THE MORPHOLOGICAL VARIETIES OF SOUTHERN RED OAK

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INTRODUCTION

Southern red oak, *Quercus falcata* Michx., also called Spanish oak, is one of the more variable of the American oaks, and for this reason there has been much confusion concerning the exact status of this taxon. It has been subdivided into as many as four separate taxa, each of which has at times been given status as an independent species. The purpose of this study is to examine the distinguishing morphological characteristics of these four varieties, to consider the validity of these taxa from a morphological standpoint, and to recommend changes in nomenclature where deemed necessary.

"Spanish oak" was known to the early settlers in America. William Penn described it to prospective colonists in 1683, as did William Byrd a half-century later (Peattie 1950), and it was recognized and named as a species, *Quercus falcata*, by Michaux in 1801 (Little 1953). The typical form is described as a tree with dark gray or blackish bark divided into heavy ridges by distinct longitudinal furrows (Brown 1961) (Fig. 1). Mature leaves, four to ten inches long, are

Fig. 1. This photograph shows the deeply furrowed bark characteristic of *Quercus falcata* (typical).

firm, dark green and lustrous above. They are coated below with a soft close pubescence, which is orange-tinged or rusty in color. The one to three pairs of falcate lateral lobes are bristle-tipped. The acuminate terminal lobe is longer than the lateral lobes, often falcate, and has bristle-tipped teeth near the end (Fernald 1950, Sargent 1922). The base is rounded or bell-shaped (Fig. 3).

This oak, found in dry woods, sandy uplands, flatwoods (Brown 1961), and other xeric areas, grows from 70 to 80 feet high with a trunk diameter of two to three feet (Small 1933). It ranges from southeastern Missouri, eastern Oklahoma, and eastern Texas eastward to the Atlantic, and from southern Illinois, southern Indiana, southern Ohio, southeastern Pennsylvania, and southern New Jersey southward to central Florida and the Gulf of Mexico (Fernald 1950). Harlow and Harrar (1958) presented a range map for the species.

The variety *triloba* (Michx.) Nutt., a variant of the typical form, was recognized by Michaux in 1801 as a separate species (Little 1953). It differs from the typical form in its leaves. These are oblong-obovate and uncleft, except toward the broad apex, where they have three short, ascending bluntish terminal lobes. The leaf base is decidedly bell-shaped (Fernald 1950) (Fig. 5). Sargent (1922) said that the *triloba* leaf and the typical leaf form usually occurred on different trees, but were sometimes found on the same tree. He also reported that variety *triloba* was a smaller tree, usually 20 to 30 feet high. In other characteristics it is like the typical form. Both Fernald (1950) and Sargent (1922) stated that this variety was rare and local throughout the range of the species.

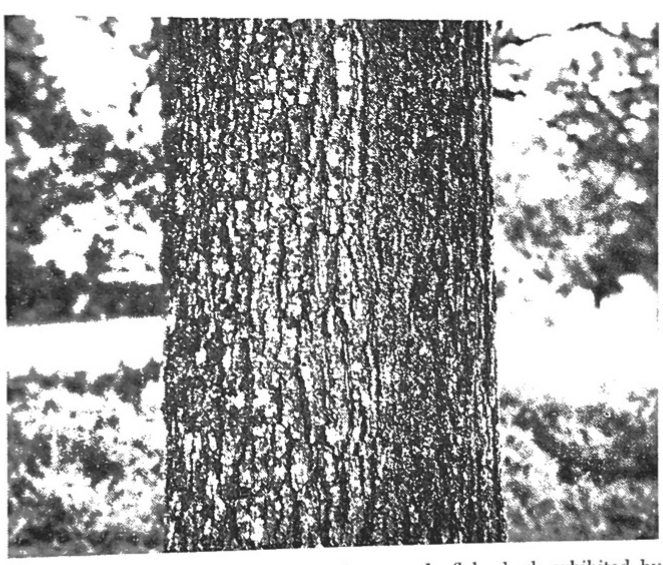

Fig. 2. This photograph shows the smooth, flaky bark exhibited by *Quercus falcata*, variety *pagodaefolia*.

Quercus falcata var. *pagodaefolia* Ell., cherrybark oak or swamp red oak, differs markedly from the typical form in leaf shape, type of bark, and habitat. It was recognized as a variety of *Quercus falcata* in 1824 by Elliott; Rafinesque in 1838 and Ashe in 1897 considered it an independent species (Little 1953). This oak has light gray, gray-brown, or dark gray bark divided by shallow furrows into flat ridges. These ridges are broken into small rectangular or square plates or scales, like the bark of mature black cherry trees (Brown 1961) (Fig. 2). The leaves, dark green and lustrous above, are coated below with white or pale yellow pubescence. They are six to eight inches long, elliptic to oblong in shape, and deeply divided into

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five to eleven spreading lobes. These lobes are attenuate, usually entire, and sometimes falcate (Sargent 1922) (Fig. 4). The base is wedge-shaped, and the leaf, which commonly hangs vertically, is often noticeable pagodiform.

