Ecology of Bottomland Oaks in the Southeastern United States

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Oaks (*Quercus* spp.) are among the most ecologically and economically valued trees of the floodplain forests which occupy the river valleys that dissect the Gulf and Atlantic coastal plains of the southeastern United States. In these floodplain forests, several species from the sections *Quercus* and *Lobatae* are commonly found distributed along a gradient of sites ranging from hydric to mesic. Bottomland oaks exhibit a wide range of flooding tolerance, a narrow range of shade tolerance, and typically occupy disturbance dependent mid-successional seres. This manuscript provides a review of the silvical characteristics, species-site associations, and ecological succession for the nine most common oak species endemic to bottomland sites of the southeastern United States.

Introduction

The moist and fertile alluvial floodplains of the southeastern United States give rise to lush broadleaf forests structured from a diverse composite of tree, vine and shrub species. It is believed the early bottomland forests, which were often depicted as having towering, moss-draped trees underlain by expansive canebrakes, encompassed well over 16 million ha. These early bottomland forests provided habitat for bygone denizens including the ivory-billed woodpecker (*Campephilus principalis* L.), the Carolina parakeet (*Conuropsis carolinensis* L.), the passenger pigeon (*Ectopistes migratorius* L.) and the red wolf (*Canis niger* Bart.). Oaks (*Quercus* spp.) were a primary component of early bottomland forests where they constituted a significant portion of the canopy species on many different site types (Tanner 1986). Over the centuries following European settlement, drainage and development have decreased the expanse of bottomland hardwood forests to about 12 million ha, 75 % of the original extent (Hodges 1994). However, oaks remain among the most common endemic tree species in contemporary bottomland forests where they continue to provide critical ecological functions and immeasurable value.

As many as 17 oak species may be found in bottomland forests of the southeastern United States, but of these, only about nine species commonly occur there. Of the nine common species, three are from the section *Quercus* (white oaks) and six are representatives of the section *Lobatae* (red oaks) (Nixon 1993). Oaks are highly desired in managed forests as a component of wildlife habitat, and they are favored for their excellent aesthetic and timber qualities. In fact, oaks currently comprise about 78 % of the planting stock established on forest restoration projects on bottomland sites of the Lower Mississippi River Alluvial Valley (King and Keeland 1999).

The aim of this manuscript is to provide a review of our existing knowledge of bottomland oak ecology, including silvical characteristics, species-site associations, and ecological succession of the nine most common oak species endemic to river bottoms of the southeastern United States.

Silvical Characteristics

Flooding Tolerance

Periodic overland flooding is among the most prevalent environmental features of alluvial floodplains, and tolerance to flooding is among the primary biological factors distinguishing bottomland oak species from their upland congeners. In southern alluvial floodplains, the most extensive flooding typically occurs during the late winter or early spring, but some floodplain sites often remain inundated for a large portion of the growing season. As a result of reduced oxygen availability in saturated soil, flooding can impact seed germination, survival, and growth of seedlings, saplings and mature trees. The response by a tree to anaerobic soil is generally governed by the capacity of the species to acclimate physiologically and morphologically. Research has demonstrated several responses of bottomland oaks to anaerobic soil including development of hypertrophied lenticels, generation of adventitious roots, reduced rates of transpiration and photosynthesis, and altered biomass accumulation patterns (Conner et al. 1998, Gardiner and Hodges 1996, Pezeshki and Anderson 1997, Pezeshki and Chambers 1986). Most of these responses enable bottomland oaks to tolerate or avoid the potential stress of relatively short-duration, periodic inundations typical of most floodplain sites. However, bottomland oaks do not appear equipped to develop aerenchyma cells or favor anaerobic root respiration which would allow them to exist under the more hypoxic condi-

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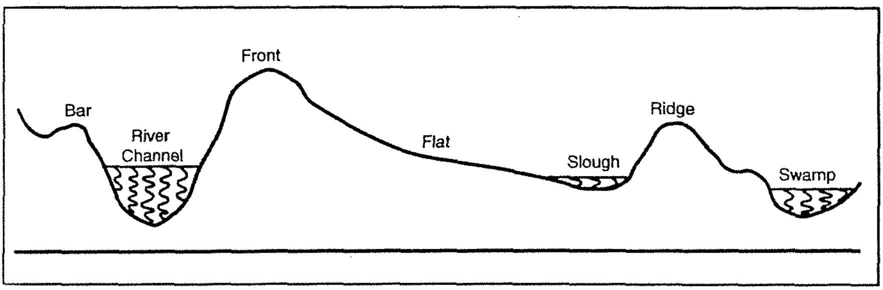
Figure 1



Schematic of geomorphological features or site types in active alluvial floodplains of the southeastern United States.

