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AN OVERVIEW OF *QUERCUS*: CLASSIFICATION AND PHYLOGENETICS WITH COMMENTS ON DIFFERENCES IN WOOD ANATOMY

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ABSTRACT

The oaks (genus *Quercus*) are one of the most important groups of flowering plants and dominate large regions of the northern hemisphere. They are most prevalent in subtropical, temperate, and montane tropical regions. *Quercus* is phylogenetically divided into at least five major groups, of which three (the red oaks, white oaks, and intermediate oaks) are native to the New World. Overall, there are more than 200 species of oak in the Western Hemisphere, and probably a larger number in Asia, and relatively few in Europe. The center of diversity in the Americas is in the highlands of Mexico, with a secondary center in the southern United States. From the standpoint of susceptibility to disease, the phylogenetic groupings have some predictive capability, and in some cases this may be related to differences in ecology, physiology, and wood anatomy. White oaks in general are more diverse in the drier parts of North America, and have heartwood that is typically blocked by tyloses, while red oaks generally have fewer tyloses. Because tyloses block water flow through the heartwood, white oak wood makes good wine barrels while red oak wood does not. Given the greater susceptibility of red oaks to both oak wilt and sudden oak death (SOD), these differences in wood anatomy may be relevant.

Key words: *Ceratocystis fagacearum*, oaks, oak wilt

The oaks (*Quercus*) are among the most recognizable trees in the Northern Hemisphere, dominating large areas of North America, Europe, and Asia. They are also among the most economically-useful trees, providing high-quality lumber, firewood, tannins for leather, natural dyes, long-lived horticultural shade trees, wildlife habitat, animal feed (acorns), and even human food (acorns are still eaten in parts of Asia). Before the advent of steel-hulled ships, oak lumber was the primary material used in the construction of both merchant and warships in Europe and the Americas (and in fact, the hull of "Old Ironsides" is not iron, but oak covered with copper sheeting). Most botanists from the Northern Hemisphere are very familiar with *Quercus*. It is also well-known to the general populace, and is prominent in literature – often as a symbol of strength or character. There are many famous oak trees, including several “treaty oaks” in various parts of the U.S.

In the context of oak wilt, the purpose of this paper is to provide an overview of the genus *Quercus*, particularly in the Americas, with the goal of providing an entry into various aspects of the relationships of oaks and oak subgroups, information about the distribution and ecology of the genus, and discussion of some selected oak species groups (e.g., the "live" oaks) that are of particular interest in the context of oak wilt (caused by *Ceratocystis fagacearum* (Bretz) Hunt).

The genus *Quercus*, with probably more than 500 species worldwide, is placed in the family Fagaceae (Nixon 1989, 1993a, b, 1997a, b, c, Manos, Doyle and Nixon 1999), which includes the genera *Castanea* (chestnuts), *Chrysolepis* (California chinquapin), *Castanopsis*, *Lithocarpus*

(including tanoak), *Fagus* (the beeches), and the rare tropical *Trigonobalanus*, *Formanodendron*, and *Colombobalanus* (Nixon 1989, Nixon 2003); these three monotypic genera are sometimes lumped under *Trigonobalanus*). The oaks and beeches (*Fagus*) are wind-pollinated, while genera in subfamily Castaneoideae (*Castanea*, *Chrysolepis*, *Castanopsis*, and *Lithocarpus*) are probably all insect-pollinated. The remaining three "trigonobalanoid" genera (*Trigonobalanus*, *Formanodendron*, and *Colombobalanus*) are poorly known, and pollination is probably by insects in *Trigonobalanus*, but by wind in the other two genera. The fossil record of trigonobalanoids and castaneoids extends to the Oligocene of North America, as do verifiable *Quercus* fossils (Crepet and Nixon 1989 a, b, Nixon 1989).

