

Redbay Survival Eleven Years after Infection with an Exotic Disease on St. Catherines Island, Georgia, USA

C. Ken Smith¹, Elise Landreaux¹, Hali Steinmann², Deborah McGrath², Christa Hayes³ & Royce Hayes³

¹The University of the South, Department of Earth and Environmental Systems, 735 University Avenue, Sewanee, Tennessee, USA

²The University of the South, Department of Biology, 735 University Avenue, Sewanee, Tennessee, USA

³St. Catherines Island Foundation, Midway, Georgia, USA

Correspondence: C. Ken Smith, The University of the South, Department of Earth and Environmental Systems, 735 University Avenue, Sewanee, Tennessee, 37383, USA. Tel: 1-931-598-3219. E-mail:ksmith@sewanee.edu

Received: December 3, 2015 Accepted: December 16, 2015 Online Published: December 22, 2015

doi:10.5539/enrr.v6n1p27

URL: <http://dx.doi.org/10.5539/enrr.v6n1p27>

Abstract

Introduced to the United States in 2002, laurel wilt (*Raffaelea lauricola*) is a fungus that causes life threatening defensive responses in the vascular system of trees within the Lauraceae family, and it is introduced to the tree by the Asian ambrosia beetle (*Xyleborus glabratus*). Redbay (*Persea borbonia*) is the preferred host species within the US coastal plains and maritime forests, and it has experienced rapid mortality throughout its range in the southeastern United States since the introduction of the ambrosia beetle and associated fungus. In this study, we inventoried all dead and live redbay trees from replicated transects inside a maritime forest, a successional old-field forest (both located on the island's Pleistocene core), and a Holocene hammock to examine the role of soils, prior land use and landscape position on redbay survival eleven years after the introduction of the exotic beetle and fungus on the island. Results indicated that the maritime forest had a significantly higher number of redbay trees prior to infection compared to the hammock or old-field sites. Eleven years post-infection, all three sites had similar densities of redbay trees and the surviving trees had similar diameter distributions among the three sites. Soils under the maritime forest had significantly higher phosphorous (P) and pH concentrations, and the Holocene hammock had a higher water table compared to the sites on the Pleistocene core. Almost all living trees at each site had signs of invertebrate herbivory and twig borer damage. Prior land use history and soils affected redbay densities before laurel wilt infection, but eleven years post-infection, all three site types had similar redbay densities, diameters, basal areas, and levels of herbivory and surviving trees did not demonstrate signs of photosynthetic stress.

Keywords: redbay, ambrosia beetle, laurel wilt, maritime forest, old-field, hammock

1. Introduction

Laurel wilt is an exotic vascular wilt disease caused by a fungus (*Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva) that was imported into the United States from Asia in 2002 through its primary vector, the exotic ambrosia beetle, *Xyleborus glabratus* Eichoff (Fraedrich et al., 2008, Harrington et al., 2011). This ambrosia beetle prefers to infest trees in the laurel family and in its introduced range, redbay (*Persea borbonia* (L.) Spreng.), is a preferred host species. Redbay mortality was first observed in South Carolina and northeast Georgia in 2003, in locations near the beetles' point of introduction to the United States, where it arrived in wood packing material at Port Wentworth, Georgia (Mayfield, 2007). Since that time, redbay mortality caused by laurel wilt has been detected on the coastal plain from North Carolina to Louisiana, and there are fears that the beetle and its fungal symbiont will attack all fifteen native plant species in the Lauraceae family across North America (Gramling, 2010).

Since its introduction in the United States, the spread of the ambrosia beetle has been rapid (up to 55 km/year), and the movement of firewood and forest products is thought to have increased rates of spread (Koch & Smith, 2008). Once it moves into a stand of healthy redbay trees, mortality of trees is rapid (within months), and research indicates that small numbers of ambrosia beetles can infect and kill a mature tree (Hanula et al., 2008). Once inside the tree, female ambrosia beetles introduce the fungus in their galleries, and as the infected tree

detects the fungus in its xylem, the tree secretes resins as a defensive response. This defensive response ultimately results in the blockage of xylem vessels, the loss of water conduction in the xylem, wilt of foliage, and tree mortality (Kendra et al., 2013).

