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Impacts of Laurel Wilt Disease on Redbay (Persea Borbonia) Population Structure and Forest Communities in the Coastal Plain of Georgia, USA

Kimberly S. Spiegel

IMPACTS OF LAUREL WILT DISEASE ON REDBAY (*PERSEA BORBONIA*) POPULATION STRUCTURE AND FOREST COMMUNITIES IN THE COASTAL PLAIN OF GEORGIA, USA

by

KIMBERLY S. SPIEGEL

(Under the direction of Lissa M. Leege)

ABSTRACT

Laurel wilt disease (LWD), a fungal disease vectored by the non-native redbay ambrosia beetle (*Xyleborus glabratus*), has caused mortality of redbay (*Persea borbonia*) in the Coastal Plain of Georgia, USA, since 2003. This disease has spread 30-100 km/year and little research has evaluated its impacts on redbay population structure and forest communities. Healthy and infested populations of redbay and their associated communities were compared in five sites infested with LWD and three un-infested sites in five counties in Georgia. Tree, shrub, and herb layers were sampled separately to determine redbay population structure and community composition and structure. Only 8% of redbay trees ≥3 cm diameter at breast height (DBH) were alive in infested sites, compared to 80% in control sites. Live redbay trees had 2 times greater average DBH in control sites. Dead tree stems had almost 3 times more stump sprouts per tree in infested sites. Impacts from LWD were found in redbay <1.00 cm diameter at ground height. Photosynthetically active radiation (PAR) was 4.8 times greater at infested sites due to loss of redbay canopy. Shrubs in control sites were taller with larger crowns than those in infested sites relative to stem diameter due to differences in light levels. Redbay trees had the greatest mean importance value (IV) at control sites compared to the 8th mean IV at infested sites for live stems.

Redbay had the greatest mean IV in infested sites when dead stems were included. Two co-dominant species to redbay, sweetbay (*Magnolia virginiana*) and loblolly bay (*Gordonia lasianthus*), ranked 1st and 2nd in mean IV at infested sites but 2nd and 3rd in mean IV at control sites and may be increasing in importance. Increases in herbaceous pioneer species were found in infested sites.

This study shows that LWD has impacted redbay populations and caused changes in associated forest communities in Georgia in 2-4 years post-infestation. Future research may show further shifts in population and community structure and consequent changes to ecosystem processes. Redbay populations may even be at risk of threatened or endangered status if this disease continues to spread throughout redbay's range.

INDEX WORDS: *Persea borbonia*, redbay, laurel wilt disease, *Xyleborus glabratus*, invasive fungal disease, population structure, community composition

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KIMBERLY S. SPIEGEL

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KIMBERLY S. SPIEGEL

Major Professor: Lissa M. Leege
Committee: Risa A. Cohen
John B. Pascarella

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CHAPTER I

Literature Review

Nonindigenous species

For millions of years the movement of the world's biota has been restricted by oceans, mountains, and other natural barriers. Human activity in the last 100 years, especially international travel and trade, has overcome these barriers and allowed species to invade new continents at an increasing rate (Liebhold et al. 1995). Simberloff (1986) noted that patterns of species introductions correspond to intercontinental commerce patterns. Approximately 50,000 nonindigenous (non-native) species have been introduced to the United States, some intentionally and others accidentally (Pimentel et al. 2000). Many of these species are beneficial, such as those introduced as food crops, livestock, or pets and for landscape restoration, biological pest control, and sport (OTA 1993, Pimentel et al. 2000). However, some nonindigenous species have proliferated and spread rapidly outside their range of introduction and become invaders that have caused major environmental damage, economic losses (Pimentel et al. 2000) and loss of biodiversity (Ruesink et al. 1995, Wilcove et al. 1998). An invasive species is defined as a non-native (or alien) species whose introduction causes or is likely to cause economic or environmental harm or harm to human health (Clinton 1999). At least 4,500 of the introduced species in the United States have become invasive (OTA 1993) and cause environmental damages and control costs of approximately $120 billion per year (Pimentel et al. 2005). Invasive species are a major or contributing cause of decline of 49 percent of all species identified as imperiled by The Nature Conservancy and federal agencies (Wilcove et al. 1998). Considering the detriment to

biodiversity and the high cost of control of invasive species, there is a vital need for continuous study and efforts to control them.