Quercus is often considered to be a taxonomically difficult group. While it is true that interspecific hybridization is relatively common in *Quercus*, it is also true that many field botanists rely almost solely on characters of leaf shape to distinguish species of oak, although leaf shape and lobing are highly plastic and mostly unreliable as taxonomic characters (Nixon 1997b). When more fundamental characters such as twig and leaf pubescence, bud characteristics, and acorn morphology are used in combination with leaf shape characters, many specimens that might otherwise be labeled as hybrids are seen to be merely leaf forms of a particular species. This is particularly true in the cases of some white oak species such as *Q. stellata*, where botanists often erroneously dismiss specimens that lack the typical "cruciate" (cross-shaped) leaf form as hybrids with other species. These specimens, more often than not, are shade or juvenile-leaved forms of *Q. stellata*, which has a wide array of leaf shapes that deviate from strictly cruciate, although hybrids between this and other white oaks are well-known.

Hybridization between species in the same group is relatively common (e.g., it is easy to cross a white oak species with another white oak species). However, crosses between species from different groups (e.g., red and white oaks) are considered to be virtually impossible, although a few reports of such crosses exist (Cottam, Tucker and Santamour 1982).

QUERCUS in the AMERICAS

With more than 200 species in the Western Hemisphere (Nixon 1997b), *Quercus* is the most important genus of the family Fagaceae in terms of species diversity as well as ecological dominance. In the Americas, the genera *Fagus*, *Castanea*, *Lithocarpus*, *Chrysolepis*, and *Colombobalanus* have only 9 additional species compared to more than 200 species of *Quercus* (Nixon 2003). As such, *Quercus* is also the most important group of Fagaceae economically in the Americas.

Ecological Diversity

Quercus is found in an astonishing array of habitats ranging from tropical and subtropical to cold temperate climates. No other tree genus in the Northern Hemisphere has species in such a diverse array of habitats. Within these climatic categories, *Quercus* is found in tropical lowland forests, dry tropical forest, cloud forest, and various montane evergreen forests, including pine-oak, pine-fir, and relatively pure stands of evergreen oak. In subtropical regions, oak is often a component or dominant in chaparral, oak woodland, pine-oak, juniper-oak, and various other phases including both mediterranean (winter-rain) and monsoonal summer-rain areas. Both the temperate deciduous forests of eastern North America and Europe are dominated over large areas by species of oak, and in the southeastern U.S., these forests grade into subevergreen types

dominated by members of the live oak group. In many regions, such as central Texas and parts of southern California (Nixon 2002), oaks are the only large native trees in the landscape.

Oak Centers of Diversity

In the Western Hemisphere, Mexico has by far the largest number of oak species, especially in the three major mountain systems, known as the Sierra Madre Occidental, Sierra Madre Oriental, and Sierra Madre del Sur (Nixon 1993a). However, oaks also become dominant elements in the mountains of the northern deserts (Chihuahuan and Sonoran) above about 1800 meters elevation. The majority of oak species in Mexico are found in oak-conifer, oak forest, cloud forest, or chaparral habitats. Several oak species, mostly with broader distributions into Central America, occur at lower elevations on both coasts of Mexico, particularly in the "cloud forests" but also in some cases extending into tropical dry forest (e.g., *Quercus corrugata*, *Q. insignis*, *Q. elliptica*, and *Q. sapotifolia*).

In Central America, the number of oak species diminishes as one heads south. There are approximately 45 species recognized from the southernmost state of Mexico (Chiapas) to Panama. The greatest number of species in Central America is on the Pacific (drier) slope. A single species of oak occurs in Colombia (*Q. humboldtii*, a member of the red oak group). Oaks are not known in South America outside of Colombia, and probably arrived in northern South America from Central America relatively recently, probably during the Pleistocene.

Oaks are also dominant in forests in Asia, especially in subtropical/temperate China. Lesser centers of diversity are found in the southeastern United States and the Himalayan belt. Europe is actually relatively depauperate in terms of oak species, probably due in large part to past glaciation which likely decimated oak populations in northern Europe.

How Do You Tell an Oak?