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tions found in swamps and sloughs that are flooded for extended periods (Gardiner and Hodges 1996, Pezeshki 1991).

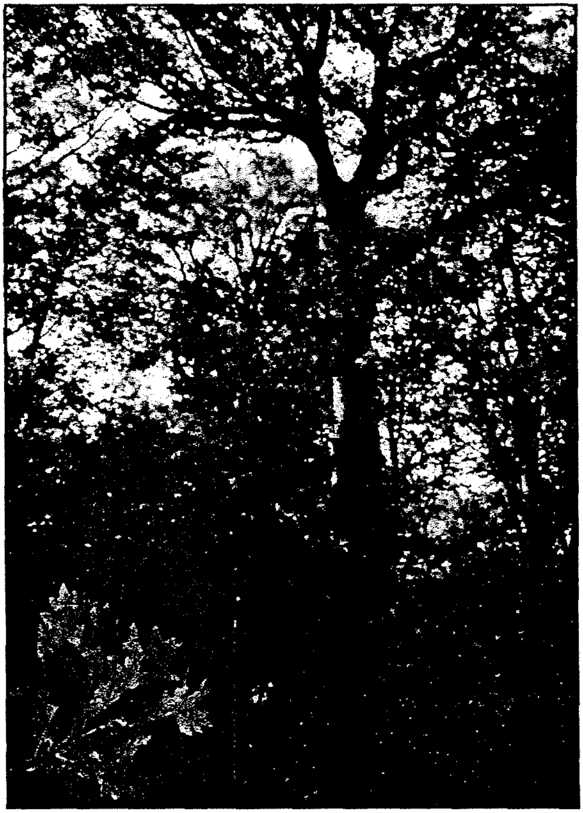
Of the bottomland oaks, overcup oak (*Q. lyrata* Walt.) exhibits the greatest tolerance of anaerobic soil conditions (Table 1). Phenology is an important mechanism of the flood tolerance of this species. Leaves typically break bud at least a month following the other bottomland oak species, and thus this species is able to avoid some of the stress associated with early spring floods (Solomon 1990). However, the other white oaks endemic to bottomlands do not exhibit this same level of flood tolerance (Table 1). Red oak species range from moderately tolerant to moderately intolerant of flooding (Table 1). For example, mature Nuttall oak (*Q. nuttallii* Palm.) trees may endure up to three years of inundation before dying, while Shumard oak (*Q. shumardii* Buckl.) trees will generally exhibit signs of stress and mortality after one year of soil saturation (Hook 1984). Of all the oaks commonly found in bottomlands, white oak (*Q. alba* L.) is the least tolerant of inundation.

It is noteworthy that oak seedlings are not as flood tolerant as mature trees of the same species (Hook 1984, McKnight et al. 1981). The full expression of flood tolerance is generally not realized until seedlings are tall enough to avoid complete inundation by floodwater. Likewise, bottomland oak acorns may retain their viability while submerged under water, but they do not have the ability to germinate when submerged and hence require an aerobic seed bed for establishment (Briscoe 1961). Nevertheless, hydrochory is probably an important aspect of the dispersal ecology of at least one bottomland oak. The acorn of overcup oak, the most flood tolerant bottomland oak, possesses a corky layer which enables the seed to float. It is common to observe evidence of hydrochory for this species in debris piles following floodplain inundations.

Shade Tolerance

A striking structural feature of many bottomland forests is the presence of well developed canopy layers, i.e. overstory, midstory, and understory. This stratification is indicative of the range of tolerance to competition exhibited by the flora endemic to bottomlands. Tree species can be found to represent a range in shade tolerance from very tolerant midstory and late successional species to very intolerant pioneer species (Putnam et al. 1960). However, very little variation in shade tolerance is observed among the different bottomland oaks. The white oak species are generally considered moderately intolerant of shade, while the red oak species are mostly labeled shade intolerant (Table 1). All bottomland oaks exhibit their best development in upper canopy positions where they receive full sunlight. Swamp laurel oak (*Q. laurifolia* Michx.) and white oak are probably the most shade tolerant of the bottomland oaks, and some authors report them as capable of developing from a sub-canopy position (McReynolds and Hebb 1990, Rogers 1990).