Only a fraction of introduced species survive and become established enough to be invasive. The rule of tens states that 10% of all introduced species will appear in the wild, 10% of those will become established, and 10% of those will become invasive (Williamson and Fitter 1996). Many hypotheses have been proposed as to what make a species successful at invasion. One is the natural enemies hypothesis, first proposed by Darwin (1859), which explains that release from natural enemies, such as herbivores or pathogens, or competitors found in its native range enables non-native species to become abundant. Escape from biotic constraints can lead to greater growth, longevity, and fitness for immigrant species (Mack et al. 2000). A second popular hypothesis is that ecosystem disturbance before or upon immigration of an invasive species leads to its success. This idea proposes that native species are not able to adapt to sudden environmental disturbances, opening up niches for non-native species to occupy (Mack et al. 2000). No single, simple, general theory explains invasions, however, because so many factors control the success or failure of invasive species (Stachowicz and Tilman 2005).

Invasive forest insects, pathogens, and disturbance

Two particularly detrimental groups of invasive organisms are invasive forest insects and pathogens. More than 2,000 alien insects are now established in the continental United States (OTA 1993, Pimentel et al. 2000); most are accidental introductions of international trade (Haack 2001). Over 360 alien insect species are known to attack woody plants in the US and Canada (Mattson et al. 1994). Many of these introduced insects have become serious forest pests and have caused widespread forest disturbance or destruction such as the hemlock woolly adelgid (*Adelges tsugae* Annand) which kills eastern hemlock (*Tsuga canadensis* (L.) Carrière), the beech

scale insect (*Cryptococcus fagisuga* Lind.), and the European elm bark beetle (*Scolytus multistriatus* Marsham) (Cox 1999). In addition to invasive insects, there are over 20 alien diseases that are known to attack woody plants in the US and Canada that have also caused major forest destruction and disturbance (Haack and Byler 1993). Some invasive fungal diseases are facilitated or introduced by an invasive insect such as beech bark disease facilitated by the beech scale insect which kills American beech (*Fagus grandifolia* Ehrh.) and Dutch elm disease introduced by the European elm bark beetle which kills American elm (*Ulmus americana* L.) (Cox 1999).

Pickett and White (1985, p. 7) define a disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." It is widely known that disturbance can facilitate invasions (di Castri 1989, Hobbs and Huenneke 1992, D'Antonio et al. 1999). However, invaders themselves can cause changes in disturbance regimes that alter community composition, and they can create entirely new disturbances and further change the ecosystem (Mack and D'Antonio 1998). For example, the near elimination of American chestnut by the chestnut blight fungus contributed to the increased dominance of oaks in northeastern North America (Liebhold et al. 1995). The transition to large expanses of forest dominated by oaks (that now exists) is also a result of reforestation of areas cleared over 100 years ago by humans (Smith 1976). These disturbances created oak dominated forests not natural to the US and are one of the reasons the gypsy moth (*Lymantria dispar* L.) has been such a successful invader in North America (Liebhold et al. 1995), since its preferred food is oak (Barbosa and Schaefer 1997).

Biological disturbances such as those due to exotic pathogens and insects can result in selective loss and replacement of a tree species (Castello et al. 1995). By selectively affecting

tree growth and mortality rates, insects and pathogens cause significant changes to ecosystem composition and processes (Castello et al. 1995, Liebhold et al. 1995). Exotic insects and pathogens can produce short- term (weeks to years after attack) and long-term (decades or centuries after attack) disturbance effects on forest ecosystems (Lovett et al. 2006). The short-term disturbance effects on individuals are tree defoliation, loss of vigor, or death (Lovett et al. 2006). Short-term effects may also be seen at the ecosystem level, and may include temporary reduction in photosynthesis and productivity, increased circulation or nutrient leaching, stimulation of decomposition and changes in microclimatic and light conditions in the forest (Webb et al. 1995, Jenkins et al. 1999, Lovett et al. 2002). Long-term disturbance effects on forests are changes in tree species composition, which then affect ecosystem characteristics such as forest structure, productivity, nutrient cycling, soil organic matter production and turnover, hydrology, and the food web (Lovett et al. 2006). Alterations in ecosystem characteristics can feedback to affect the pests (e.g., increased nitrogen availability can increase the survival of phytophagous insects), the trees (e.g., increased light availability from tree death may improve conditions for survivors), or the forest composition (e.g., increased light, water, and nutrients may change the relative competitiveness of different tree species) (Lovett et al. 2006). Some specific examples of invasive pests and pathogens will elucidate how invaders have caused disturbances in forest ecosystems in North America.

Cryphonectria parasitica*, chestnut blight fungus*

One of the best known examples of invasive pathogens in the United States is the chestnut blight fungus (*Cryphonectria parasitica* (Murr.) Barr) which is responsible for the eradication of the American chestnut (*Castanea dentata* (Marsh.) Borkh.). American chestnut once comprised 25% of the eastern hardwood forests in the United States, or 200 million acres of land (Kuhlman

1978) and until its demise it was one of the most important timber trees of eastern forests (Cox 1999). The fungus probably entered North America prior to 1904 on Chinese or Japanese chestnut trees introduced as urban ornamentals (Cox 1999). Chestnut blight spread at a rate of 40 km/year and within 40 years had spread throughout the entire range of the American chestnut in eastern North America (Kuhlman 1978). The fungus invades the bark and spreads through the xylem and phloem tissues, which creates cankers that eventually girdle and kill the tree (Cox 1999). The fungal spores are spread to chestnut hosts by wind and rain and can also reproduce on dead substrates (Liebhold et al. 1995).

