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The Silvics of *Persea borbonia* (L.) Spreng., Red Bay, and *Persea palustris* (Raf.) Sarg., Swamp Bay, Lauraceae (Laurel Family)

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ABSTRACT

Red bay [*Persea borbonia* (L.) Spreng.] and swamp bay [*Persea palustris* (Raf.) Sarg.] are aromatic, broadleaved, evergreen tree species native to the southeastern Atlantic Coastal Plain of the United States. Confusion exists over whether red bay and swamp bay should be considered separate species; nonetheless, certain physical and chemical characteristics, as well as associated flora and soils, are commonly used to distinguish the species. Both species flower in late spring and produce dark blue drupes in the fall. They are highly tolerant of shade, commonly occurring as understory trees with irregularly shaped stems, but also grow well in full sun. Hundreds of thousands of red bay and swamp bay trees have been killed by laurel wilt, a vascular disease caused by a nonnative insect/pathogen complex. In infected stands, laurel wilt disproportionately kills the largest red bay and swamp bay trees, usually eliminating all but the smallest diameter stems and sprouts. Although it is not a major timber species, red bay and swamp bay are rich in essential oils and have been used for numerous culinary, cultural, and medicinal purposes.

Keywords: Ambrosia beetle, laurel wilt, red bay, silvics, swamp bay.

COVER PHOTO: Swamp bay (*Persea palustris*) Fruit(s). Courtesy photo by Chris Evans, University of Illinois, Bugwood.org.

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INTRODUCTION

Red bay [*Persea borbonia* (L.) Spreng.] and swamp bay [*Persea palustris* (Raf.) Sarg.] are woody plant species in the family Lauraceae native to the Southeastern United States. Informally, the two species are often grouped together and broadly defined as "red bay" (sometimes spelled as one word, "redbay"). Both are shade tolerant, broadleaved, evergreen, midstory trees, seldom growing large enough to make them commercially important. However, their ecological and cultural value, coupled with dramatic reductions in their populations caused by a disease known as laurel wilt, has generated recent interest in these species.

The genus *Persea* has been revised several times throughout history. First applied in 1601, the word *Persea* was derived from Greek, referring to a sacred fruit-bearing tree in Persia and Egypt (Coder 2007, Kopp 1966). In 1753, Linnaeus incorporated *Persea* into the genus *Laurus* which included the New World species, red bay, and avocado, under the names *L. borbonia* and *L. persea,* respectively (Coder 2007, Kopp 1966). Since that time, the genus has had many names, including *Borbonia*, *Farnesia, Menestrata, Tamala*, and *Nothaphoebe* (Coder 2007). Of the roughly 150 to 200 *Persea* species worldwide, only three species, red bay, swamp bay, and silk bay (*Persea humilis* Nash), are native to the Southeastern United States. Catesby (1771) is credited with first describing and illustrating red bay under the name *Laurus caroliniensis* (Kopp 1966, Sargent 1895). Catesby's description of the tree suggests that he was actually sketching swamp bay (McMillan and others 2013, Reveal and others 2014). However, his illustration of red bay is somewhat ambiguous, and the leaves lack the pubescence of swamp bay. Further, the red peduncles and the leaves somewhat resemble lancewood (*Damburneya coriacea*), another lauraceous species that Catesby described in the Bahamas, suggesting that the red bay illustration may be a composite of all three species (Reveal and others 2014).

The ambiguity of Catesby's red bay illustration exemplifies the confusion on whether these are indeed separate species or varieties of the same species. Swamp bay was first described in 1814 as a variety of red bay by Frederick Pursh but is recognized by many authorities as a separate species with ascending (versus appressed) rusty hairs (trichomes), peduncles 4–7 cm (versus 1–3 cm) and more acute leaf blades than red bay (Weakley 2015). Silk bay was noted by Nash in 1895, described by Kopp (1966) as another variety of red bay, and later described as a separate species by some authors. Endemic to Florida, silk bay is distinguished by having very dense, appressed silky hairs on the underside of the leaves (Weakley 2015). Henceforth in this paper, we limit our discussion to red bay and swamp bay.