Seedlings of most bottomland oaks are considered to be slightly more shade tolerant than mature trees, but they still require moderate sunlight availability for quick, early development (Gardiner and Hodges 1998, Lockhart et al. 2000, Putnam et al. 1960). In the absence of adequate sunlight, bottomland oak seedlings often exhibit a shoot dieback-resprout response that allows them to persist for many years (in some cases) in the low light environment. Rela-



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Quercus lyrata, *like the ancient specimen shown here, is the North American oak species most capable of surviving long term flooding.*

tive to other species in bottomlands, oak seedlings are generally poor competitors with more tolerant species when light availability is low, and are weak competitors with more intolerant species when light availability is high. This relates to the morphology and physiology of the species including the propensity to favor root growth over shoot growth, poor physiological acclimation to low light availability, and a slow response to increased light availability (Hodges and Gardiner 1993).

Species-site associations

A clear understanding of bottomland oak distribution within alluvial floodplains can not be fully grasped without knowledge of floodplain geomorphology. This is because the edaphic, hydrologic, and biological factors which determine species growth, i.e. the site factors, are intrinsically linked to floodplain geomorphology. The geomorphology of a river valley will typically include an active floodplain and a series of ancient floodplains, or terraces (Hodges 1994, Putnam et al. 1960). Bottomland oaks generally attain their best growth and dominance on the active floodplain, because terrace soils are relatively lower in fertility, lower in moisture availability, and may possess developed genetic pans (Hodges 1994). On the active floodplain, sites are distinguished according to topographical features created from the erosional and deposition processes of the river as it meanders over the floodplain.

Site types most commonly recognized in alluvial floodplains of the southeastern United States include bars, fronts, flats, ridges, sloughs and swamps (Hodges 1994, Putnam et al. 1960) (Figure 1). These sites represent a gradient of hydroperiod, physical soil properties, and chemical soil properties, i.e. site quality, within the floodplain. Bars are the most recently deposited alluvium within the river channel and along its margins. The alluvium deposited on the bar is typically very coarse, well drained,

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and lacks pedogenic development. Fronts are the natural levees of the river channel. They are formed from relatively recent alluvial deposits of sand and silt, and are often the highest, best drained sites in the floodplain. Ridges are historical fronts or bars, and as such also contain relatively coarse soil particles. However, ridges exhibit a greater degree of pedogenic development and may not be as well drained as fronts. Swamps are depressional areas within the floodplain, typically old channels of the river that are permanently flooded receiving fine textured sediments. Sloughs, which have developed from swamps by accretion of sediments, are typically poorly drained and are flooded seasonally based on elevation. Flats are generally broad areas between fronts or ridges and sloughs or swamps. They are intermediate in soil texture, soil drainage, and hydroperiod (Hodges 1994, Putnam et al. 1960).

Edaphic and hydrologic characteristics of the specific site types listed above will govern bottomland oak establishment and growth. Because bottomland oak species differ in their flooding tolerance and other site requirements, they are typically observed stratified along the gradient associated with particular site types (Table 1). For example, Tanner (1986) reported that overcup oak can comprise about 60 % of the canopy in mixture with water hickory (*Carya aquatica* (Michx. f.) Nutt.) on the hydric soils of poorly drained sloughs and low flats of the Lower Mississippi River Alluvial Valley. Several oak species including Nuttall oak, water oak (*Q. nigra* L.) and willow oak (*Q. phellos* L.) are found along a continuum from the ridges to the low flats (Tanner 1986). Along this continuum, bottomland oaks develop in various proportions with other bottomland species including sweetgum (*Liquidambar styraciflua* L.), green ash (*Fraxinus pennsylvanica* Marsh.), American elm (*Ulmus americana* L.), and sugarberry (*Celtis laevigata* Willd.). Very old, alluvial deposits which are no longer inundated by the river, such as ridge sites on terraces, are generally occupied by white oak and a mixture of hickories (*Carya* spp.) (Tanner 1986). Bottomland oaks do not occur on the most recently developed sites, i.e. bars, nor do they occur on the lowest, most hydric sites in the floodplain, the swamps (Table 1).