Although in eastern North America and Europe, the typical lobed leaf of most oaks species is diagnostic, and recognizable by the general populace, throughout the range of *Quercus* the lobed leaf is not common. Only a few of the species found in Mexico, the subtropical Mediterranean region, and subtropical and tropical areas of Asia have lobed leaves. By far the most common leaf form in *Quercus* is an entire (neither lobed nor toothed) or regularly-toothed leaf without lobes. Thus, the acorn (a nut subtended by or enclosed by a hardened cup) is the most important diagnostic feature. Unfortunately, the genus *Lithocarpus* also has a similar acorn fruit, but for North America, there is just a single species of *Lithocarpus* (*L. densiflorus*, the "tanoak") in California and southern Oregon. In this case, *Quercus* is separated from *Lithocarpus* by the different form of the male catkins in the two genera, lax and hanging in *Quercus*, and upright in *Lithocarpus* (which is insect-, not wind-, pollinated). In summary, the genus *Quercus* is reliably recognized by the combination of the acorn and lax male catkins.

Some confusion persists about the term acorn. An acorn is technically the entire fruit of the oak, which is made up of both the cup and the single-seeded nut that it encloses. However, the nuts, after falling from the cup in the fall, are often referred to simply as acorns, which is technically (botanically) incorrect, but because of common usage must be considered an alternate, popular definition of acorn.

***Quercus* Subgroups**

The oaks are divided into two subgenera (Nixon 1993b, Manos, Doyle and Nixon 1999), subgenus *Cyclobalanopsis* (sometimes recognized as a separate genus), restricted to eastern

Asia, and subgenus *Quercus*, with the remainder of species, including all species native to North America and Europe. Within section *Quercus*, there are four recognized sections: Section *Cerris* (Europe, Mediterranean, Asia), Section *Lobatae* (red oaks – New World only), Section *Protobalanus* (southwestern U.S., northwestern Mexico), and Section *Quercus* (white oaks) in the Americas, Europe, and Asia.

Name Issues in *Quercus*

Although in North America the name *Quercus* is consistently and generally applied to oaks, there has been considerable confusion regarding subgeneric groupings of oak, both in terms of common names and scientific nomenclature. This is in large part due to vague designations of rank in some of the older literature, where often no distinction was made between the rank of subgenus and section below the level of genus (e.g., Trelease 1924). The problem is compounded by the use of various common names for different groupings. Thus, for the white oak group, one may see the names *Lepidobalanus* or *Leucobalanus*; because the type of the genus (*Quercus robur* L.) is a white oak, the white oak group is correctly referred to as Section *Quercus* (within Subgenus *Quercus*). Likewise, one may see the red oak group referred to as subgenus *Erythrobalanus*; based on recent molecular and morphological work, it is best recognized as a section with subgenus *Quercus*, and the correct name for the red oaks is then *Quercus* subgenus *Quercus* section *Lobatae* (Nixon 1993b). It also is worth noting here that the red oaks are sometimes also referred to as the black oaks, particularly in the western U.S., where the common eastern red oak (*Q. rubra*) does not occur naturally, and the common lobed-leaf red oak of California is *Q. kelloggii*, or California black oak.

Morphological Variation in Oaks

Along with incredible habitat variation, there is corresponding morphological variation in New World *Quercus*, particularly in leaf form. Most *Quercus* species, except for several from eastern North America, do not have lobed leaves – entire, toothed or spinescent leaves are more typical. Many of the montane tropical species, particularly in the red oak group, have similar, entire, glossy leaves, and the taxonomy of the tropical oaks remains problematic. This, along with hybridization and a lack of adequate fruiting material in collections, adds to the difficulty in understanding the taxonomy of these tropical groups, and these are perhaps the most difficult species in the genus.

Ecology of Red Oaks vs. White Oaks

In a very broad sense, based on numbers of species in various habitats, it is clear that white oaks occupy a greater range of habitats than do red oaks, particularly drier habitats. Thus, red oaks are less diverse in the dry regions of the southwestern U.S., and red oaks predominate in the wetter areas of Central America. That said, particular species of red oak may be more drought adapted than particular white oaks; such is the case with various red oak species from the drier phases of Mexican highlands.

