee and Illinois seedlots had a mean height at age 25 years of 15.5 m, a slight superiority over the growth of Virginia and Alabama trees. Survival differences were not source-related. Of the 3 provenances represented in Ohio, trees from the one Virginia provenance were 36% faster-growing at age 11 years than the mean of 2 Tennessee provenances. Scarlet oaks from Alabama seedlots did not survive in Ohio.

Willow oak

Six seedlots of 4 provenances of willow oak (*Quercus phellos* L) were tested in Pennsylvania. The provenances were Mississippi, Arkansas, Virginia and Maryland. Willow oaks of Virginia origin were tallest with a mean height of nearly 16 m at age 25 years, but only one-third of the trees survived the winters. The survival rate of trees in the Arkansas collections was about twice that of the others. Only Arkansas trees were winter-hardy in Ohio, but growth was slow, averaging 1.5 m at age 11 years.

Shingle oak

Shingle oak (*Quercus imbricaria* Michx) was represented in both Pennsylvania and Ohio by 3 sources (Illinois, Indiana and Ohio). There were no clear source-related differences in growth rate or hardiness in either location. At age 25 years in Pennsylvania, trees of Indiana origin averaged 15.6 m in height and were taller than those from Illinois and Ohio.

Blackjack oak

One progeny of each of 4 provenances of blackjack oak (*Quercus marilandica* Muenchh) was tested in southeastern Pennsylvania. The provenances were in Texas, Kansas, Arkansas and New Jersey. Height growth in 25 years varied from a mean of 9.4 m for trees of Texas origin to 7.2 m for trees from the New Jersey seed source. The survival rate of blackjack oak varied from 10% in the Texas progeny to 38% in the progeny from nearby southern New Jersey.

CONCLUSIONS

With the exception of results from tests of *Quercus rubra*, information on variation in growth and adaptive traits of the North American oaks is still very limited. Even *Q. rubra* is inadequately sampled, considering its abundance and wide distribution. The distribution of *Q. falcata* has been more completely sampled than has that of the wider-ranging *Q. rubra*, although the future of the South Carolina tests of southern red oak is uncertain. However, some useful information is now available about intraspecific variation in growth rate and winter hardiness in this species. Studies of variation in *Q. pagoda* are yielding valuable information, but they do not cover the entire species range. Considering the economic importance of *Q. alba*, we should be much farther ahead than we are in our research on this species. Our white oak tests are very limited, both geographically and in sampling intensity. Because of its drought-resistance in the prairie regions of North America, *Q. macrocarpa* merits further research on vigor and hardiness. The recently initiated effort under way with *Q. nigra*, focusing on the western part of the species range, will provide some information on this previously untested fast-growing species. Tests of scattered seed sources of 6 other oaks provide fragments of information that may reduce the risk of plantation failure and increase productivity in certain regions, although they are at best only indicative and in no case descriptive of variation of the species as a whole. Indications of variation in resistance to iron chlorosis in *Q. palustris* may be useful in urban forestry. As far as other North American oaks are concerned, including the western species, their intraspecific variation is virtually unknown.

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