Since 2003, southeastern U.S. coastal plain and maritime forests have seen dramatic changes in forest community structure due to laurel wilt. In coastal Georgia, 90% of redbay trees with diameter at breast height (DBH) > 3 cm were killed across five infested sites, and mortality was noted among the smallest stem diameter classes (Speigel & Leege, 2013). In northern Florida, one year after infection was observed, redbay mortality was 100% in the overstory component resulting in significant changes in forest stand structure (Shields et al., 2011). On St. Catherines Island, Georgia, 98% of redbay main stems died across six 1 ha plots from 2004 - 2009 (Evans et al., 2013). On Ft. George Island, Florida, 132 redbay stems (DBH > 2.5 cm) were monitored from 2004 - 2006, and 92% of these trees died over this time span (Fraedrich et al., 2008).

Despite the numerous studies documenting redbay mortality, little is known about abiotic factors or site characteristics that may precipitate mortality or improve chances of survival in infected redbay populations. St. Catherines Island, Georgia, was home to an extensive redbay population before the wilt was first observed in 2004, and the island has a well-documented land use history and a variety of soils supporting maritime forests. Before the laurel wilt infection, redbay dominated the sub-canopy in many locations across the island, and original populations of redbay are still evident from dead standing trees, some of which now host young basal sprouts. Thus, St. Catherine's Island presents an opportunity to study the influence of site characteristics on redbay survival and regeneration following extensive wilt-induced mortality. The primary objectives of this study were to (i) estimate the density and diameter distributions of redbay, eleven years after the initial exposure to laurel wilt and (ii) examine the role of prior land uses, landscape position and soils on redbay survival and health.

2. Methods

2.1 Site Description

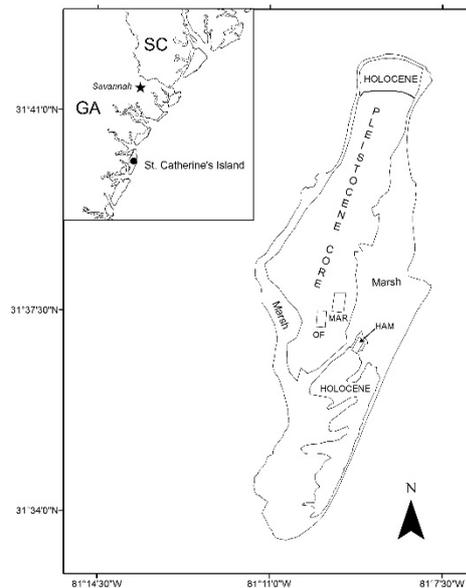


Figure 1. The location of St. Catherines Island, Georgia on the southeastern coast of the United States. OF = maritime forest in old-fields (Foxworth soils), MAR = maritime forest (Echaw soils), HAM = maritime forest in hammock (Fripp-Duckston soils)

St. Catherines Island, Georgia (USA, 31°39'N, 81°09'W) is approximately 13 km long and 5 km across at its widest point. It is located 6 km from the mainland, between Ossabaw Island to the north and Blackbeard-Sapelo Islands to the south (Figure 1). The three sites investigated in this study were located in the southeastern corner of the island with parent materials consisting of marine sediments. Soils on the Holocene hammock sites were sandy and deep (>2 m) and primarily classified as Fripp series (Entisols, Typic Quartzipsammets) on small ridges (old dunes) and Duckston series (Entisols, Typic Psammaquents) in the swales or low areas between the

old dunes (NRCS 2015). Soils of the maritime forest on Pleistocene core were sandy and deep (>3m) and on the border of soils classified in the Foxworth (Entisols, Typic Quartzipsamments) and Echaw series (Spodosols, Oxyaquic Alorthods). These soils were on flat terrain and were moderately well-drained. Forested sites with soils in the Echaw series were typically not cultivated in the 1800s. Soils of the old-field sites on the Pleistocene core were sandy and deep, and classified in the Foxworth series. These soils were on flat terrain and were well-drained and very permeable. These soils were cleared of forest and used for cotton cultivation in the 1800s in the central and southern portion of the island's Pleistocene core. The hammock site was above the high tide line, thus it is not regularly exposed to salt water overwash. The maritime forest and old-field sites were approximately 5 meters above sea level.

