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NOTES ON THE TAXONOMY, ECOLOGY, AND DISTRIBUTION OF *NYSSA BIFLORA* (NYSSACEAE)

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ABSTRACT

Nyssa biflora Walt., a wetland tree of eastern North America, grows primarily on organic soils in bogs, streamheads, and blackwater swamps. First described by Mark Catesby, unrecognized by Linnaeus, and given its current binomial by Walter, it is often confused with other *Nyssa* species. Long regarded as a variety of *Nyssa sylvatica*, *N. biflora* is now considered a distinct species by most authors. It is compared here in morphology and ecology to the other four North American species, *N. aquatica*, *N. ogeche*, *N. sylvatica*, and *N. ursina*.

Nyssa biflora Walt., also commonly known as *N. sylvatica* var. *biflora* (Walt.) Sargent, has an interesting taxonomic history. "The Tupolo Tree" was first described by Mark Catesby in *The Natural History of Carolina, Florida, and the Bahama Islands* (1754) as "*Arbor in aqua nascens, foliis latis acuminatis & non dentatis, fructu Elaeagni minore*" (tree arising in water, leaf flat and acuminate with no teeth, fruit like small *Elaeagnus*). Catesby also described "The Water-Tupolo"—as *"Arbor in aqua nascens, foliis latis acuminatis & dentatis, fructu Elaeagni majore*" (tree arising in water, leaf flat and acuminate *with* teeth, fruit like *large Elaeagnus*) (remember, Catesby's work predated binomial nomenclature). Linnaeus (1753) cited Catesby's descriptions of the two species (he had visited the Oxford University herbarium in 1736 while researching *Species Plantarum* and either saw Catesby's specimens or reviewed an early edition of *The Natural History of Carolina*) but consolidated the two descriptions into *Nyssa aquatica* L., not recognizing *N. biflora* in his *Species Plantarum*. The "*Nyssa biflora*" binomial, therefore, had to wait until the publication of *Flora Caroliniana* (1788) by Thomas Walter, who also recognized it as a good species, separate from *Nyssa aquatica*. Not until 1785 was the closely-related *Nyssa sylvatica* (black gum, sour gum, tupelo, upland tupelo, pepperidge), now known to be the most widespread species of *Nyssa* in North America (Tucker & Park 2016), described by Humphry Marshall (Marshall 1785).

Since its original description, *Nyssa biflora* has been absorbed into *N. aquatica* (by Linnaeus) and into *N. sylvatica* (as *N. sylvatica* subsp. *biflora* (Walt.) A.E. Murray and as *N. sylvatica* var. *biflora* (Walt.) Sargent). Burckhalter (1992) somewhat humorously pointed out that Sargent "lowered the species to a variety in 1893 and twelve years later elevated it back to a species." He also concluded (1990, 1992) that *N. biflora* is "unquestionably a separate species," based on flavonoid and phylogenetic work. Recently, *N. biflora* was accepted as a species by Tucker & Park (2016) in their treatment of *Nyssa* for FNANM.

Distinctions

Partially because of common names, *Nyssa biflora* (swamp tupelo, swamp black gum), *Nyssa sylvatica* (black gum, sour gum, tupelo), and *Nyssa aquatica* L. (water tupelo) have often been confused. *Nyssa biflora* has narrowly lanceolate leaves, 1-3 small fruits (despite its name), while *N. aquatica* has a variable number of larger fruits (over twice as large as those of *N. biflor*a), often called "swamp olives." The leaves of *N. biflora* (to 8 cm) are usually less than half as long as those of *N. aquatica* (to 18 cm), and, as Catesby pointed out, have no teeth (measurements here are from Tucker & Park 2016).

Nyssa biflora is similar to *Nyssa sylvatica* and the small Florida panhandle endemic *N. ursina* Small (bear or Apalachicola tupelo) in that all three have elliptical leaves. Leaves of *N. sylvatica* are more ovate-elliptical with a cuspidate tip (*N. sylvatica* leaves are highly variable from south to north and from coastal populations to those in the Appalachians). *Nyssa sylvatica* also usually has 4-5 drupes, compared to 1-3 in *N. biflora*. Small (1927) thought *N. ursina* to be closely related to *N. biflora*, with which it is occasionally found. Wen and Steussy (1993), however, regarded *ursina* as a variety of *N. sylvatica*, as *N. sylvatica* var. *ursina* (Small) Wen & Stuessy.