Fernald (1945) expressed the frustration of distinguishing between red bay and swamp bay, writing that he "abandoned the futile attempt to see two species or two varieties in the glabrous-leaved material and that with leaves densely pubescent beneath," he "cannot look upon them as anything but glabrous and pubescent forms of one species, *P. borbonia*." Coker and Totten (1945) likewise argued for describing red bay and swamp bay as one species claiming that the distinguishing characteristics between the two are "vague and unsatisfactory," citing an example specimen from North Carolina with short peduncles (suggesting red bay), but with "copiously pubescent" leaves (suggesting swamp bay). However, Wofford and Pearman (1975) conducted a scanning electron microscope (SEM) study on the leaves of native *Persea* species of the Southeastern United States and found that the pubescence of swamp bay was distinct from red bay. Although hair density was variable, hair length was statistically different between the two species, with red bay averaging hairs of 0.16 mm and swamp bay averaging hairs of 0.58 mm (Wofford and Pearman 1975). The SEM study also emphasized the difference between the appressed hairs of red bay and the ascending, or lanate, hairs of swamp bay. Wofford (1974) conducted a chemical study on flavonoids in red bay and swamp bay to further separate the species. He suggests that the two are closely related, evolving from a common ancestor, but red bay lacks one unidentified compound and has trace amounts (present in 25 percent of samples) of three other compounds (orientin, isoorientin, and quercetin 3-O-glucoside) while swamp bay consistently contains these compounds

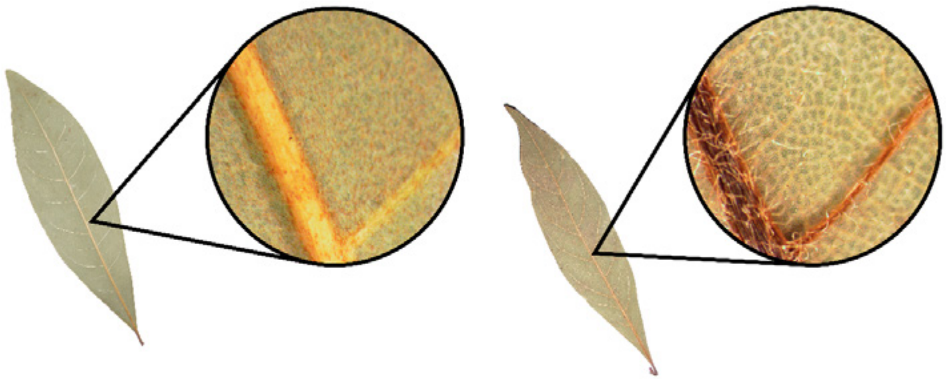

Figure 1—Distinguishing characteristics of red bay showing appressed trichomes (left) and swamp bay showing ascending trichomes (right). (from Shearman 2016).

(Wofford 1974). Niogret and others (2011) also found chemical differences between the two species, with red bay and swamp bay having qualitative and quantitative differences in volatile terpenoids in freshly rasped wood samples. Weakley (2015) emphasizes that the hairs of red bay and swamp bay are distinctly different (appressed versus ascending, respectively) and are the most consistent identifiable features (fig. 1). Authorities are increasingly recognizing red bay and swamp bay as different species.

The literature, however, seldom distinguishes between the species. Many studies refer to red bay in their sites, but their site description would suggest that it is actually swamp bay. Once laurel wilt began to occur in the Southeastern United States (see damaging agents section below) and mortality of the *Persea* species drew the attention of more researchers, most studies used Brendemuehl's (1990) broader definition of red bay while acknowledging that there may be two different species (e.g., Cameron and others 2008, 2010, 2015; Fraedrich and others 2008; Spiegel and Leege 2013). This report attempts to distinguish between the two species where possible; however, more detailed population genetic studies on the native *Persea* spp. of the United States are needed.