The variety *pagodaefolia* is a larger tree than the typical form, growing up to 120 feet high and four to five feet in diameter (Sargent 1922). Its wood is regarded as being superior to that of the variety *falcata*, since it is harder, stronger, and heavier. Peattie (1950) reported the density of *Quercus falcata* to be 41 pounds per cubic feet, and the density of variety *pagodaefolia* to be 48 pounds per cubic foot. Sargent (1922) reported that cherrybark oak was manufactured into lumber in the Mississippi valley, and was valued almost as highly as white oak. In contrast, the wood of southern red oak was used primarily for fuel.

The range of cherrybark oak corresponds approximately to that of southern red oak, though the range of cherrybark oak does not extend quite so far north or west as that of the typical form (see map, Harlow & Harrar 1958). Yet, the habitat of the two forms is very

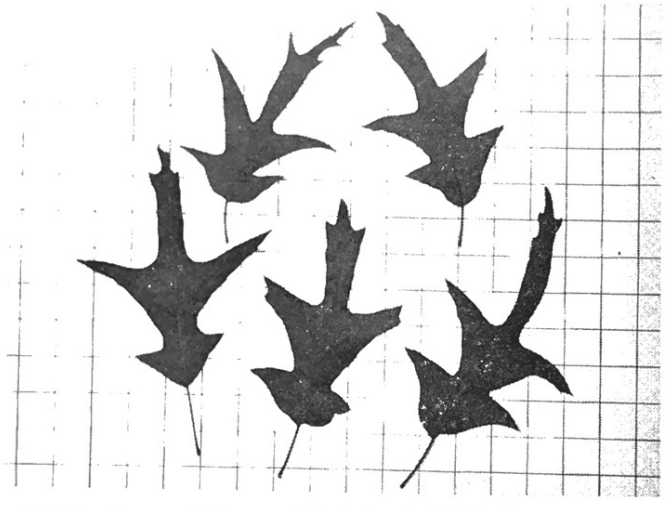

Fig. 3. Leaves of *Quercus falcata* (typical). The large squares on the background of this photograph and those following are 1″ x 1″.

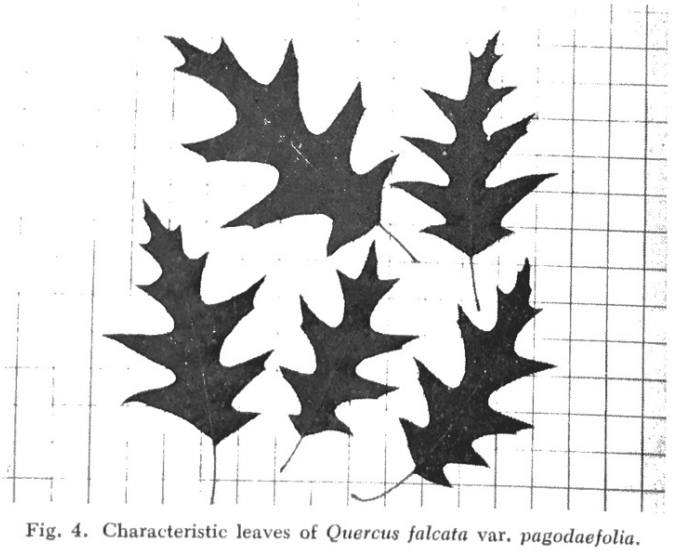

Fig. 4. Characteristic leaves of *Quercus falcata* var. *pagodaefolia*.

Fig. 5. Characteristic leaves of a tree which might be called *Quercus falcata* var. *triloba*.

Fig. 6. Characteristic leaves from the lowest branches of a tree which might be identified as *Quercus falcata* var. *leucophylla*.

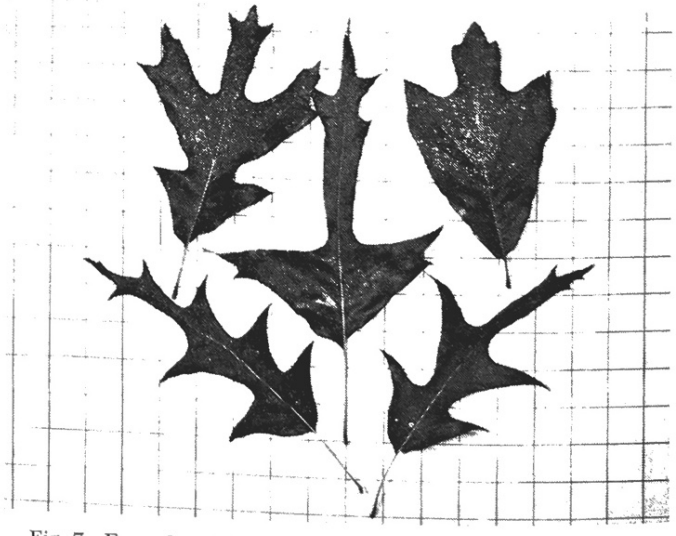

Fig. 7. Examples of leaf variability on *Quercus falcata* (typical). All these leaves came from the same tree.