The other two North American *Nyssa* species are easily separated from *N. biflora. Nyssa ogeche* Bartram ex Marshall, the Ogeechee tupelo or lime, has large ovate leaves and bright, large fruit, maturing as yellow to red-orange drupes. *Nyssa aquatica*, as discussed earlier, has much larger fruits than *biflora* and longer, elliptic-ovate leaves. Finally, *biflora* leafs out earliest of all *Nyssa* species in the spring and begins to drop leaves before other *Nyssa* species.

Habitat

All species of *Nyssa* may grow in wetlands. *Nyssa biflora* prefers acidic, organic soils, while *N. aquatica* is usually found on mineral soils. Both inhabit large Atlantic and Gulf Coastal Plain floodplains, but *N. biflora* is often found in seepage bogs along the base of floodplain bluffs, while *N. aquatica* is found in sloughs, oxbows, and other old river channels. *Nyssa biflora* is found in Carolina bays, pocosins, Blue Ridge and Piedmont bogs, and on other acidic soils where *aquatica* is usually absent. In the deep organic soils of "gum swamps," *N. biflora* is often a dwarfed tree less than 15 m tall, but in Congaree Swamp National Park in South Carolina several 30 meter-tall trees, including the national record, grow in rich mineral soils mixed with organic matter. Most of the time, however, *N. aquatica* is the larger tree of the two. Sloughs of mature *N. aquatica* trees approaching 30 m in height are occasionally found in large southeastern river floodplains. *Nyssa ogeche* is found along blackwater streams, while *N. ursina* is found in savannas and flatwoods depressions. Finally, *N. sylvatica* is found in upland mixed forests in the southern portion of its range, but in New England and northward it is a tree of swamps and wetlands.

Geography

Nyssa biflora ranges widely in eastern North America, north to New Jersey, Kentucky, Illinois, Missouri, south to Florida, and west to Arkansas and Texas. It is rare in Kentucky, Illinois, and Missouri, where it is a peripheral species. Although it is most commonly seen in the Atlantic and Gulf Coastal Plains, *N. biflora* is now known from mountain bogs in the Carolinas, Piedmont seepage bogs in South Carolina, and acidic wetlands in nearly every county in Alabama. It is usually found at low elevations, but I recently found a mature *Nyssa biflora* in a mountain bog in Oconee Co., South Carolina, at just over 750 meters elevation.

Nyssa sylvatica has the widest range of the five species of North American *Nyssa*. It is found from Ontario to Florida west to Oklahoma and Texas, with disjunct montane populations in several states of Mexico. *Nyssa aquatica* is known from the District of Columbia south to Florida and west to Texas and up the Mississippi drainage to Missouri and Illinois.

Nyssa ursina is a narrow endemic found only in the Florida panhandle, and *Nyssa ogeche* ranges from just north of the Savannah River in South Carolina through the Outer Coastal Plain of Georgia, Alabama, and Mississippi west to Louisiana (all range information from Tucker & Park 2016). As mentioned above, *N. biflora* usually grows in floodplains with *N. aquatica*, although not in the same habitat. As *N. sylvatica* often grows in high floodplains and on floodplain bluffs, there are probably places along tributaries of the lower Savannah River in South Carolina and Georgia where one may see four species of *Nyssa*, including *N. ogeche*, in one long panorama. All four indeed occur in Jasper Co., South Carolina (South Carolina Plant Atlas 2021).

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LITERATURE CITED

Burckhalter, R. E. 1990. Flavonoid and phylogenetic analyses of the genus *Nyssa* (Cornaceae) in North America. Ph. D. diss., Univ. of Alabama, Tuscaloosa.

Burckhalter, R.E. 1992. The genus *Nyssa* in North America: A revision. Sida 15: 323–342.

Catesby, M. 1754. The Natural History of Carolina, Florida, and the Bahama Islands. Volume I. C. Marsh, London.

Linnaeus, C. 1753. Species Plantarum. Laurentius Salvius.

Marshall, H. 1785. *Nyssa sylvatica*. Upland Tupelo Tree or Sour Gum. Pp. 97–98, in Arbustrum Americanum: The American Grove, or, an Alphabetical Catalogue of Forest Trees and Shrubs, Natives of the United States.

Small, J.K. 1927. A new *Nyssa* from Florida. Torreya 27: 92–93.

South Carolina Plant Atlas. 2021. <www. herbarium.biol.sc.edu> Accessioned 17 October 2021.

Tucker, G.C. and T.J. Park. *Nyssa*. Pp. 458–461, in Flora of North America North of Mexico, Vol. 12. Oxford Univ. Press, Oxford and New York.

Walter, T. 1788. Flora Caroliniana. J. Fraser, London.

Wen, J. and T.F. Steussy. 1993. The phylogeny and biogeography of *Nyssa* (Cornaceae). Syst. Bot. 18: 68–79.