In this region, annual rainfall averages approximately 110 cm per year, and the average annual temperature is approximately 19°C (Georgia Coastal Systems LTER, 2014). An analysis of rainfall data from nearby Sapelo Island indicated that from 2000-2014, St. Catherines experienced nine years with below average rainfall, and five of those years were 20 cm below average rainfall, including 2004 (90 cm), 2007 (84 cm), 2008 (84 cm), 2010 (86 cm) and 2011 (85 cm).

2.2 Sampling Sites

We inventoried redbay populations along transects spanning three land use histories: maritime hammock without cultivation, maritime forest without cultivation and maritime forest that was previously under cultivation (old fields). The island's Pleistocene core was home to twenty antebellum cotton fields abandoned in the late 19th century that were largely colonized by naturally regenerated slash pine (*Pinus elliottii* Engelm.), loblolly pine (*Pinus taeda* L.), longleaf pine (*Pinus palustris* Mill.) and a variety of hardwood species. In the mid-20th century, many of the stands were logged and left to naturally regenerate. Over the past 15 years, several of these stands experienced surface fires caused by lightning and patchy mortality due to a southern pine beetle infestation, and switch cane (*Arundinaria tecta* Walter (Muhl.)) is now common in the understory. Intact maritime forest was located in-between the antebellum cotton fields, and was dominated in the overstory by live oak (*Quercus virginiana* Mill.), laurel oak (*Quercus laurifolia* Michx.), sabal palm (*Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.), pignut hickory (*Carya glabra* (Mill.) Sweet) and loblolly pine. The maritime forest mid-story was dominated by wax myrtle (*Morella cerifera* (L.) Small), yaupon (*Ilex vomitoria* Aiton), sparkleberry (*Vaccinium arboreum* Marshall), American holly (*Ilex opaca* Aiton), and redbay. The understory of these forests consisted of a variety of grasses and occasionally very dense cover of saw palmetto (*Serenoa repens* (W. Bartram) Small). These forests are remnants of what once covered much of the island's interior. The eastern edge of the island's Pleistocene core is adjacent to a series of old dunes and hammocks formed during the Holocene. The forests within these landforms are dominated by live oak in the overstory and saw palmetto within the understory. The hammock was never cleared for agricultural purposes, but livestock roamed these forests in the 1900s.

To identify old-field boundaries, an 1867 map of the antebellum cotton fields was rectified on a recent satellite image with ARCGIS to help us identify remnant maritime forest between the old fields. The old-field boundaries were still visible on the aerial images (by differences in vegetative cover), and the location of the old-field and maritime sampling points were determined by their position on this map. Old-field boundaries were field checked during transect installation, and the old-field boundaries could still be identified on the ground by small ditches that were dug around the fields in the 1800s.

Once the three sampling sites representing different land uses were established, a three hectare sampling area was designated at each of the three sites. At each site, a 300 meter transect was established parallel to a reference road which marked the boundary of each site. Three sampling transects were established 20 meters from the road with centers established at 50, 150, and 250 meters along the 300 meter reference transect. Using these centers, three 60x100 meter (0.6 ha) east-west trending transects were established. Each transect included a 40 meter buffer located between each transect.

2.3 Redbay Inventory

In each transect at each site (3 transects X 3 sites), we located all living and dead redbay stems and measured height, diameter at breast height, and percent canopy cover (directly above the stems). Trees were assigned a number and classified as a snag (standing dead), an original living main stem, a living basal sprout, or a dead sprout. All live redbay were assigned a GPS coordinate for future study. On occasion, snags had fallen over, and we obtained a DBH (diameter at breast height, 1.3 m above ground) from the stem on the ground. Most of the dead stems were still standing at the time of this study. We measured basal area three times within each transect using an angle gauge (10 factor). Readings were taken 25, 50, and 75 meters down the center of each transect.

Persea palustris (Raf.) Sarg. (swamp bay) was present on the island, but we did not identify any swamp bay in our plots.