The Significance of Wood Anatomy of Oaks

Species of the white oak group typically have smaller diameter vessel elements, that are thinner-walled and angular in outline, in contrast to the larger, round, thick-walled vessels of red oaks (Fig. 1). Tillson and Muller (1942) surveyed a large number of species, however, they found that many evergreen white oaks from the southwestern U.S. and Mexico had vessels resembling

those of red oaks, that were larger, thick-walled and rounded in outline. These included both *Q. fusiformis* and *Q. virginiana* in the live oak group. However, Tillson and Muller did not survey the occurrences of tyloses. In mature wood the heartwood of white oaks typically fills with tyloses (see Fig. 1). Tyloses are intrusions into the vessels of the heartwood that become lignified and impregnated with tannins, literally "plugging" the vessels (Fig. 1b). This not only reduces the rate of flow of water/sap in the heartwood, but also creates a mechanical (and chemical) barrier to the growth of some wood-infecting fungi.

Because red oaks have fewer tyloses in healthy mature wood, the wood is much more porous than that of white oaks, and red oak lumber is not as resistant to fungal decay and insect damage, nor is red oak suitable for construction of items that must hold water, including barrels, kegs, and ships. Indeed, certain white oaks such as *Q. stellata* (post oak), because of their decay-resistant wood, were preferred not only for fence posts but also for railroad ties and structural and support timbers in contact with ground or in lower portions of buildings. Until recently, oak flooring was almost entirely from white oak sources, due to its resistance to decay in humid climates. But recently, this has been largely replaced by flooring cut from faster-growing red oak species such as *Q. velutina* (black oak) and *Q. falcata* (southern red oak). Although it is clear that red oak lumber is much more susceptible to decay when in contact with the ground than is white oak lumber, this does not necessarily translate directly to fungal disease resistance in living plants. However, the general pattern of greater susceptibility of red oaks to oak wilt may be related at least in part to these wood-anatomical differences.

The Live Oak Group: ***Quercus virginiana, Q. fusiformis, Q. minima, Q. geminata, Q. brandegei,* and *Q. oleoides*.**

It is important to note that although many oaks in various regions are referred to as “live oaks,” some are not members of series *Virentes* (for example, the California live oak, *Q. agrifolia*, is a red oak species; see Nixon 2002). The discussion here will focus on only the phylogenetically-related group of live oaks centered around *Q. virginiana*. The live oak group is one of the dominant elements of the oak flora of the southeastern coast of the U.S., extending into central Texas, and in isolated pockets through Latin America (as *Q. oleoides*) as far south as Costa Rica.

***Quercus* series Virentes Trelease (1924): A Subgroup of the White Oaks**. Distinctive features: very drought tolerant. An unusual feature of the live oak group (shared with the Glaucoideae) is the occurrence of fused cotyledons in all species. On germination, the petiolar region of the cotyledons elongates as a cotyledonary tube, pushing the hypocotyl/epicotyl axis deep into the soil, sometimes as much as 15 cm. The adaptive significance of this feature appears to be both drought and fire tolerance, since the crown of the plant is buried deep under the soil and less likely to either desiccate or be damaged in a quick-burning fire. All of the live oak group also regenerate extensively after fires by root-sprouts, often forming thickets for the first years before trees become emergent; or in the case of *Q. fusiformis*, such clones eventually form copses ("shinneries") that are connected extensively by both rhizomes and root grafts. This, of course, is one of the major considerations in developing strategies in treating oak wilt in live oak in central Texas and elsewhere.

Q. virginiana (live oak): The most widespread and famous of the live oak group, *Q. virginiana* is found from Virginia to Florida, and westward along the coastal states into Texas. It forms distinctive evergreen woodlands usually on deeper, better soils. Live oak was an

important resource for shipbuilding in the 18th and 19th centuries, providing structural beams and framework. A typical leaf-form is illustrated in the herbarium specimen in Figure 2.