The size structure of American chestnut has been severely altered. All large stems have been killed but chestnut roots are not killed by the fungus and they sprout clonal shoots (Cox 1999). However, the sprouts become re-infected by the fungus and die back so sexual reproduction is rare (Stephenson et al. 1991). This cycle continues to repeat so that an understory, or "shrub" stage of chestnut now exists (Paillet 1984).

The rapid disappearance of the American chestnut led to major changes in the composition of forests of the eastern United States. Studies of forest composition after chestnut blight spread through the U.S. showed oaks and maples replaced chestnut (Augenbaugh 1935, Woods and Shanks 1959, Stephenson 1974) and shifts from oak-chestnut to oak-hickory forests (Keever 1953, McCormick and Platt 1980).

Little data are available on how the loss of chestnut has affected ecosystem processes but many speculations have been made. Since it once dominated a wide range of habitats, its decline is thought to have altered both terrestrial and aquatic processes (Ellison et al. 2005). Chestnut wood has a high tannin content and leaves have a relatively low C:N ratio, therefore its decline probably altered forest ecosystem processes such as decomposition, nutrient cycling and

productivity (Ellison et al. 2005). Chestnut wood decomposes slower than other co-occurring species and its high tannin concentration could have restricted the mobilization of nutrients in soils (Ellison et al. 2005). Because chestnut wood decomposes slowly, when present in stream channels it provides long term habitat for aquatic organisms (Ellison et al. 2005). For example, Wallace et al. (2001) showed that 24% of large woody debris (>10 cm in diameter) in an Appalachian headwater stream was wood from American chestnut that had died 50 years prior. Chestnut also has a fast growth rate (Jacobs and Severeid 2004) which might have resulted in rapid sequestration of carbon and nutrients (Ellison et al. 2005). Chestnut leaves rapidly decay and have a high nutritional quality which could have been important for aquatic shredding macroinvertebrates, whose life cycles are closely associated with the dynamics of decaying detritus (Ellison et al. 2005). Replacement by other species such as oak with more slowly decaying leaves and lower nutritional quality would decrease leaf-processing and consumption rates in shredding macroinvertebrates, thus lowering their adult body mass and growth rates (Smock and MacGregor 1988).

Evidence from the southern Appalachians suggests the abundance of chestnut in riparian corridors was due to production of allelopathic chemicals that prevented establishment of the present riparian shrub and tree composition, including eastern hemlock and rhododendron (Vandermast et al. 2002). Ironically, the loss of American chestnut may have facilitated the establishment of another species, eastern hemlock, which is now threatened by an invasive organism.

Adelges tsugae*, hemlock woolly adelgid*

The hemlock woolly adelgid (HWA) has been a cause of large scale destruction of hemlock trees in the US. It is a sap-feeder and inserts its sucking mouthparts into the vascular

tissue to feed on the phloem fluid of the tree (Watson 1992). Heavy infestations drain the tree of its vital nutrients, and damage to the tree or death occurs as a result of stress (Watson 1992). Main tree limbs often die within a year of infestation and whole trees die within 4-10 years (McClure 1991). Adelgid eggs, nymphs, and wingless adults are dispersed by wind, birds and mammals on their feathers or fur, but winged adults also exist and can disperse on their own (McClure 1990). The HWA is native to eastern Asia and invaded the Pacific Northwest in the 1920s, beginning its invasion on western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and by 1953 it had spread to eastern North America attacking eastern hemlock (*Tsuga canadensis* (L.) Carrière) and Carolina hemlock (*Tsuga caroliniana* Engelm.) (Cox 1999). Its rate of spread is between 12.5 km/year and 20.8 km/year, depending on various factors (Evans and Gregoire 2007). It has caused up to 95% of eastern hemlock mortality in some forests (Orwig and Foster 1998).