2.4 Redbay Leaf Damage and Browse

All live redbay in each transect underwent a series of visual foliar analyses. For each live tree, evidence of the Palamedes or spicebush swallowtail caterpillar (*Papilio palamedes* Drury and *Papilio troilus* L.) or the black twig borer (*Xylosandrus compactus* Eichhoff) was noted as a yes or no per tree. The presence of the caterpillars was noted if any leaves were found with the tip evenly chewed off in a relatively straight line, a characteristic regionally associated with the 5th instar of the caterpillar. Black twig borer damage was noted if trees had evidence of flagging (dead branches), dead twigs, or dead terminal shoots that were hollowed out in the center. If the redbay had evidence of foliar damage from other unknown invertebrates, this was quantified as a percentage of damage on the whole tree. Deer browse was recorded as yes or no for each tree (Table 4).

2.5 Soil Sampling

Surface soil samples (0 - 10 cm) were taken at each of the three sites. At each site, bulked samples were taken at 25, 50, and 75 meters down the centers of each transect. The composite soil samples were air dried, sieved through a 2-mm sieve, and then oven-dried at 45°C for 24 hours prior to chemical analyses. Soil pH was measured using a glass electrode in a 1:1 slurry with deionized water. Concentrations of Mehlich-3 (M-3) extractable elements (P, K, Mg and Ca) were determined using Inductively Coupled Plasma (ICP) emission spectroscopy. We focused on these elements because prior work on the island indicated that these elements and soil pH were indicative of the presence of shell, which is a major driver of soil variability across the island (Smith & McGrath, 2011). Cation exchange capacity was estimated as the sum of M-3 extractable bases. Percent organic matter was measured using a Walkley-Black colorimetric procedure. All soil chemical analyses were conducted by A & L Analytical Laboratories (Memphis, TN). At each site, depth to water table was measured using a hollow stem auger during June 2014. On the maritime and old-field sites, three samples were taken and spaced 20 meters apart. At the hammock site, five samples were spaced 20 meters apart with three on a dune, two in a swale and one mid-slope on a dune.

2.6 Fluorescence

As a means of assessing stress within individuals, we measured pre-dawn fluorescence using a Licor 6400 XT equipped with a fluorometer chamber. Under periods of stress, chlorophyll *a* emits a photon within the PSII system, and by measuring fluorescence, we can understand the effects of stress within the tree's overall photosynthetic performance (Maxwell & Johnson, 2000). Within one transect at each site, five healthy sprouts were selected at random for measurement. At 4:00 am, pre-dawn fluorescence readings were taken on four healthy leaves of each selected tree at each transect. Methods were repeated two other mornings to conduct readings on the two remaining sites. This sampling method ensured readings were taken before the first light activated the photosystems within the trees.

2.7 Sampling Design and Statistical Analysis

As previously mentioned, three 0.6 ha transects were established at each of the three experimental units which represented maritime forest growing on three different soil types (soil series). Thus, each transect was considered as a replicate inside each of the three experimental units, and we used this single factor experimental design to evaluate the response of redbay growing on different soil types to the laurel wilt infection. Mean forest and soil properties were compared among the three sites (three sites X three transects = 9 total sampling units) using a one-way analysis of variance. Within subject differences in soil chemistry and for forest variables among the three sites were identified using a post-hoc Tukey's HSD multiple comparison procedure. Prior to conducting parametric statistical tests, the normality of all variables was verified using a Shapiro-Wilk procedure. If variables were not normally distributed, they were log transformed prior to analysis of variance.

3. Results

3.1 Soil Sampling

We detected significant differences in soil pH, phosphorus (P), and potassium (K) among the three sites (Table 1). Surface soils at the maritime site had significantly higher pH and P (Tukey's, $p = 0.02$), and K levels were higher in the hammock. Depth to water table among the three sites was significantly different ($p = 0.03$), with depths at the hammock site (1.6m) significantly higher than at the old-field site (2.6m) and maritime site (2.8 m).