different. Cherrybark oak is found largely in bottomlands, near streams (Fernald 1950), and in other areas of high water availability (Caplener *et al.*, in press), as opposed to the usually more xeric habitat of *Quercus falcata* var. *falcata*.

A fourth variety of *Quercus falcata* is variety *leucophylla* (Ashe) Palmer & Steyerm. Ashe distinguished this form from variety *pagodaefolia* in 1916 (Little 1953). It differs from variety *pagodaefolia* in its leaves. On the upper branches they are described as nearly as broad as long, deeply divided into five to seven lobes, and as being thickly covered below with pale pubescence. The leaves on the lower branches constitute the only characteristic by which this variety is recognized. These are obovate, shallowly divided, thin, dark green, glabrous above, and often covered below with white or brownish pubescence (Sargent 1922) (Fig. 6). Vines (1960) said that the lower leaves resembled those of black oak in shape. This variety grows in moist rich soil throughout the range of variety *pagodaefolia*.

NOTE ON NOMENCLATURE.

Although Linnaeus applied the name *Quercus rubra* to the composite taxon of 'red oak,' DuRoi in 1772 limited this name to the northern red oak (Svenson 1939); southern red oak was later named *Quercus falcata* Michx. After 1915, however, the name *Quercus borealis* Michx. f. was applied to northern red oak, and many authors adopted the name *Quercus rubra* for southern red oak (Little 1953). Sargent (1922) and Small (1933) were among these authors. Britton and Brown (1913) and Stemen and Myers (1937) used *Quercus triloba* as a name for southern red oak. In recent years the practice has been to restore the original name of *Quercus falcata* to southern red oak. Gleason (1952) proposed to eliminate the term *Quercus rubra* from the nomenclature, since it was the source of confusion, but most authors are now restoring the name *Quercus rubra* to northern red oak. Svenson (1939) discussed the nomenclatural confusion and suggested the procedure followed in this paper. Here, southern red oak is called *Quercus falcata*, regardless of which synonym the source used for it, and *Quercus rubra* refers to the northern red oak.

Review of Literature

All four varieties of *Quercus falcata* were described by Sargent (1922) and Vines (1960). Kelsey and Dayton (1942) also listed all four varieties. Peattie (1950), Gleason (1952), Little (1953), West and Arnold (1956) in Florida, Radford, Ahles and Bell (1964) in the Carolinas, and Chapman (1860) recognized only two varieties: the typical form of *Quercus falcata*, and variety *pagodaefolia*. Small (1933), Britton and Brown (1913), Brown (1961) in Louisiana, and Bailey (1933) recognized only two forms, but they gave variety *pagodaefolia* rank as a separate species.

Fernald (1950) recognized the typical form and varieties *pagodaefolia* and *triloba*. Little (1953) listed the variety *triloba* as a synonym for *Quercus falcata* var. *falcata*, and Stemen and Myers (1937), Bailey (1949), and Britton and Brown (1913) also regarded *triloba* as a synonym for *falcata*. Steyermark (1963) treated *triloba* as a forma of *Quercus falcata*.

Harrar and Harrar (1946), in their work on Southern trees, recognized the typical form and variety *pagodaefolia*, but they also distinguished the form *leucophylla*. They agreed with Kelsey and Dayton (1942) that the name 'cherrybark oak' should be restricted to variety *leucophylla*, with variety *pagodaefolia* being called 'swamp red oak.' Little (1953) and Steyermark (1963) listed *leucophylla* only as a synonym for *pagodaefolia*.

In Mississippi there has been much confusion about the true identity of variety *pagodaefolia*. Hilgard (1860) reported that there was a common oak in northern Hinds county which was often not distinguished from black oak (*Quercus velutina* Lam.), and was considered by many to be a variety of *Quercus falcata*. Actually, he said, it was 'true,' or northern, red oak, *Quercus rubra*. Since recent studies have found no *Quercus rubra* in this area, and *Quercus falcata* var. *pagodaefolia* is one of the more common oaks, it is probable that Hilgard's 'true red oak' was actually variety *pagodaefolia*.