Many changes to forest ecosystems have been noted as a result of HWA infestations and the decline of eastern hemlock. Severe hemlock mortality decreased basal area and increased canopy gaps (Orwig and Foster 1998, Jenkins et al. 1999, Small et al. 2005). In canopy gaps, the microclimate of the forest floor changed dramatically, with greater levels of light (Orwig and Foster 1998, Jenkins et al. 1999, Eschtruth et al. 2006), increased temperatures (Jenkins et al. 1999) and changes in moisture content (Cobb and Orwig 2002, Small et al. 2005, Orwig et al. 2008). Consequently, increases in density of clonal saplings, herb richness and abundance, vegetation cover, and several invasive shrubs and woody vines were found (Orwig and Foster 1998, Jenkins et al. 1999, Small et al. 2005, Eschruth et al. 2006). As a result of severe hemlock mortality, forest composition shifts from coniferous forest to oak and mixed hardwood forests have been observed (Jenkins et al. 1999, Orwig et al. 2002, Small et al. 2005, Stadler et al. 2005).

Shifts from coniferous to deciduous forests alter understory microclimates and change the leaf litter from slowly decomposing coniferous needles to more rapidly decaying deciduous litter (Small et al. 2005). Several studies showed increased litterfall, soil organic matter, inorganic nitrogen availability and nitrification rates with hemlock mortality (Jenkins et al. 1999, Orwig et al. 2008) which may potentially increase nitrogen to forest streams (Cobb and Orwig 2002, Orwig et al. 2008). Regenerating stands after HWA infestation had increased decomposition, which could decrease nutrient availability in forests and affect stream water quality (Jenkins et al. 1999, Yorks et al. 2003).

Results by Daley et al. (2007) showed greater evapotranspiration rates of a replacement species, black birch (*Betula lenta* L.), than eastern hemlock which suggests alterations in the annual water balance. Another study showed forest water use would decrease immediately after hemlock mortality, but replacement by deciduous species would increase water use (Hadley et al. 2008). Ford and Vose (2007) found hemlock mortality decreased transpiration resulting in increases in discharge from forest streams.

Hemlock often grows on moist stream banks and loss of hemlock may remove shade and increase stream temperature, algal growth, and bank erosion, which could affect fish, salamanders and other animals (Brooks 2001, Ellison et al. 2005). Hemlock forests are important habitats for many bird species and hemlock mortality resulted in a decline of populations of black-throated green warbler (*Dendroica virens*) (Tingley et al. 2002).

Cryptococcus fagisuga, ***beech scale insect and beech bark disease***

The beech scale *(Cryptococcus fagisuga* Lind.) causes beech bark disease on American beech (*Fagus grandifolia* Ehrh.) via various *Nectria* fungi which causes significant mortality and damages to beech trees in eastern North America (Houston and O'Brien 1983). Beech bark

disease occurs when the beech scale insect damages the tree by making minute feeding wounds in the bark, making a hospitable environment for *Nectria* fungi to then infest the tree (Houston and O'Brien 1983). The beech scale insect was accidentally brought to Nova Scotia from Europe in 1890 on ornamental European beech (*Fagus sylvatica* L.) for the Halifax Public Gardens (Houston 1994). The disease is now found as far south as Tennessee and North Carolina and as far west as Wisconsin (Wisconsin DNR 2009). Morin et al. (2007) estimated the rate of spread as 14.7 km/year. The first instars of the beech scale are transported by air currents (Wainhouse 1980) and it is possible that migratory birds transport nymphs (Houston 1994). The *Nectria* fungal spores are also wind dispersed (McCullough et al. 2005). According to Houston (1994) often more than 50% of the beech trees ≥ 25 cm in diameter are killed and many more are severely damaged. Such losses can be significant. For example, as of 1977 the estimated loss in merchantable timber volume attributed to beech bark disease in Vermont was nearly 300 million board feet (including trees dead, dying, or damaged beyond use) (Houston 1994).

Beech bark disease causes a slow death of beech, which can take 10 years or more, and leads to "gradual gaps" in the forest (Lovett et al. 2006). These gaps are filled in by lateral growth of neighboring trees or by growth of understory saplings (Lovett et al. 2006). Death of mature beech stems is often followed by sprouting from roots, which increases density of small stems, but the disease also infects these stems as they mature (Houston 1994, Latty 2001, Forrester et al. 2003, Van Leaven and Evans 2005). The main effect of beech bark disease is a shift in size and age structure of beech populations rather than shifts in tree composition (Lovett et al. 2006). But some studies have shown beech decline increases numbers of competing species (Twery and Patterson 1984, Runkle 1990, DiGregio et al. 1999, Griffin 2005). McNulty and Masters (2005) found an increase in species richness and abundance of shrub layer species in

forests affected by beech bark disease. Shifts in species composition are likely to affect nutrient cycling in beech bark affected forests. Beech is an important species in northern hardwood forests and dominates many stands in terms of basal area, density, and leaf litter (Lovett et al. 2006). Beech leaves are high in lignin and are slower to decompose than hardwood co-dominants such as sugar maple (Lovett et al. 2006). Replacement of beech by sugar maple (*Acer saccharum* Marsh.) would result in lower forest floor mass (Finzi et al. 1998), increased nitrification and increased nitrate leaching into streams (Lovett and Mitchell 2004).