Table 1. Surface soil (0-10cm) chemical properties (mean \pm se) on sites representing three land use histories on St. Catherines Island

Soil variable	Maritime	Old-Field	Hammock
pH	5.5 (0.2)a*	5.0 (0.4)ab	4.0 (0.1)b
phosphorus (mg/kg)	171 (0.7)a	147 (50.0)ab	27 (2.2)b
potassium (mg/kg)	24 (2.0)a	28 (1.4)a	44 (0.5)b
calcium (mg/kg)	615 (231)a	451 (110)a	283 (50)a
magnesium (mg/kg)	77 (14)a	74 (9)a	56 (7)a
% OM	3.8 (0.5)a	4.1 (0.5)a	4.6 (0.1)a

*Letters indicate significant differences among the three sites (Tukey's post-hoc, $p < 0.05$).

3.2 Basal Area

Total basal area was similar among the three sites and ranged between 23 and 25 m² per hectare (Table 2). Live oak was a dominant species within the hammock and old field (71-91% of total basal area, Table 2). Loblolly pine was a large component within the maritime site and comprised 50% of total basal area. Sabal palm was present at all three sites but at relatively low basal areas.

Table 2. Basal area by tree species at the three sampling sites (m² per hectare)

Species	Maritime	Old-Field	Hammock
<i>Quercus virginiana</i>	8.9	18.1	21.1
<i>Pinus taeda</i>	12.7	4.5	0.8
<i>Sabal palmetto</i>	3.3	2.3	1.0
<i>Ilex opaca</i>	0.5	0.0	0.2
<i>Ilex vomitoria</i>	0.0	0.0	0.2
total	25.4	24.9	23.3

3.3 Redbay Inventory

During the 2014 inventory, we found significant differences in the number of dead redbay found at each site with higher numbers of dead stems in the maritime forest (Table 3). In 2014, there were no significant differences in the number of living redbay among the three sites (Table 3, $p = 0.32$). There were no significant differences among the three sites for average DBH, which ranged from 3.1 – 3.8 cm among the three sites (Table 3). The hammock sites experienced the lowest mortality rate.

Table 3. Numbers of living and dead redbay stems (per ha) and diameters of living trees (mean \pm se) from the 2014 transects

Site	Dead stems*	Living Stems	DBH
Maritime	174.4 (17)a	51.0 (4.1)a	3.4 (0.3)a
Old-Field	73.3 (5)b	29.4 (12.9)a	3.1 (0.1)a
Hammock	44.9 (7)b	32.2 (10.5)a	3.8 (0.6)a

*Maritime significantly higher (Tukey's, $p = 0.02$)

3.4 Redbay Leaf Damage and Deer Browse

Close to 100% of living trees showed signs of invertebrate herbivory on foliage among the three sites (Table 4). Only one tree in the maritime forest and one tree in the hammock did not have any signs of herbivory. Damage attributed to the black twig borer ranged from 78 to 89% of trees, and evidence of deer browse among the three

sites was low, ranging from 3 and 12 percent of living trees. Sixty-two to sixty-nine percent of trees within the three sites had leaf herbivory attributed to the Palamedes or spicebush swallowtail caterpillars (Table 4).

Table 4. Percentage of live redbay stems affected by invertebrate herbivory, twig borer damage, the swallowtail caterpillar (Palamedes or Spicebush) or deer browse

Foliar agent	Maritime	Old-field	Hammock
invertebrate	99	100	98
twig borer	89	82	78
swallowtail caterpillar	62	65	69
deer	4	3	12

3.5 Fluorescence

Average readings for the fluorescence measurements were 0.798, 0.804 and 0.809 ($F_v/F_m \pm 0.1$), and there were no significant differences among the three sites ($p = 0.19$). F_v/F_m is the ratio of variable to maximum fluorescence or the quantum efficiency of open photosystem II centers (Maxwell and Johnson, 2000). Trees that are not under stress typically have F_v/F_m values ranging from 0.7 to 0.83 (Ritchie, 2006), indicating that the trees among the three sites were not experiencing environmental stress during our measurement period.

4. Discussion

The maritime site, which originally had the highest redbay density, was never cleared for agriculture and had higher surface soil pH and concentrations of P compared to the other two sites. Potentially, these soil factors favored the development of the higher number of pre-wilt stems. The higher soil pH and P concentrations at the maritime site were likely due to its proximity to shell middens deposited by Native Americans, a practice that started 5000 years before present (Thomas, 2008a). The island's fire history likely affected redbay distribution prior to infection with laurel wilt, and according to the island's superintendent, only one light surface fire had passed through the maritime or old-field site over the past 40 years. Redbay is not well adapted to fire and experiences high mortality following moderate to high severity fires (Van Deelen, 1991).