Mattoon and Beal (1925), in their guide to Mississippi forest trees, recognized only the typical form of *Quercus falcata*. Lowe (1913) and Brown (1945) treated *pagodaefolia* and *falcata* as synonyms. Therrill (1949) discussed the typical form and varieties *pagodaefolia* and *leucophylla* and commented that the wood of both the latter varieties was superior to that of the typical form. Sargent (1922) reported that variety *leucophylla* was common in central Mississippi, and was one of the largest and most valuable timber trees of the Yazoo Basin in Mississippi.

It can be seen that there is considerable disagreement among botanists about the correct division of the *Quercus falcata* complex. However, from the literature three distinct patterns can be recognized. These patterns were noted by Vines (1960). First, most botanists consider the evidence for the separation of the variety *triloba* insufficient, and they include this form with the variety *falcata*. Second, many botanists recognize a morphological difference between the types *leucophylla* and *pagodaefolia*, though there is little agreement on exactly what the differences are. Some botanists, such as Little (1963) and Steyermark (1963), consider the difference insufficient for recognition of the type *leucophylla* as a variety. Third, most botanists think that the differences between the varieties *falcata* and *pagodaefolia* are sufficient for recognizing two separate varieties, and to some botanists, these differences are sufficient to give the two forms rank as separate species.

Methods

A dichotomous key (Table I) was prepared based on the descriptions and illustrations of Vines (1960), Fernald (1950), and Sargent (1922). This key was used to distinguish the four forms of *Quercus falcata*. During the winter of 1963, trees which appeared to be of

the varieties *falcata* and *pagodaefolia* were located and distinguished on the basis of bark and fallen leaves.

TABLE I.

KEY TO THE VARIETIES OF *QUERCUS FALCATA*

A. Bark divided into heavy ridges by distinct longitudinal furrows; leaf base rounded, leaf pubescence yellow to rusty beneath ..... B

B. 1-3 pairs of lateral lobes spreading to spreading-ascending, often falcate; terminal lobe elongate, acuminate, often falcate 1

1. ..... *Quercus falcata* var. *falcata*

B. 3 short bluntish lobes at broad apex of obovate leaf; leaf base prolonged, bell-shaped 2

2. ..... *Quercus falcata* var. *triloba*

A. Bark divided into at ridges by shallow furrows, the ridges broken into small squarish flakes; leaf base short wedge-shaped; pubescence whitish, greenish or brownish C

C. Leaves ovate to oblong with 3-5 pairs of spreading attenuate lateral lobes; often pagodiform in shape. 3

3. ..... *Quercus falcata* var. *pagodaefolia*

C. Leaves elliptic to obovate with 2-3 pairs of broad spreading lobes on lower branches; leaves of upper branches more deeply and narrowly lobed.. 4

4. ..... *Quercus falcata* var. *leucophylla*

Study was begun before buds opened in the spring, and as buds opened, twigs, leaves, and inflorescences were collected and preserved for later study. Collections were made from individual trees in widely scattered areas, and at regular intervals to secure leaves and flowers at various stages of maturity. During this critical period of flowering and leaf maturation, sketches were made and notes taken daily. After the emergence of leaves, trees which exhibited the characteristics of the varieties *triloba* and *leucophylla* were selected for careful study. Frequent observation and careful comparison of differences among the varieties were continued through the period of maturation of fruit until the fall of the leaves in November and December. Photographs and sketches were used frequently to record observed differences. Leaves were collected at different stages of growth, on different portions of the tree, and in various degrees of shade and sun to reflect normal variation due to maturity and aging, self-shading, and other factors.

Tree-ring studies and acorn and winter bud measurements were made on the varieties *falcata* and *pagodaefolia*. After acorns matured in October and November, they were collected from numerous trees in widely scattered areas, but most were collected on the Millsaps College campus in Jackson, Mississippi and at Bluff Forest Experimental Station near Vicksburg, Mississippi. These acorns were measured with vernier calipers to determine top-to-bottom height and side-to-side diameter. Vernier calipers were also used to measure length and greatest diameter of winter buds.

Wood corings were taken from representative trees of each type in the study of growth rings. Trees in the same type of environment were selected, and where possible, cores were taken from neighboring trees of different varieties.

Branches which bore typical *Quercus falcata* leaves in the summer of 1963 were noted, and used in the spring of 1964 in experiments designed to test the effect of shading on the shape of leaves. Before buds opened, branchlets were shaded with single and double thicknesses of mosquito netting, or left unshaded as a control. Daily observations of the three conditions were made for three weeks, until vandals tore down the netting and destroyed most of the branchlets in the process. The same experiment being carried out on variety *pagodaefolia* was also prematurely terminated by vandals.

To insure that the range of the study was not too limited, herbarium specimens were secured from areas outside of Mississippi. Specimens were collected in Alabama and Tennessee, and herbarium specimens were secured from southern Illinois. Correspondence with several botanists throughout the country gave access to experienced opinion about the taxonomic status of *Quercus falcata* outside the area of direct study.