Succession

Autogenic and allogenic processes drive ecological succession in alluvial floodplains of the southeastern United States (Hodges 1997). The primary allogenic process in a floodplain is deposition, and it may serve to advance, reverse, or hold succession static (Hodges 1997). Thus, the rate and direction of succession in bottomlands is tied closely with site stability. In addition, the rate of succession is influenced by the relative "wetness" of a site, as fewer tree species are adapted to compete on hydric sites versus mesic sites. Furthermore, succession is associated with the type of river system, i.e. major versus minor river (Hodges 1997). Hodges (1997) recognized three distinct patterns of succession for major and minor river bottoms based on whether a site is well drained, poorly drained, or permanently flooded, and based on stability of these site conditions.

As mentioned above, bottomland oaks are not found on permanently flooded sites such as swamps and deep sloughs. Succession into a species association with an oak component will not occur on these wet sites until sufficient accretion has occurred to reduce flooding and improve drainage of the site. Bottomland oaks are also not found on bars, the most recently formed and dynamic sites. The newly deposited alluvium forming the bar is too recent and not stable enough to support bottomland oak species. Site stability is required and soil genesis, particularly a decreased in pH, will have to advance before bottomland oaks will occupy such sites.

On the remainder of the bottomland sites, the fronts, ridges, flats and shallow sloughs, bottomland oaks are components of mid-successional, disturbance dependent seres. For example, water oak and willow oak can be found growing in association with sweetgum on flats of the Lower Mississippi River Alluvial Valley. This species association usually follows disturbance to a sere of American elm, green ash, and sugarberry. In the absence of additional disturbance, the oak and sweetgum dominated sere will revert to the more tolerant elm-ash-sugarberry association within 200 years (Hodges 1994, 1997). Bottomland oaks can also be a minor component in a variety of species associations, dominating other seres. For example, Nuttall oak is often a component in the elm-ash-sugarberry association described above, and water oak is commonly found as a component of a river front association of American sycamore, sweet pecan, and American elm (Hodges 1997). Bottomland oaks can develop into relatively pure stands on high flats in the floodplain, but these pure oak stands are generally a result of severe disturbance, such as burning, mowing or grazing, during stand establishment (Aust et al. 1985).

Because of the dynamic nature and age of alluvial floodplains, the regional oak - hickory climax is not often observed there. The climax sere can not be achieved in bottomlands until sites have advanced beyond the influence of the river (Shelford 1954). Hence, the allogenic driver of succession is removed. When deposition no longer occurs, autogenic processes primarily drive succession. With increased pedogenesis, oaks and hickories become dominant species. Several of the bottomland oak species, including cherrybark oak (*Q. pagoda* Raf.), Shumard oak, and especially white oak, growing in association with hickories, are indication of late succession on a bottomland site (Hodges 1994). This climax sere is more readily seen in minor river bottoms rather than major river bottoms.

Summary

Nine species of bottomland oaks from the sections *Quercus* (white oaks) and *Lobatae* (red oaks) are commonly found on the floodplains of river systems which dissect the Gulf and Atlantic coastal plains of the southeastern United States. These bottomland oaks exhibit shade tolerance rankings ranging from moderately intolerant for the white oak species to intolerant for the red oak species. Distribution of bottomland oaks within floodplains, however, is primarily driven by flooding tolerance of the individual species. Flooding tolerance among the bottomland oaks ranges from tolerant for overcup oak to intolerant for white oak. These flood tolerance characteristics drive a stratified distribution of bottomland oaks among topographical sites in the floodplain. On active floodplains, bottomland oaks achieve their greatest dominance in mid-successional seres resulting from stand disturbance.

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References

Aust, W. M., J. D. Hodges and R. L. Johnson. 1985. The origin, growth and development of natural, pure, even-aged stands of bottomland oak. Pp. 163-170 in E. Shoulders, Ed., Pro-

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ceedings of the Third Biennial Southern Silvicultural Research Conference. USDA-FS General Technical Report SO-54.