Q. fusiformis (Texas or plateau live oak): This species intergrades broadly with *Q. virginiana* in the areas between the Edwards Plateau and coastal Texas; material from Brazos County eastward is typical *Q. virginiana*, while material to the west and north is more typical of *Q. fusiformis*. Because of this broad zone of intergradation, some botanists prefer to lump *Q. fusiformis* as a variety of *Q. virginiana*. However, in its extreme forms in northern Mexico (e.g., in the mountains near Monterey, Nuevo Leon), *Q. fusiformis* is very distinctive with long, tapered acorns (not shown), and usually narrower more acute leaves (Fig. 3). In these features, *Q. fusif*ormis from northern Mexico approaches the morphology of *Q. brandegei* from Baja California. Based on the completely different habitat preferences and distinctness of the material from northern Mexico, I prefer to follow Muller and treat the two taxa as separate species with a broad zone of intergradation in central Texas (Fig. 4). This better reflects the very different ecological parameters that coincide with the two distributions, including far less rainfall and a distribution almost entirely on limestone in the range of *Q. fusiformis*.

Q. minima (dwarf live oak): This species is found only on deeper sands in the southeastern U.S. and forms extensive rhizomatous colonies, usually less than 1 meter tall. It is characterized by a tendency to produce two different leaf forms on the same stems, a "juvenile" leaf form toward the lower portion of the stem that is often irregularly toothed and asymmetrical, and usually more entire, less lop-side leaf on the upper portions of the stem. Unfortunately, sprouts and regenerating colonies of both *Q. geminata* and *Q. virginiana* can resemble populations of *Q. minima*, and there is much confusion in the identification of these species.

Q. geminata (sand live oak): *Q. geminata*, although placed by some taxonomists as a synonym or variety of *Q. virginiana*, is distinct in morphology, ecological distribution, and also has a later flowering time than the latter. It is identifiable by the narrow, revolute leaves with impressed venation (Fig. 5). It occurs on deep sands more or less with the same coastal distribution as *Q. virginiana*, which is typically found on better loam or poorly-drained clay soils. The later flowering time and different edaphic preference of *Q. geminata* probably helps to maintain its distinctness from *Q. virginiana*, and putative hybrids are relatively rare, although these are noticeable for example at the western limits of *Q. geminata* in the regions of Biloxi and Gulfport, Mississippi.

Q. brandegei: This species is endemic to the Cape Region of Baja California, Mexico, extending from lower pine-oak forest into very dry thorn scrub habitats. In morphology, it is similar to the extreme forms of *Q. fusiformis* found in northeastern Mexico, but has even longer, acute acorns and narrow, acute leaves.

Q. oleoides: This is the most geographically widespread species of the live oak group, extending from northeastern Mexico (Tamaulipas) to Costa Rica, but only found in relatively restricted populations at low elevations in very tropical localities, in a variety of soils from sand dunes to volcanic and seasonally-inundated ("savannah") clays. On the western end of Cuba, there is a population of live oak that has been called *Q. oleoides* var. *sagraeana*, and is the only known oak stand in the Caribbean. This population is highly variable and seems to combine features of both *Q. oleoides* and *Q. geminata*.

SUMMARY

Oaks are extremely diverse in habit and habitat. However, broad patterns of correlation between oak groups and ecological environmental parameters are apparent, including some generalities

about wood anatomy that are relevant to disease resistance and susceptibility. White oaks in general are more drought adapted and also have more tyloses in the vessels of mature wood. Both of these features may contribute to greater resistance to infection and/or the symptoms of oak wilt in white oaks. However, the live oak group, a subgroup within white oaks, is also susceptible to oak wilt as evidenced by the severe infections in central Texas. Thus, wood anatomy alone is not a sufficient predictor of susceptibility within the oaks. Even so, given the phylogenetic patterns of susceptibility within oak groups, it is likely that oak wilt could become a major problem in Latin America, where red oaks dominate high elevations and wetter forests from Mexico to Colombia. Extrapolating from wood anatomy (and assuming a correlation with susceptibility), other mostly Asian groups of *Quercus*, the *Cerris* and *Cyclobalanopsis* groups (which have in general a red-oak like wood), as well as the genus *Lithocarpus*, may also ultimately be at risk.