AREA OF STUDY.

Major areas of observation were all in Mississippi. These were the campus of Millsaps College; Bluff Forest Experiment Station, near Oak Ridge in Warren County; Caney and Oakahay Creek bottoms in Smith County; and an area about 1.5 miles north of Stringer, in Jasper County. Other areas of observation and collection or photography were the northern sections of the city of Jackson; Kickapoo Boy Scout Camp, four miles north of Clinton, in Hinds County; an area in Bienville National Forest five miles northeast of Morton, in Scott County; Blakely Plantation, ten miles north of Vicksburg in Warren County; an area near Canton, in Madison County; and the campus of the University of Mississippi at Oxford. Roadside observations were made between Jackson and Columbia, Mississippi, along U. S. 98 and Miss. 13; between Jackson, Mississippi, and Nashville, Tennessee, along the Natchez Trace and U. S. 45; and between Stringer, Mississippi, and Mobile, Alabama, on U. S. 98 and Miss. 15. Collections were made along the latter two routes, once in southern Tennessee on U. S. 45, and once just across the Alabama line on U. S. 98.

OBSERVATIONS AND EXPERIMENT RESULTS

Quercus falcata, varieties *falcata* and *triloba*

The only morphological difference found between typical *Quercus falcata* individuals and trees which might be called variety *triloba* was the difference in leaf shape described previously. The number of *triloba*-type leaves of any given tree varied from a few near the trunk at the base of the crown of typical *Quercus falcata* trees, to almost all the leaves of saplings and some young trees. All seedlings exhibited the *triloba*-type leaf, and not a single tree was found without some of those leaves. There seemed to be three general types of leaves exhibited by these two varieties. Besides the *triloba* leaf (Fig. 5) and the typical *Quercus falcata* leaf (Fig. 3), there is an intermediate type of leaf with only three lobes, but with the central lobe elongated, and the side lobes ranging from ascending to spreading. The first type was found on seedlings, saplings, and at the base of the crown of all trees. The intermediate leaf form was generally found on saplings, and on the lower

branches of most mature trees. In forests this type was found throughout the crown of young trees and high in the crown of mature trees. The typical leaf form is found on almost all branches of large lone trees, and in the upper crown of forest trees.

The proportion of leaves of the first (*triloba*) and intermediate types was much greater in the forest; trees standing alone tended to have almost all leaves (except those very near the trunk) of typical form. Most large trees exhibited leaves of all three types. Leaves of the *triloba* type tended to be larger than the typical leaf, and often had less pubescence on the lower side. No pattern of differences could be found between the fruit, buds, bark, or color and pubescence of young twigs of trees which were separated into these two varieties on the basis of leaf form.

Quercus falcata, varieties *pagodaefolia* and *leucophylla*

No morphological differences could be found between trees identified as the variety *pagodaefolia* and variety *leucophylla*, except for leaf differences described previously. No pattern of differences in acorns, bark, twigs, or amount and color of pubescence was found between trees which had been separated on the basis of leaf shapes into these two varieties. Large lower leaves of both types of trees tended to have less pubescence underneath.

The number of leaves of each leaf-type varied considerably from tree to tree. Some trees, noticeably those which stood in the open, had no leaves of the *leucophylla* type (Fig. 6), except a few at the base of the crown. Most trees had a considerable number of leaves of the *leucophylla* type in the lower part of the crown. Seedlings and saplings had all their leaves of the *leucophylla* type. In addition to these two characteristic leaf-types, there appears to be a third type, intermediate in form between the other two. Its lobes are narrower and more sharply defined than those of the *leucophylla* type, but they are not so numerous as the lobes of the *pagodaefolia* type, and the leaf is not so strongly pagodiform. This intermediate type of leaf is generally common in the lower crown of trees standing alone, and in the middle crown of trees with many lower leaves of the *leucophylla* type. Most mature trees exhibit all three types of leaves. Generally, the number of *leucophylla*-type leaves increases greatly in the forest; some understory forest trees have all their leaves of the *leucophylla* and intermediate types. Leaves taken from the crown of trees with almost no *leucophylla*-type leaves were not different from leaves taken from the top of trees with many *leucophylla*-type leaves, either in size, shape, or amount and color of pubescence.

Quercus falcata (typical) and the variety *pagodaefolia*

In the field, two major characteristics make the distinction of *Quercus falcata* var. *falcata* from the variety *pagodaefolia* quite easy. The smoother, flaky bark of the variety *pagodaefolia* is quite different from the darker, rougher bark of the typical form (Figs. 1 and 2). Two features of the leaf of the typical form, the long terminal lobe and the rounded base, give this leaf a silhouette easily distinguishable from that of the leaf of variety *pagodaefolia*, which has a wedge-shaped base and more numerous sub-equal lateral lobes. Besides these differences, there are a whole series of differences in development, pigmentation, and pubescence of the leaves of these two forms of oak, beginning with the first emergence of the leaves in early spring.