HABITAT

Native Range

Collectively, red bay and swamp bay have been reported in the Atlantic Coastal Plain from Maryland south to Florida and along the Gulf Coast west to eastern Texas (fig. 2). In the core part of their range, swamp bay has the larger distribution, with red bay being restricted to the coastal fringe and swamp bay extending inland. Weakley (2015) suggests that reports of red bay located north of North Carolina are likely to be swamp bay misidentified as red bay or use the larger definition of red bay. Fossil evidence suggests that one of the species (likely swamp bay, although reported as red bay) was once present as far north as New Jersey (Hollick 1892). High densities of red bay and/or swamp bay occur in South Carolina and Georgia, and the highest densities are found in eastern North Carolina on the Albemarle Peninsula (Koch and Smith 2008). Occasionally, the two species can be found together on the same site which suggests the possibility of interbreeding populations.

Climate

The climate for both species ranges from warm-temperate to semitropical (Brendemuehl 1990). Mean annual precipitation ranges from 40 inches (1020 mm) in the northern part of swamp bay's range to approximately 52 inches (1320 mm) along the Atlantic coast to a maximum of 64 inches (1630 mm) along the Gulf Coast (Brendemuehl 1990). Red bay likely experiences a similar precipitation range, but a slightly higher minimum precipitation of around 49 inches (1250 mm) due to its coastal fringe distribution. Collectively, the two species have a high frost-free period from 200 to 365 days, with more than 250 days for most of their range (Brendemuehl 1990).

Soils and Topography

The two species differ with regard to the sites and soils in which they are typically found. Red bay is primarily found in hammocks, dunes, and maritime forests of barrier islands with dry and sandy soils (Weakley 2015). Swamp bay, as its common name implies, is

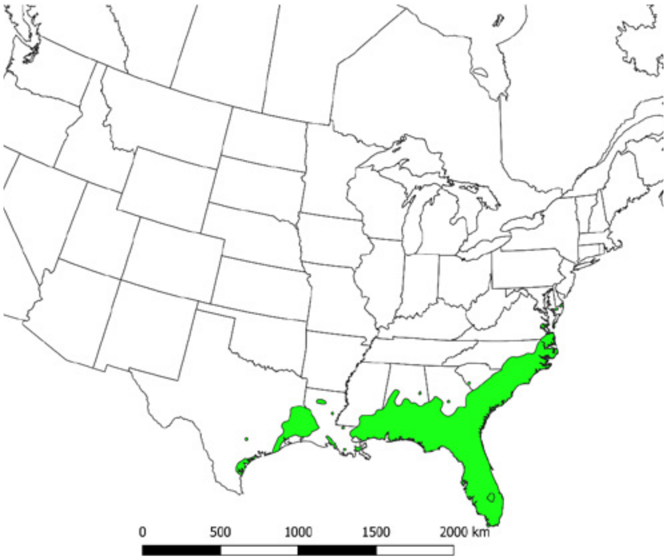

Figure 2—Distribution of red bay and swamp bay (combined) in Eastern North America based on Little (1977).

typically found on the borders of swamps, pocosins, and bay forests, as well as maritime forests with wet, mucky, or peaty soils (Brendemuehl 1990, Weakley 2015). However, maritime forests with dry, sandy soils can also support swamp bay.

Soil nutrient requirements—Soils for both species are generally acidic with pH ranging from 3 to 7.5 but averaging around 4.5. Little has been published on growth response to different soil nutrient levels. Soils, where red bay is often found, are generally higher in calcium, pH, and phosphorous than soils supporting swamp bay populations (Shearman and others 2018).

Soil moisture regime—Soil moisture varies throughout the red bay and swamp bay range. Red bay soil is generally drier due to the high percentage of sand. Swamp bay can tolerate both very moist and very dry conditions.