Briscoe, C. B. 1961. Germination of cherrybark and Nuttal(l) oak acorns following flooding. Ecology 42:430-431.

Conner, W. H., K. W. McLeod, and J. K. McCarron. 1998. Survival and growth of seedlings of four bottomland oak species in response to increases in flooding and salinity. Forest Science 44:618-624.

Edwards, M. B. 1990a. *Quercus michauxii* Nutt. Swamp Chestnut Oak. Pp. 693-696 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2. Hardwoods. USDA-FS Agriculture Handbook No. 654.

Edwards, M. B. 1990b. *Quercus shumardii* Buckl. Shumard Oak. Pp. 734-737 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2. Hardwoods. USDA-FS Agriculture Handbook No. 654.

Filer, T. H., Jr. 1990. *Quercus nuttallii* Palmer Nuttall Oak. Pp. 704-707 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2. Hardwoods. USDA-FS Agriculture Handbook No. 654.

Gardiner, E. S. and J. D. Hodges. 1996. Physiological, morphological and growth responses to rhizosphere hypoxia by seedlings of North American bottomland oaks. Annales des Sciences Foretières 53:303-316.

Gardiner, E. S. and J. D. Hodges. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. Forest Ecology and Management 108:127-134.

Hodges, J. D. 1994. The southern bottomland hardwood region and brown loam bluffs subregion. Pp. 227-269 in J. W. Barrett, Ed. Regional Silviculture of the United States, 3rd ed., John Wiley & Sons, Inc.

Hodges, J. D. 1997. Development and ecology of bottomland hardwood sites. Forest Ecology and Management 90:117-125.

Hodges, J. D. and E. S. Gardiner. 1993. Ecology and physiology of oak regeneration. Pp. 54-65 in D. L. Loftis and C. E. McGee, eds. Oak Regeneration: Serious Problems, Practical Recommendations. USDA-FS General Technical Report SE-84.

Hook, D. D. 1984. Waterlogging tolerance of lowland tree species of the South. Southern Journal of Applied Forestry 8:136-149.

King, S. L. and B. D. Keeland. 1999. Evaluation of reforestation in the Lower Mississippi River Alluvial Valley. Restoration Ecology 7:348-359.

Krinard, R. M. 1990. *Quercus falcata* var. *pagodifolia* Ell. Cherrybark Oak. Pp. 644-649 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2.

Hardwoods. USDA-FS Agriculture Handbook No. 654.

Lockhart, B. R., J. D. Hodges and E. S. Gardiner. 2000. Response of advance cherrybark oak reproduction to midstory removal and shoot clipping. Southern Journal of Applied Forestry 24:45-50.

McKnight, J. S., D. D. Hook, O. G. Langdon and R. L. Johnson. 1981. Flood tolerance and related characteristics of trees of the bottomland forests of the southern United States. Pp. 29-69 in J. R. Clark and J. Benforado, Eds. Wetlands of Bottomland Hardwood Forests. Elsevier Scientific Publishing Co., New York.

McReynolds, R. D. and E. A. Hebb. 1990. *Quercus laurifolia* Michx. Laurel Oak. Pp. 677-680 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2. Hardwoods. USDA-FS Agriculture Handbook No. 654.

Meadows, J. S. and J. A. Stanturf. 1997. Silvicultural systems for southern bottomland hardwood forests. Forest Ecology and Management 90:127-140.

Nixon, K. C. 1993. Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names. Ann. Sci. For. 50:(Suppl 1), 25s-34s.

Pezeshki, S. R. 1991. Root responses of flood-tolerant and flood sensitive tree species to soil redox conditions. Trees 5:180-186.

Pezeshki, S. R. and P. H. Anderson. 1997. Responses of three bottomland species with different flood tolerance capabilities to various flooding regimes. Wetlands Ecology and Management 4:245-256.

Pezeshki, S. R. and J. L. Chambers. 1986. Variation in flood-induced stomatal and photosynthetic responses of three bottomland tree species. Forest Science 32:914-923.

Putnam, J. A., G. M. Furnival and J. S. McKnight. 1960. Management and inventory of southern hardwoods. USDA-FS Agriculture Handbook No. 181, 102 pp.