In central and south Mississippi, the buds of these two oaks burst in late March, earlier than those of most other species of oaks. The emerging leaves of the variety *falcata*, though very small, already have the shape of the mature leaf, but they are pale green, wrinkled, and covered above and below with white pubescence. They increase in size slowly. Pubescence is gradually lost from the upper surface of the leaf, and the pubescence underneath acquires its rusty color. The pubescence on the petiole also becomes rusty. When the leaves are a month old, they have reached full size, but the upper surface of the leaf has not yet lost all pubescence, and the leaf is still neither as dark green nor as thick and leathery as it will become when fully mature.

The leaves of the variety *pagodaefolia* burst from the buds and fold back to a right angle with the twig. These ovate to ellipsoidal leaves are very rugose with the lateral veins in deep grooves, and have no visible sinuses. Each leaf is covered above and below with white pubescence, but the entire upper surface of the leaf is colored a deep red. Sargent (1922) noted this pigmentation, but reported that it was the pubescence which was red. The pubescence is always white or greenish, however, with the pigmentation in the leaf proper. These leaves expand very rapidly; the leaf smoothes out, the sinuses become visible and widen, and the leaf quickly acquires the shape of the mature leaf of variety *pagodaefolia*. The red pigment begins to fade, but still pervades the entire upper leaf surface. The leaves reach full size 3½ weeks after emerging, earlier than the typical form of the species. By this time they have lost their red pigmentation, except along the veins of the leaf and at the bottom of the basal sinuses. This last coloring soon disappears, and the pubescence is gradually lost from the upper surface of the leaf. The pubescence underneath the leaf and on the petiole remains whitish, but the tomentum of the leaf axil may turn rusty. The leaves are now mature in size and shape, but still are thin, papery, and light green. They become darker green and thicker with age, though they are never as dark and leathery as the leaf of the variety *falcata*.

Sargent (1922) noted a difference in the autumn coloration of the leaves of these two oaks. The leaves of the variety *pagodaefolia* begin to change color before those of the typical form. They first turn bright yellow and pass through orange to red-brown before beginning to fall. In central Mississippi the leaves begin changing in early November and begin falling by early December. The leaves of the typical variety begin changing later, around middle to late November in central Mississippi, and begin falling soon after the color change

begins. They go directly from green to dull red or red-brown, without the colorful intermediate stages that characterize variety *pagodaefolia.*

The year-old twigs of the typical form have rusty pubescence, while those of the variety *pagodaefolia* have greenish or light brown pubescence. Though Sargent (1922) noted a difference of coloration and pubescence between two- and three-year-old twigs of the two trees, no such pattern was discerned in this study.

No pattern of difference was recognized between staminate flowers of the two types of oaks, but the tepals of pistillate flowers of variety *falcate* are red, whereas those of the variety *pagodaefolia* are not.

A growth ring study carried out as a part of this project was inconclusive, giving no significant information. Measurement of length and greatest diameter of winter buds produced no consistent pattern of variation, but there is a slight difference in coloration, the buds of variety *pagodaefolia* being not so dull as those of the typical form.

Results obtained in this study did not indicate significant and uniform differences between the acorns of the two forms. Unpublished work by Darrel S. English indicated that there is no significant difference in the weight of acorns of the two varieties. Sargent (1922) reported that the acorns of variety *pagodaefolia* were sessile, but this study revealed that both oaks bear their acorns on short peduncles.

Discussion

Quercus falcata, var. *triloba*

This variety was distinguished from the typical form solely on the basis of the shape of its leaves, except for a mention by Sargent (1922) that it was a smaller tree than the typical form. However, Sargent (1922) also noted that both the trilobed leaf and the typical leaf sometimes occurred on the same tree. Vines (1960) reported that sometimes practically all the leaves on a tree were of the *triloba* type; sometimes half were of this type and half were of the typical form; and sometimes only a few trilobed leaves were found on a tree. He said that many botanists felt that *triloba* was not a variety. Harrar and Harrar (1946) did not recognize variety *triloba,* and described the typical form as having dimorphic leaves, with the leaves in the lower crown being mostly three-lobed. These observations correspond with those of this study (Fig. 7). It is believed that the three-lobed leaf is not an expression of varietal differences, but instead an expression of shading.