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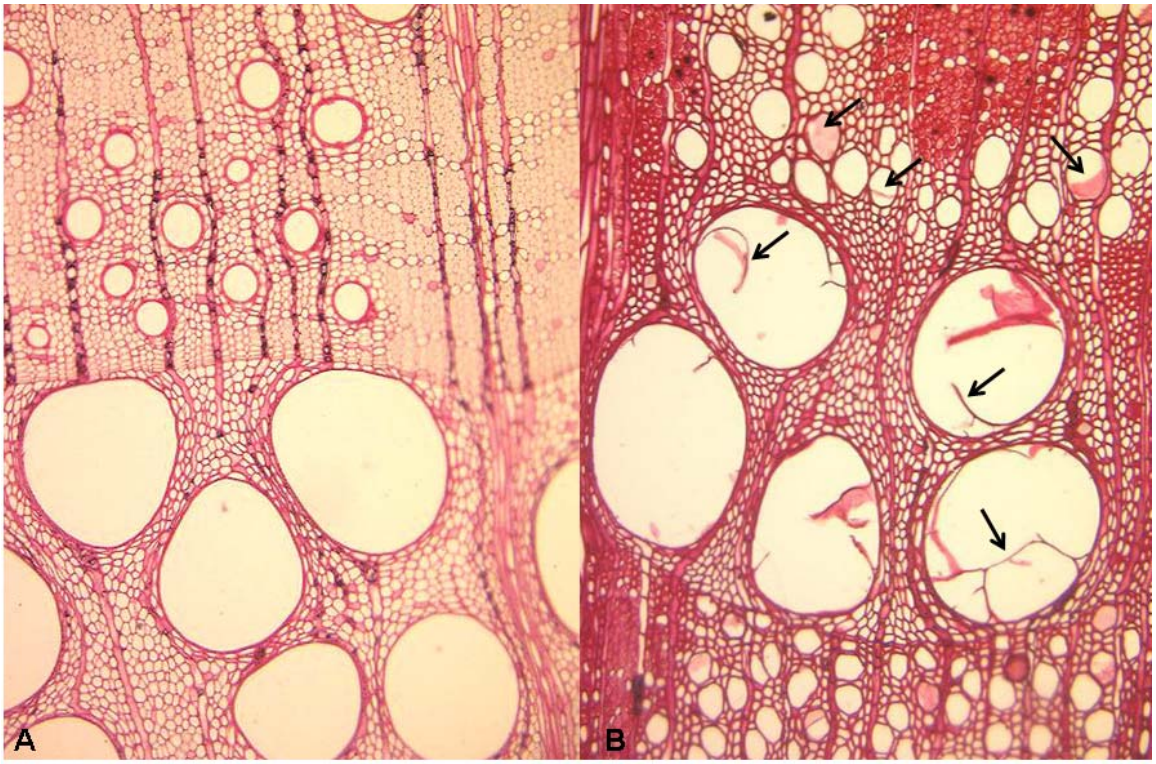

Figure 1. Standard light microscope preparation of cross sections of mature wood of *Quercus*. A. *Quercus rubra* with thicker-walled, more rounded vessels. B. *Quercus alba* with thinner-walled, more angular vessels in cross-section Note tyloses indicated by arrows in the large spring vessels and summer vessels of *Q. alba*, lacking in *Q. rubra*. (Magn. X).

Figure 2. Typical leaf form of *Quercus virginiana* in Florida (Muller 9830, BH).

Figure 3. Typical leaf form of *Quercus fusiformis* in Mexico (Rzedowski 7574, BH).

Figure 4. Typical leaf form of *Quercus fusiformis* in Texas. (Dyal, Hazard and Fisher 152, BH).