Associated Forest Cover

Red bay and swamp bay communities are distinctly different, and the two species can often be distinguished based on other associated species (Shearman and others 2018). Red bay is usually found in maritime live oak forests on barrier islands with live oak (*Quercus virginiana* Mill.), devilwood [*Cartrema americanum* (L.) Raf.], southern magnolia (*Magnolia grandiflora* L.), and cabbage palm [*Sabal palmetto* (Walter) Lodd. Ex Schult. & Shult.f.]. The presence of yaupon (*Ilex vomitoria* Aiton) in the understory is highly associated with red bay (Shearman and others 2018). Swamp bay is often associated with floodplain forest and swamp species: black tupelo (*Nyssa sylvatica* Marshall), water tupelo (*Nyssa aquatica* L.), loblolly-bay [*Gordonia lasianthus* (L.) Ellis], sweetbay magnolia (*Magnolia virginiana* L.), sweetgum (*Liquidambar styraciflua* L.), Atlantic white cedar (*Chamaecaparis thyoides* [L.] Britton), water oak (*Quercus nigra* L.), laurel oak (*Q. laurifolia* Michx.), baldcypress [*Taxodium distichum* (L.) Rich.], and pondcypress (*Taxodium ascendens* Brongn.), along with understory species such as shining fetterbush [*Lyonia lucida* (Lam.) K. Koch] and lizard's tail (*Saururus cernuus* L.). Swamp bay is often found in pocosins, where it can be associated with loblolly-bay, big gallberry (*Ilex coriacea* Pursh), honey-cups [*Zenobia pulverulenta* Bartram ex Willd. (Pollard)], pond pine (*Pinus serotina* Michx.), and laurel greenbrier (*Smilax laurifolia* L.). Similarly, in baygall swamps, swamp bay is found with buckwheat-tree [*Cliftonia monophylla* (Lam.) Britton ex Sargent] and titi (*Cyrilla racemiflora* L.). In maritime hardwood forests, swamp bay is found with white oak (*Quercus alba* L.), American beech (*Fagus grandifolia* Ehrh.), red mulberry (*Morus rubra* L.), and mockernut hickory [*Carya tomentosa (*Poir.) Nutt.]. When *Persea* is found with longleaf pine (*Pinus palustris* Mill.), it is usually swamp bay (Shearman and others 2018). Associates of both species include wax myrtle (*Morella cerifera* L.), American holly (*Ilex opaca* Aiton), eastern redcedar (*Juniperus virginiana* L.), American beautyberry (*Callicarpa americana* L.), darlington oak (*Q. hemisphaerica* Bartram ex. Willd.), Spanish moss [*Tillandsia usneoides* (L.) L.], and saw palmetto [*Serenoa repens* (W. Bartram) Small].

LIFE HISTORY

Reproduction and Early Growth

Flowering and fruiting—Small, white, bisexual flowers bloom from May to June on peduncles. Red bay flowers, and presumably swamp bay flowers, exhibit heterodichogamy, where flowers temporally alternate between female and male phases. On some individuals, all flowers open in a female phase, with receptive stigmas in the morning, and then re-open in the afternoon in a male phase where pollen is released. On other individuals, all flowers open in the female phase in the afternoon and re-open in the male phase and shed pollen the following morning (Chanderbali and others 2006). The fruit of both species is a dark blue drupe approximately ½ inch in size. Fruits ripen in the fall from September to October.

Seed production and dissemination—Fruits are produced annually. Seeds are disseminated largely by wildlife from birds, deer, and black bears (Brendemuehl 1990).

Seedling development—There is little information on seedling development in the literature other than that germination is hypogeal (Brendemuehl 1990).

Vegetative reproduction—Both species resprout readily after being damaged. Stumps from toppled stems can have multiple sprouts growing from the base. At least one source suggests that *Persea* can spread vegetatively through root suckers, which eventually form independent seedlings when the root suckers decay (Titus 1990).