Beech produces a nut that is an important food source for wildlife including rodents, birds, and bears (Faison and Houston 2004). Shifts of beech to smaller size structure will result in decreased nut production and could reverberate through the food web (Lovett et al. 2006). Reduced beech nut production could directly affect bears which use beech nut as an important food source before hibernation (Faison and Houston 2004).

Scolytus multistriatus, ***European elm bark beetle and Dutch elm disease***

Another example of an invasive insect that has caused large scale disturbance in North America is the introduced European elm bark beetle (*Scolytus multistriatus* Marsham). This beetle is the vector of an *Ophiostoma* fungus that causes Dutch elm disease in elm species (*Ulmus* spp.), most severely in American elm (*Ulmus americana* L.) (Sutherland et al. 1997, Paine 2006). Dutch elm disease was first observed in the U.S. in 1931 on trees in Cleveland and Cincinnati, Ohio (Campanella 2003). Then in 1933 trees infested with Dutch elm disease were found in New Jersey and New York (Campanella 2003). In 1933 the fungus was detected on logs imported for making furniture and the following year, dish crates made of elm were found harboring the bark beetles (Campanella 2003). The beetles feed on sapwood of elm and the fungal spores are passed into the tree's vascular tissues (Campanella 2003). The fungal spores produce protrusions in the

vascular tissues which block the flow of water and nutrients and the tree dies in a few months (Campanella 2003). The beetles are capable of flying 4.8 km and can be dispersed even further by wind currents (Campanella 2003). American elm was a common tree in eastern hardwood forests and was extensively used as an ornamental tree in urban areas in the eastern U.S. (Sinclair and Campana 1978). The value of trees lost due to this disease is estimated at several billion dollars (Sinclair and Campana 1978).

Density and basal area of larger elms were substantially reduced from Dutch elm disease, but increases in density of smaller size classes were seen (Root et al. 1971, Johnson and Bell 1975, Grittinger 1978, Parker and Leopold 1983). Forest composition shifted where elms became absent, and other trees of their moist bottomland habitats increased in abundance (Boggess and Bailey 1964, Root et al. 1971, Grittinger 1978, Cox 1999). McBride (1973) found more individuals and more species under dead elm canopies, which suggested variable light and soil moisture in canopy gaps likely led to increases in both tolerant and intolerant species. McBride (1973) also proposed these increases could be from seed-eating birds using dead elms to roost in, as the types of species found were bird dispersed. In some forests, regeneration in the understory was dominated by shrub species, which could increase the food supply for seed- and fruit-eating herbivores and inhibit tree regeneration (McBride 1973, Huenneke 1973). The seeds of elm are consumed by many species of birds and small mammals and their decline could mean a loss of food for wildlife (Waldron 2003). Death of elm could decrease nesting sites for birds in the U.S. as they have in other elms affected by Dutch elm disease in the United Kingdom (Osbourne 1985). American elm leaves decompose more rapidly than some of its associated species and have high concentrations of postassium and calcium. Therefore, their removal from forests could affect nutrient cycling (Bey 1990).

Xyleborus glabratus *and laurel wilt disease*

Beetles, order Coleoptera, are the most commonly intercepted order of insects associated with wood packing materials, accounting for 92% of all insect introductions on wood articles in the United States (Haack 2001, Haack 2006). Of the introduced Coleoptera, 58% belong to the family Scolytidae, the bark and ambrosia beetles (Haack 2001). In the United States, an estimated 90% of all tree mortality is caused by insects and more than 60% of the total is caused by members of the Scolytidae (Anderson 1960). The recently introduced redbay ambrosia beetle (*Xyleborus glabratus* Eichoff) is the vector of a fungus (*Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva) that causes laurel wilt disease in woody members of the plant family Lauraceae (Fraedrich et al. 2008, Harrington et al. 2008). It was named after the tree it was first found using as its host in the United States, redbay (*Persea borbonia* (L.) A. Sprengel).

Ambrosia beetles do not consume wood, but create galleries in trunks or stems of the host in which they culture a symbiotic fungus as a food source (Kuhnholz et al. 2001). The fungi are carried in specialized structures (mycangia) found at the base of each mandible (Fraedrich et al. 2008) and both the adults and larvae feed on the spores (Wood and Bright 1992). The genus *Xyleborus* is diverse with over 500 species and can be found on every continent except Antarctica (Rabaglia 2003). In general, members of this genus have a wide host range (Rabaglia et al. 2006). Males are haploid and wingless but the winged females seek out new hosts and establish galleries (Wood and Bright 1992).