In 2014, the redbay population on St. Catherines consisted primarily of small diameter sprouts, with very few original or large diameter stems remaining in any of our plots. Across the three sites, 90% of all living stems were <5cm diameter, and we found only one living tree >15cm diameter. The largest snags among the three sites included trees of 77, 38 and 33 cm DBH in the maritime, old-field and hammock sites, respectively. Evans et al. (2013) reported large declines in redbay densities across all diameter classes on the island from 2004-2009, and by 2014, the species, although persisting in the midstory at small diameters, was no longer a component in the canopy among our three sites. Recent studies indicated that the ambrosia beetle can persist in redbay stands that have trees with 2-3cm root collar diameters (Maner et al., 2014), so in future years, it will be interesting to track growth and survival of the remaining stems as they move into larger diameter classes.

The high redbay mortality rates among all three sites were likely exacerbated by rainfall patterns during the height of the infection. As previously mentioned, once a tree has the fungus introduced into its xylem by the ambrosia beetle, the tree defense mechanism involves the disruption of water conduction in the xylem. This defensive reaction, combined with several years of below average rainfall and soil moisture stress, likely contributed to the high mortality rate across the island. In a separate study on one of the island's driest environments (at 6 m elevation) known as the hickory ridge, redbay, which was an important subcanopy species, almost disappeared after 2012 (Smith et al., 2015). We also note that the hammock site, which had the lowest initial mean redbay density and the highest water table, experienced the lowest mortality rate among our three sites. In 2014, when rainfall was at or above mean levels, our fluorescence study indicated that the surviving trees were not physiologically stressed during our sampling period. In addition, during the summer of 2014, no trees in our three site types were showing signs of stress from laurel wilt.

The reduction in redbay densities across the southeastern United States has created concern about the long-term health of the Palamedes swallowtail since redbay is the primary larval host for this butterfly species (Chupp & Battaglia, 2014). Our herbivory data, although qualitative, indicated that in 2014, swallowtail caterpillars and other insects were actively utilizing the remaining redbay as a host plant and food source. In addition, previous studies on the island indicated that redbay regeneration might be in jeopardy due to high deer browse (Evans et

al., 2013), but we found low levels of deer browse on sprouts within our study sites and most sprouts had reached heights above the browse line. Past studies on an adjacent island indicated that redbay fruits and leaves were a minor component of annual browse by whitetail deer (Thomas, 2008b). Although we did find several trees with redbay fruits in 2014, we did not find any redbay seedlings among our sites, so deer browse of trees germinated from seed may be problematic, particularly during dry years when available forage is low.

The reduction of redbay densities in the midstory within another coastal Georgia forest resulted in an open forest, changing the amount of light reaching the forest floor (Speigel & Leege, 2013). On St. Catherines, herbaceous species, grasses, *Sabal palmetto* and vines appear to have filled many of the canopy gaps created by redbay mortality, and the increased light on the forest floor and shift in species may increase fire susceptibility in this forest type, particularly during dry summers.

In conclusion, prior land use history and soils affected redbay densities before laurel wilt infection, but eleven years post-infection, all three site types had similar redbay densities, diameters, basal areas, and levels of herbivory and surviving trees did not demonstrate signs of photosynthetic stress. Despite a large reduction in redbay densities, the species has continued to persist in the midstory and in smaller diameter classes. Drought, changes in fire regimes, and the potential for future laurel wilt infections will likely be stressors on this important species in the future, and it will be important to follow the growth and health of the survivors of the initial and devastating infection.

Acknowledgements

The authors would like to thank anonymous reviewers for making contributions to the paper as well as the St. Catherines Island Foundation for logistical support on the island. Sewanee's Environmental Studies Program and Forestry and Geology Department provided stipends for the student authors on this paper, which enabled them to conduct fieldwork on the island in 2014. Nicole Nunley of Sewanee's Earth and Environmental Systems Department provided valuable GIS and mapping support.

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