Sapling and Pole Stages to Maturity

Growth and yield—Growth varies widely throughout the range, possibly due to site quality (Brendemuehl 1990). Different sources suggest differences in growth between red bay and swamp bay. Kirkman and others (2007) state that red bay grows up to 60–70 feet tall and 2 feet in diameter, while swamp bay does not usually grow over 25–50 feet. In contrast, Duncan and Duncan (2000) state that red bay achieves slightly shorter stature (up to approximately 60 feet in height and about 2 feet in diameter) while swamp bay can grow to up to 65 feet in height and 3 feet in diameter (fig. 3).

Rooting habit—No studies could be found that examine the rooting habits of either species. Observations of seedling roots indicate that both species develop taproots with relatively large carbohydrate reserves. Roots contain borbonol, an antifungal compound that protects the roots from rot infections such as that from *Phytophthora cinnamomi* (Zaki and others 1980).

Reaction to competition—Red bay and swamp bay are highly shade tolerant but also grow well in full sun. Irregular stems are common for individuals growing under a closed canopy, likely due to light competition (fig. 4).

Damaging agents—The major damaging agent for red bay and swamp bay is laurel wilt, a vascular disease caused by the fungal pathogen *Raffaelea lauricola* T.C. Harrington, Fraedrich, & Aghayeva sp. nov. (Fraedrich and others 2008). The laurel wilt pathogen is a fungal symbiont of the red bay ambrosia beetle (*Xyleborus glabratus* Eichhoff), which bores into healthy host trees and inoculates the sapwood with *R. lauricola*. The pathogen moves rapidly in the xylem cells, and diseased red bay trees typically die within a few weeks or months after initial infection. Symptoms include dark discoloration of the outer sapwood and wilted foliage that can persist on the tree for many months (Hughes and others 2015) (fig. 5). Both *X. glabratus* and *R. lauricola* are native to Asia, and the beetle vector was first detected in North America near Savannah, GA in 2002 (Rabaglia and others 2006). Laurel wilt has killed hundreds of millions of red bay and swamp bay trees throughout the southeastern Atlantic and Gulf Coastal Plain regions of the United States. The disease also affects other plant species in the family Lauraceae including avocado (*Persea americana* Mill.), pondberry [*Lindera melissifolia* (Walter) Blume],

Figure 3—A large red bay tree on Jekyll Island, GA. (USDA Forest Service photo by Stephen Fraedrich).

Figure 4—In shaded environments, red bay (pictured here) and swamp bay trees can develop twisted, irregular-shaped trunks. (USDA Forest Service photos by A.E. Mayfield).

Figure 5—Symptoms of laurel wilt in red bay: wilted and discolored foliage that may remain on the tree for several months (left); and bark removed to show dark discoloration in the outer sapwood (right). (USDA Forest Service photos by A.E. Mayfield).

pondspice [*Litsea aestivalis* (L.) Fernald], Gulf triandra [*Licaria triandra* (Se.) Kosterm.], and sassafras [*Sassafras albidum* (Nutt.) Nees] (Cameron and others 2015, Hughes and others 2017).

In forest stands, laurel wilt disproportionately affects the largest red bays and commonly eliminates all but the smallest diameter stems and sprouts (Fraedrich and others 2008, Shields and others 2011). Shearman and others (2015) found that once laurel wilt is detected in a county, the odds of topkill increase 153.7 percent every year. Nearly all *Persea* spp. in a stand are topkilled within the first 2 years of laurel wilt, with the exception of smaller stems under 2.5 cm in diameter (Shearman 2016). After being topkilled, red bay and swamp bay resprout readily from underground buds and basal area gradually increases from years 2 to 10 post infection (Shearman 2016). Small diameter stems (1–5 cm, diameter at breast height) predominate in the years following a laurel wilt epidemic, and it is uncertain whether stems in this diameter range will reach maturity or be attacked again after reaching larger diameters.

Small branches can be attacked by the black twig borer (*Xylosandrus compactus* Eichhoff), a non-native beetle introduced in the United States in 1941 (Ngoan and others 1976). This ambrosia beetle creates brood chambers in the pith of branches. The attack by the black twig borer leads to dieback of the twig, which can be mistaken as an early symptom of laurel wilt but does not result in the death of the entire tree.