The redbay ambrosia beetle is native to Asia and has been recorded from India, Bangladesh, Japan, Myanmar, and Taiwan (Wood and Bright 1992). Its host species in its native range include the following members of Lauraceae: Asian spicebush (*Lindera latifolia* Hook. f.), yellow litsea (*Litsea elongata* (Nees) Benth. et Hook. f.) (Wood and Bright 1992), and *Phoebe*

lanceolata (Wall. ex Nees) Nees in India (Maiti and Saha 2004). It is also known to use the following as hosts: one member of the Fagaceae, Japanese stone oak (*Lithocarpus edulis* (Makino) Nakai), in Japan (Murayama 1936), one member of Fabaceae, white popinac (*Leucaena glauca* (L.) Benth) (Nobuchi and Ono 1973), and a member of Dipterocarpaceae, sal tree (*Shorea robusta* C. F.) (Wood and Bright 1992).

The redbay ambrosia beetle was first discovered in the United States in a funnel trap at Port Wentworth, Georgia in 2002 (Rabaglia et al. 2006) and it was most likely introduced via international transport of wood products containing beetles (Rabaglia 2003). The redbay ambrosia beetle vector has since spread laurel wilt disease into more than 60 counties in the Coastal Plain of South Carolina, Florida, and most recently into Mississippi as of August 2009 (Figure 1.1a). It has steadily expanded its range since its introduction at a calculated rate of 55 km/year based on 2004-2006 data (Koch and Smith 2008). Rates of spread are due to natural beetle dispersal and possible movement of infested wood by humans. *Xyleborus glabratus* found in Indian River County, FL in 2006, >200 km from the closest other county known to be infested at that time (Koch and Smith 2008), suggests anthropogenic introductions.

Flight activity of *X. glabratus* populations were tracked from March 2006 to September 2007 on Hunting Island State Park, South Carolina by Hanula et al. (2008). The number of beetles trapped and density of beetle entrance holes increased with increasing density of redbay (Hanula et al. 2008). The flight activity of beetles increased from spring to summer and peaked in September and declined to 0 in winter (Hanula et al. 2008). No distinct generations were found, which could suggest a single generation per year or multiple overlapping generations (Hanula et al. 2008). It took ~8 weeks for eggs to develop to adults in spring (Hanula et al. 2008). The first male was captured on June 3rd, and few beetles were captured from March through May, which

suggests they most likely do not overwinter in all life stages (Hanula et al. 2008). Boring dust was also first noted on June 3rd until September, when beetles stopped attacking trees (Hanula et al. 2008). Host material may no longer have been attractive at this point, or beetles had dispersed (Hanula et al. 2008), or possibly went into dormancy. Redbay wood remained attractive for at least 68 days after wounding, suggesting redbay's aromatic compounds attract beetles for several months (Hanula et al. 2008). Several beetles were even found on Hilton Head Island, South Carolina, in late stages of infestation at the time of Hanula et al.'s study (2008). If beetles remain present, redbay sprouts will eventually become infested.

Most species of ambrosia beetles restrict their breeding activity to one or a few host plant species (Wood 1982). Most live only in recently cut or injured wood or wood that is in the process of dying (Wood 1982), but a few attack healthy living tissue that causes tree mortality (Wood 1982). Members of the genus *Xyleborus* attack weak, dead, or dying host trees and there is no evidence of *X. glabratus* as an important pest in its native range (Wood and Bright 1992, Rabaglia 2003). In its introduced range it causes mortality of healthy redbay trees within a matter of weeks to a few months (Mayfield 2008) and it only takes one redbay ambrosia beetle to inoculate and kill a tree (Fraedrich 2010). Sassafras (*Sassafras albidum* (Nutt.) Nees) affected with laurel wilt disease has been found in four locations in Georgia (Fraedrich et al. 2008) and the fungus has been isolated from wilted pondspice (*Litsea aestivalis* (L.) Fern) at a location in South Carolina and one in Georgia (Fraedrich et al. 2008). Pondspice is state-threatened species in Georgia and state-endangered in Florida and Maryland (USDA Plants Database 2010). The fungus was also isolated from wilted pondberry (*Lindera melissifolia* (Walt.) Blume), a federally endangered species, at a site in Georgia (Fraedrich et al. 2008). Significant concern exists that laurel wilt disease could negatively impact the commercial avocado (*Persea americana* Mill.)

industry in Florida (Mayfield et al. 2008). Laurel wilt was found in an avocado tree in a residential neighborhood in Jacksonville, FL in 2007 (Mayfield et al. 2008). In pathogenicity tests, spicebush (*Lindera benzoin* (L.) Blume), cultivated avocado, and swampbay (*Persea palustris* Raf. (Sarg.) were found to succumb to the ambrosia fungus (Fraedrich et al. 2008). Fraedrich (2008) also found California laurel (*Umbellaria californica* (Hook. & Arn.) Nutt.) was susceptible to laurel wilt. Fraedrich et al. (2008) found two other species of exotic ambrosia beetles, the Asian ambrosia beetle (*Xylosandrus crassiusculus* Motschulsky) and the black twig borer (*Xylosandrus compactus* Eichoff), in the stems and twigs of dead and dying redbay trees. This could possibly be a case of "invasional meltdown," in which invasion by one exotic species facilitates invasion by additional exotic species (Simberloff and Von Holle 1999).