Leaves grown in shade tend to be broader and thinner than those leaves with full isolation; this holds true for shaded and unshaded individual plans, as well as shaded and unshaded portions on the same tree (Weaver and Clements 1929). These differences occur frequently in trees with a dense crown of leaves; those leaves fully exposed to the sun are very different from those of the shaded interior of the crown. A forest tree may have sun leaves at the top and, as a result of shading by neighboring trees or by its own crown, have shade leaves on the sides and near the base (Oosting 1956). Apparently this is true of *Quercus falcata,* for leaves of the *triloba* type are found at the base and in the interior of the crown of trees that are definitely the typical form of *Quercus falcata.* In a forest, the trees shade each other so that on some trees sun leaves occur only at the very tip of the tree; the rest of the tree has leaves produced by various degrees of shading. Such a tree would be identified as variety *triloba.* Understory trees would be more likely to receive considerable shading, and thus be identified as variety *triloba;* overstory trees, receiving more sunlight, would have more of the typical leaves. This may explain why Sargent (1922) reported that the variety *triloba* was smaller than the typical form.

There may be a maturity factor involved in this relationship, explaining the tendency of seedlings and saplings to have shade type leaves even when exposed to sunlight. Stebbins (1950) noted that there is a definite tendency of seedlings and saplings of lobed-leaved plants to have more nearly entire leaves. This is especially true of oaks.

No evidence was found to indicate that there is any difference, other than those resulting from the shading and maturity factors. However, if, as Sargent (1922) reported, there is an area in Baldwin, Co., Georgia, where a form exists which is morphologically different from the typical tree, then this type might be called a *forma,* which Fernald (1950) defined as having "minor departures in vegetative characters, . . . but without fundamental or constant trend over large areas, occurring here and there in the broad range of the species." Steyermark (1963) treats the trees in Missouri with three-lobed leaves as *Quercus falcata* var. *falcata* forma *triloba.*

Quercus falcata var. *leucophylla*

The principal difference between the *pagodaefolia* and *leucophylla* forms of *Quercus falcata* lies in the broader, more irregularly lobed leaf of the variety *leucophylla,* which also has large, less deeply cut leaves at the base of its crown. Harrar and Harrar (1946) did not describe the variety *leucophylla,* but said only that it was a tree with "considerable leaf variation." Therrill (1949) reported that the lower leaves were larger with shallower lobes, and that the tree was "easily recognized." No mention was made of dimorphism in the variety *pagodaefolia.* Yet every tree examined in this study, whether identified as the variety *pagodaefolia* or variety *leucophylla,* exhibited the other type of leaf. It appears that the leaf differences between the two types are the result of different amounts of shading.

Weaver and Clements (1929) reported that plants with lobed or divided leaves, when shaded, produced leaves with more nearly entire margins. They also reported that shade leaves would be broader, and sun leaves narrower, and that the largest leaves of many plants occurred in partial shade. Thus the three general types of leaves observed on these two types of oaks are products of different amounts of shading: the typical

pagodiform leaf is produced with full insolation; the type of leaf characteristic of the upper crown of trees identified as the variety *leucophylla* may be a product of intermediate shading; and the large, broad leaf characteristics of the lower branches of variety *leucophylla* is a product of denser shading.

Ashby (1963) reported that in southern Illinois, near the northern limit of the range of *Quercus falcata* var. *pagodaefolia*, the tree exhibits the same type of dimorphism observed in the area of study, and herbarium specimens received from him confirm this. Shade leaves collected from the variety *pagodaefolia* are like those of trees identified as variety *leucophylla;* sun leaves from the same trees are typically pagodiform.

Fernald (1950) did not recognize the variety *leucophylla.* Little (1963) noted a difference in pubescence, but did not think that this difference was sufficient for varietal separation. In the area of study a great deal of variation in amount and color of pubescence was noted, but no pattern was found in this variation. Deeply shaded leaves sometimes had relatively little pubescence underneath, as would be expected (Talbert and Holch 1957). No correlation between color of pubescence and size or shape of leaf was found.

It should be noted that there is a great deal of variation in leaf shape among individuals in variety *pagodaefolia.* Part of this may involve a maturity factor similar to the one discussed for *Quercus falcata* (typical), for seedlings and young saplings always exhibit leaves of the *leucophylla* type. Observations indicate that individual sensitivity to sunlight may play a large part in this variability. Some trees had *leucophylla*-type leaves when shading is very slight, and typical leaves only in full sun. Others produced leaves of the *leucophylla* type only in heavy shade, and typical ones in moderate shade. No other morphological differences could be distinguished between these trees. This great variability among individuals is probably the basis that taxonomists have used in separating variety *leucophylla* from variety *pagodaefolia.*

All trees in this study exhibited the dimorphism said to be characteristic of variety *leucophylla,* though most of them are definitely variety *pagodaefolia.* Differences in amount of shading had an obvious effect on the relative proportions of the two types of leaves on any given tree. Even trees whose upper crown exhibited primarily leaves of the *leucophylla* type also usually had definitely pagodiform leaves at the very tip of the crown. It appears that there is no sound morphological basis for the recognition of variety *leucophylla* as separate from variety *pagodaefolia.* If in some parts of the range of this oak there is actually a genetically-based morphological difference in the two types of trees, then the *leucophylla* type might qualify as a *forma,* as defined previously. However, all results of this study indicate that the two names are synonyms applied to shade and sun variations of the same plant. Steyermark (1963) treats these two names as synonyms, stating that, "It does not appear possible to maintain var. *leucophylla* as a separate variety, the character of . . . pubescence, and diversity in types of leaves on lower branches not appearing to be consistent or reliable differences."