Fire is also a likely damaging agent. Typically, red bay and swamp bay are very minor components, if present at all, in communities maintained by frequent fire such as those dominated by longleaf pine (*Pinus palustris* Mill.). *Persea* abundance can increase in such communities in the absence of fire (Menges and others 1993).

It is common to find numerous galls on the leaves of red bay and swamp bay. These galls are formed by the nymph of the red bay psyllid (*Trioza magnolia* Ashmead). The nymphs feed on the phloem from within the gall until they emerge as adults. Damage from the red bay psyllid is generally minor and only cosmetic. For example, Leege (2006) found no relationship between the number of galls on a plant and seed production.

Other minor damaging agents include the larvae of the palamedes swallowtail butterfly (*Papilio palamedes* Drury), which feeds exclusively on red bay and swamp bay leaves.

SPECIAL USES

Several authors state that red bay wood is used locally as cabinet wood and in boat building (Brendemuehl 1990, Kirkman and others 2007, Kopp 1966), a statement apparently originating with Sargent (1895); however, no information can be found that these uses are still in practice today. Indeed, it may be the case that the use of red bay wood may have once been much more prominent than it is now. Sargent (1895) stated that red bay was one of the most valuable evergreen species in North American forests, reaching sizes of 2.5 to 3 feet in diameter. The Forest Inventory and Analysis data suggests that trees of this size are rare (even more so since laurel wilt), with a median tree size of 2.4 inches (FIA Database 2021). However, the wood is occasionally used as smoke wood in barbecues. It is likely that the movement of wood infected with laurel wilt for smoking or as firewood has aided in the spread of the disease throughout the Southeast.

Historically, red bay has been used for numerous culinary, cultural, and medicinal purposes. Dried leaves have been used to flavor soups, gumbos, and other traditional southern U.S. dishes (Coder 2012). Various Native American Tribes have employed red bay, medicinally, to treat a wide variety of ailments and used it in cultural celebrations and ceremonies (Coder 2012, Hughes and others 2015). Prior to the spread of laurel wilt disease in the Southeast, red bay was considered an excellent landscape tree due to its aromatic evergreen foliage, tolerance of a range of sunlight and soil conditions, attractive bark, wildlife use, and adaptability to pruning (Gilman and others 2018).

GENETICS

Few studies have analyzed the genetics of red bay or swamp bay. Chen and others (2015) found high diversity levels among 24 red bay gSSR markers. This high diversity may be due to using the larger definition of red bay in the study. Li and others (2011) used ITS and LEAFY intron II sequences to analyze 78 *Persea* species, including red bay and swamp bay. They estimated that the divergence of the *Persea* group occurred roughly 55.3 million years ago. In their results, red bay and swamp bay were closely related along with a third species, *P. haenkeana*.

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Red bay [*Persea borbonia* (L.) Spreng.] and swamp bay [*Persea palustris* (Raf.) Sarg.] are aromatic, broadleaved, evergreen tree species native to the southeastern Atlantic Coastal Plain of the United States. Confusion exists over whether red bay and swamp bay should be considered separate species; nonetheless, certain physical and chemical characteristics, as well as associated flora and soils, are commonly used to distinguish the species. Both species flower in late spring and produce dark blue drupes in the fall. They are highly tolerant of shade, commonly occurring as understory trees with irregularly shaped stems, but also grow well in full sun. Hundreds of thousands of red bay and swamp bay trees have been killed by laurel wilt, a vascular disease caused by a nonnative insect/pathogen complex. In infected stands, laurel wilt disproportionately kills the largest red bay and swamp bay trees, usually eliminating all but the smallest diameter stems and sprouts. Although it is not a major timber species, red bay and swamp bay are rich in essential oils and have been used for numerous culinary, cultural, and medicinal purposes.

Keywords: Ambrosia beetle, laurel wilt, red bay, silvics, swamp bay.

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