Laurel wilt is a vascular disease that in redbay is characterized by wilting leaves that turn brown and often persist on branches for more than a year after the tree dies (Fraedrich et al. 2008). A dark black staining of sapwood also occurs as the fungus spreads through the vascular tissues (Fraedrich et al. 2008). Redbay seedlings are less affected and attacked less frequently by the beetle than saplings or mature trees, and sprouting occurs at some stumps of dead primary redbay trunks (Fraedrich et al. 2008). In experimental inoculations of the LWD fungus all seedlings of spicebush, sassafras, redbay and swampbay died within 5 weeks after inoculation Fraedrich et al. (2008).

Objectives

Laurel wilt disease is a newly emerged disease with a rapid rate of spread which has resulted in redbay mortality in the southeastern U.S. No research has yet been published on the effects of laurel wilt disease on population structure of redbay or on its associated plant communities. Following the pattern of other fungal diseases in the U.S., laurel wilt disease is

likely to alter redbay structure and forest composition, with subsequent ecosystem level effects. The goals of this research were to determine the changes in redbay population structure and the changes in forest communities that might occur as a result of redbay mortality. The specific objectives of this study were: 1) to compare the size structure of redbay populations in infested and uninfested sites; 2) to examine the effects of redbay mortality on forest composition and community structure; and 3) to examine the effects of redbay mortality on abiotic factors such as light level (canopy cover) and litter depth.

CHAPTER 2

Redbay Population Structure

Introduction

Invasive fungal diseases have had a severe impact on the population structure of several tree species in the United States, such as American elm (*Ulmus americana* L.), American beech (*Fagus grandifolia* Ehrh.), and American chestnut (*Castanea dentata* (Marsh.) Borkh.). American chestnut has been practically eliminated from eastern forests as a result of the chestnut blight, leaving gaps in communities for other species to fill, and thus, shifting community composition (Korstian and Stickel 1927, Keever 1953). However, in some former chestnut stands, individual stems still exist as root sprouts. These survive until fissures develop in the bark, but they eventually die back to the ground (Parker et al. 2003). New sprouts arise nearby and the cycle repeats, which can go on for decades (Parker et al. 2003). Because of the chestnut blight, chestnuts rarely grow mature enough to fruit and flower (Parker et al. 2003). Many young elms survive long enough to reproduce before being killed by the pathogen, unlike chestnut (Castello et al. 1995), but significant mortality has occurred. American beech still persists following Dutch elm disease and beech scale invasion because of natural resistance (Wainhouse and Deeble 1980). Although elm and beech have not been completely eliminated like chestnut, their populations have shifted in structure from larger individuals to a predominance of sprouts and smaller individuals in greater densities (Barnes 1976, Karnosky 1979, Forrester et al. 2003, Van Leaven and Evans 2005).

Laurel wilt disease (LWD), caused by the fungus *Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva, is a recently introduced disease in the southeastern US which has drastically altered populations of redbay (*Persea borbonia* (L.) A. Sprengel). The vector of laurel wilt disease is the

introduced redbay ambrosia beetle (*Xyleborus glabratus* Eichoff), which was first trapped in Port Wentworth, Georgia in 2002 (Figure 1.1a) as part of the USDA Forest Service Early Detection and Rapid Response Pilot Project (USDA Forest Service 2010). Redbay mortality was first observed in 2003 in the lower Coastal Plain of South Carolina and locations around Savannah, GA (Fraedrich et al. 2008) and on barrier islands off the Georgia coast (Cameron et al. 2008). Initial reports on the cause of mortality were drought related, but no substantial evidence to support this was found (Fraedrich et al. 2008). In 2004, a team of members from the USDA Forest Service, South Carolina Forestry Commission, Georgia Forestry Commission, Florida Division of Forestry, and other agencies and organizations worked together to uncover the cause of redbay mortality (USDA Forest Service 2010). In November 2004, on Hilton Head Island, SC, redbay trees with wilt symptoms were observed with streaks of black discolored sapwood, from which a fungus was consistently isolated (Fraedrich et al. 2008). Also found in the affected redbay were several species of ambrosia beetles, two of which are native to the US (Fraedrich et al. 2008). A third species was the introduced *X. glabratus*, which was determined to be the vector of the laurel wilt disease fungus (Fraedrich et al. 2008).