Quercus falcata* var. *falcata* and the variety *pagodaefolia

The typical form of *Quercus falcata* does not grow as large as variety *pagodaefolia;* it also tends to have lacier foliage, a more open crown, and a darker coloring due to its darker, more leathery leaves and the rusty pubescence underneath them. Nearer the tree, the differences in texture of bark and shape of leaf become obvious, as does the difference in color of the pubescence underneath the leaves and on the petioles and young twigs. The red pigment of the emerging leaves of the form *pagodaefolia* and the differences in pigmentation of the leaves in autumn also separate it from var. *falcata.*

Another difference mentioned in the literature is the heavier, more easily worked, and commercially more valuable wood of variety *pagodaefolia.* Besides these differences mentioned above, this study revealed some other morphological differences which, though not as obvious as these, were quite consistent in pattern. One of these differences is in pigmentation of the female flowers, and another is the difference in the coloration of buds.

Other than these morphological differences, there is a very pronounced ecological difference between these two forms of oak. It has long been noted that variety *pagodaefolia* grew in more moist situations than the typical form. Braun (1950) reported *Quercus falcata* var. *falcata* as a component of pre-climax mixed oak, oak-hickory, and oak-pine forests throughout the Western Mesophytic Forest Region and in the southern portions of the Oak-Hickory, Oak-Chestnut, Mixed Mesophytic, and Oak-Pine Forest Regions. Oosting (1942) found it a canopy component of both pre-climax and climax oak-hickory forest in the Piedmont of North Carolina. Braun (1950) reported the variety *pagodaefolia* as a component of post-climax mixed bottomland hardwood communities throughout its range, often becoming an important dominant, with the variety *falcata* rare in these communities. A good substantiation of the correlation between moisture and distribution is work by Caplenor *et al.* (in press). Their work in West-Central Mississippi indicated that the variety *pagodaefolia* was consistently present, almost to the exclusion of the typical form, on soils with uniformly higher water content (lowlands) or on those soils with a high percentage of available water (relatively undisturbed loess). In the loess they found that the typical form occurred almost exclusively in openings formed by disturbance, while variety *pagodaefolia* was generally limited to relatively undisturbed forests. This may indicate a difference in shade tolerance of the two taxa, or some other aspect of competitive advantage afforded variety *pagodaefolia* in areas of high moisture availability.

Quarterman and Keever (1963) found that *Quercus falcata* var. *falcata* was an important climax dominant

in the Southern Mixed Hardwood Forest of the southeastern Coastal Plain. They did not find variety *pagodaefolia* in the climax, indicating the post-climax nature of the loess communities where this variety is an important component.

There appears to be little hybridization between these two forms of oak. Of the thousands of trees throughout Mississippi which were examined during the fifteen months of this study, only three were found which were thought to be hybrids between these two oaks. According to Stebbins (1950), speciation in the genus *Quercus* is determined by accumulation of gene mutations, and this accumulation is due to geographic or ecological isolation of a population. Unlike speciation based on chromosomal changes, which would discourage hybridization, the type of speciation which *Quercus* exhibits allows frequent hybridization, even between well established and quite different species. Such infrequent hybridization between trees of a genus which is notorious for hybridization, especially since the trees often grow in close proximity, indicates that speciation is well establised.

Because of pronounced morphological and ecological differences, and because there is very little hybridization between the two forms, it is concluded that the variety *pagodaefolia* deserves rank as a separate species. It is recommended that *Quercus falcata* var. *pagodaefolia* Ell. be given the name first proposed by Ashe (1897) when he recognized this form as a species. That name is *Quercus pagodaefolia* (Ell.) Ashe—a species in its own right.

Conclusions

1. There is no apparent morphological basis in the area of study for distinguishing variety *triloba* from the typical form of the species.
2. There is no valid morphological basis, at least in the area of study, for distinguishing variety *leucophylla* from variety *pagodaefolia*.
3. The consistent pattern of morphological and ecological differences between the typical form of *Quercus falcata* and the form *pagodaefolia*, plus the absence of evidence of frequent hybridization, indicate that these two forms should be recognized as separate species.

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