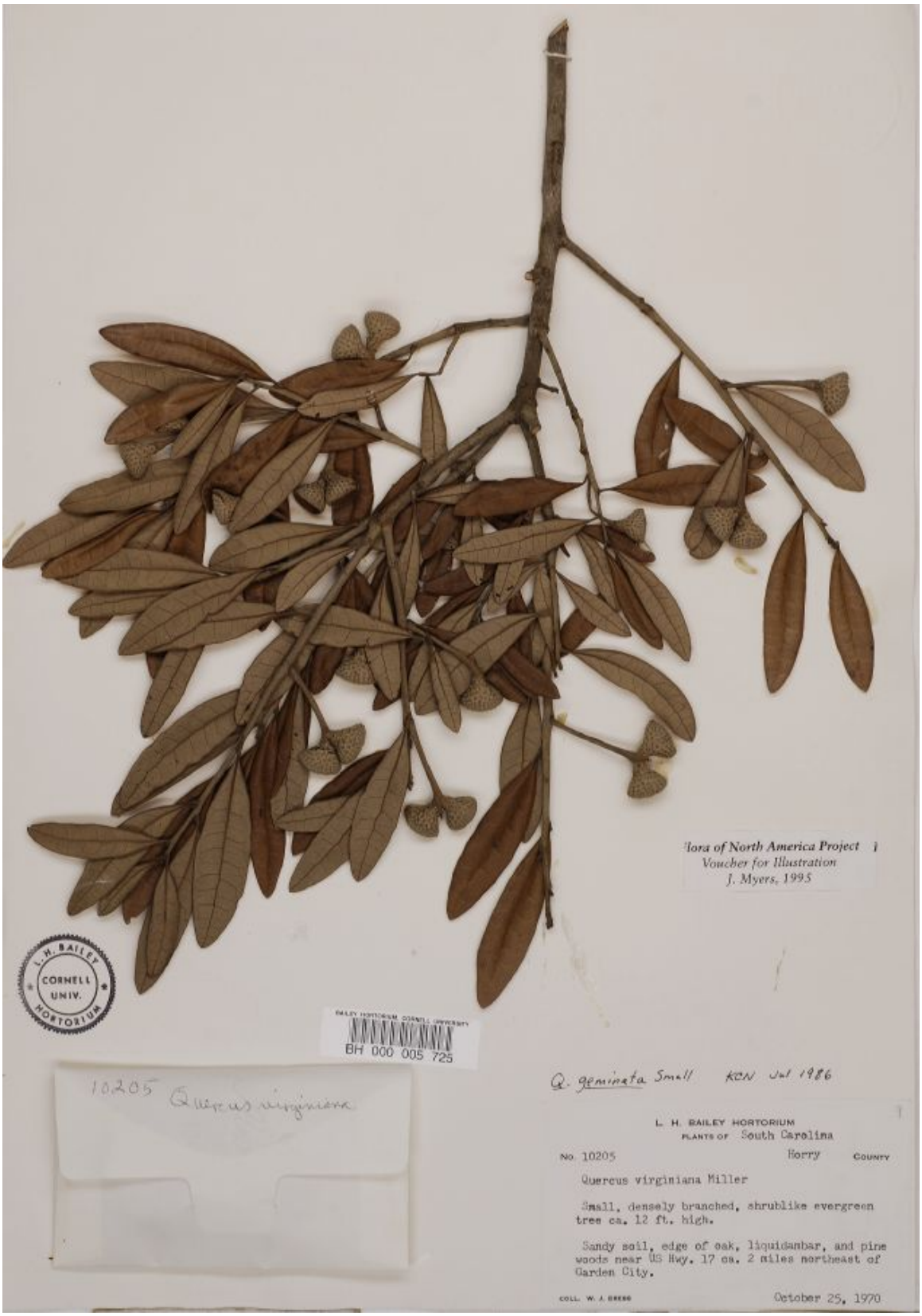

Figure 5. Typical leaf form of *Quercus geminata* (Dress 10205, BH).