Rogers, R. 1990. *Quercus alba* L. White Oak. Pp. 605-613 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2. Hardwoods. USDA-FS Agriculture Handbook No. 654.

Schlaegel, B. E. 1990. *Quercus phellos* L. Willow Oak. Pp. 715-720 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2. Hardwoods. USDA-FS Agriculture Handbook No. 654.

Shelford, V. E. 1954. Some lower Mississippi Valley floodplain biotic communities: their age and elevation. Ecology 35:126-142.

Solomon, J. D. 1990. *Quercus lyrata* Walt. Overcup Oak. Pp. 681-685 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2. Hardwoods. USDA-FS Agriculture Handbook No. 654.

Tanner, J. T. 1986. Distribution of tree species in Louisiana bottomland forests. Castanea 51:168-174.

Vozzo, J. A. 1990. *Quercus nigra* L. Water Oak. Pp. 701-703 in R. M. Burns and B. H. Honkala, Tech. Coords., Silvics of North America 2. Hardwoods. USDA-FS Agriculture Handbook No. 654.

Errata

This table was inadvertently left out of Emile Gardiners's article, Ecology of Bottomland Oaks in the Southeastern United States, from the last issue of *International Oaks* (Journal # 12). Our apologies to the author and our readers.

Table 1. Summary of flood tolerance rating, shade tolerance rating and species-site associations of 9 common bottomland oak species endemic to the southeastern United States (adapted from Putnam et al. 1960).

Species	Flood Tolerance[1]	Shade Tolerance[2]	Species-Site Associations[3]
Section *Quercus*			
overcup oak (*Q. lyrata* Walt.)	Tolerant	Moderately intolerant	common on poorly drained flats or sloughs with water hickory
swamp chestnut oak (*Q. michauxii* Walt.)	Moderately intolerant	Moderately intolerant	common on loamy, well-drained sites, particularly ridges of older alluvium with cherrybark oak, sweetgum and hickories
white oak (*Q. alba* L.)	Intolerant	Moderately intolerant	infrequent on well drained, older alluvium with Shumard oak, cherrybark oak, sweetgum, hickories, and loblolly pine (*Pinus taeda* L.)
Section *Lobatae*			
swamp laurel oak (*Q. laurifolia* Michx.)	Moderately tolerant	Moderately intolerant	common on poorly drained clay flats and margins of sloughs and swamps of Gulf coastal plain bottoms with willow oak, water oak and Nuttall oak
Nuttall oak (*Q. nuttallii* Palm.)	Moderately tolerant	Intolerant	common on poorly drained clay flats in recent alluvium of the Gulf Coastal Plain, and the Mississippi and Red River Valleys with green ash, sweetgum, and American elm
willow oak (*Q. phellos* L.)	Moderately tolerant	Intolerant	common on many site types but primarily on high flats and loamy ridges of recent alluvium with water oak and sweetgum

Species	Flood Tolerance[1]	Shade Tolerance[2]	Species-Site Associations[3]
water oak *(Q. nigra* L.)	Moderately tolerant	Intolerant	common on well drained loamy ridges and high flats with willow oak, cherrybark oak, sweetgum, and others, but also found on poorly drained flats with swamp laurel oak and Nuttall oak
cherrybark oak *(Q. pagoda* Raf.)	Moderately intolerant	Intolerant	common on loamy, well-drained sites, particularly ridges of older alluvium with swamp chestnut oak, water oak, Shumard oak, sweetgum, and hickories
Shumard oak *(Q. shumardii* Buckl.)	Moderately intolerant	Intolerant	scattered on well drained ridges of older alluvium, with cherrybark oak, white oak, sweetgum and hickories

[1] Rankings range from Very tolerant, Tolerant, Moderately tolerant, Moderately intolerant, Intolerant, and Very intolerant. Additional sources include Hook (1984) and McKnight et al. (1981).

[2] Rankings range from Very tolerant, Tolerant, Moderately tolerant, Moderately intolerant, Intolerant, and Very intolerant. Additional sources include Edwards (1990a, 1990b), Filer (1990), Krinard (1990), McReynolds and Hebb (1990), Meadows and Stanturf (1997), Rogers (1990), Schlaegel (1990), Solomon (1990) and Vozzo (1990).

[3] Additional sources include Hodges (1994, 1997).