Large redbay trees and shrubs have succumbed to the effects of laurel wilt disease in the Coastal Plain of Georgia and significant mortality has occurred (Fraedrich et al. 2008, Cameron et al. 2008). Sprouting from roots of dead stems frequently occurs in redbay (Fraedrich et al. 2008) as in American chestnut. Canopy loss from redbay mortality may have a significant impact on regeneration of redbay in the understory (personal observation). No research has been published on the effects of laurel wilt disease on population structure of redbay. Therefore, an examination of differences of redbay size structure in infested and control sites may aid in determination of such changes. The objectives of this study were to: 1) determine the abundance, density, and size

structure of redbay populations in infested and control sites; 2) determine the relationship of redbay shrub diameter to height and crown area to see if differences in growth patterns exist in infested and control sites; 3) compare redbay regeneration by stump sprouts in infested and control sites; and 4) determine redbay canopy and basal area loss due to LWD in infested sites.

Methods

Study Species

Redbay (*Persea borbonia* (L.) A. Sprengel) is an aromatic evergreen tree native to the Atlantic and Gulf Coastal Plain forests of the southeastern U.S. (Brendemuehl 1990; Figure 1.1b). It is also found in the Bahamas (Duncan and Duncan 1988). Some taxonomists recognize a second species of *Persea*, swampbay (*P. palustris* (Raf) Sarg.) (Sargent 1922, Duncan and Duncan 1988) or consider it to be a variety of redbay *(P. borbonia* var. *pubescens* (Pursh) Little) (Coker and Totten 1945, Little 1979). A third species of *Persea*, silk bay, is found in Florida (*P. humilis*) (Wofford 1997). In the research presented here, I followed the same protocol as the Georgia Forestry Commission and USDA Forest Service and did not attempt to differentiate between species or varieties, and referred to redbay as *P. borbonia sensu lato* (Cameron et al. 2008, Fraedrich et al. 2008).

Redbay thrives in a variety of conditions ranging from wet to well-drained (Coder 2007). It can be found in hammocks, mixed hardwoods, low pinewoods, coastal dunes, maritime forests (Wofford 1997) and evergreen hardwood forests known as bayheads or bay swamps where fresh water flows out of a spring or seep (Coder 2007). Redbay is tolerant of shade but is also found growing well in open sunlight, in both young and old forest stands (Brendemuehl 1990). Coastal forests of Georgia and South Carolina support an average density of 200-400 redbay trees (2.5 cm or larger) per hectare (Hanula et al. 2008).

Most redbay are midstory trees or understory shrubs, but mature redbay trees can grow 18-21 m in height with diameters of 60-90 cm (Harrar and Harrar 1946). Leaves are aromatic, leathery, alternate, simple, entire, elliptic to oblong, 5-20 cm long, dark green and glabrous above, and pubescent below (Brown and Kirkman 1990). Twigs are light brown, smooth to slightly pubescent, and the terminal winter buds are naked, densely hairy, and about 6 mm long (Brown and Kirkman 1990). Redbay bark is grayish to reddish brown, with deep irregular fissures that turn into scaly ridges on older trees (Brown and Kirkman 1990).

Redbay flowers are perfect, yellow, about 6 cm long, found in axillary panicles and appear May through June (Brown and Kirkman 1990). They are primarily pollinated by insects, mostly by bees, but may also be wind pollinated (Bremdemuehl 1990). The fruit is a small dark blue drupe about 13 mm long that matures in the fall from September to October (Brown and Kirkman 1990). Fruit are produced annually and are eaten and seeds are dispersed by songbirds, white-tailed deer, bobwhite, wild turkey, and black bear (Brendemuehl 1990). Redbay fruit were in 15th place in a list of 63 food items in order of volumetric importance to wildlife (Goodrum 1977). The leaves are eaten by deer and black bear (Goodrum 1977). Redbay and other varieties of *Persea* and sassafras are the primary food plants of the Palamedes swallowtail (*Papilio palamedes* Drury) caterpillar (Minno et al. 2005).

Study Sites

For this research, eight sites were sampled in the Coastal Plain of Georgia; five sites where laurel wilt disease was present (hereafter infested) and three sites where it had not yet invaded (hereafter control) (Figures 2.1 and 2.2). Sites were located in wet areas in bayheads (3) or mixed hardwood forests (4) and Carolina Bays (1). Bayheads are evergreen hardwood swamps composed primarily of loblolly bay (*Gordonia lasianthus* (L.) Ellis), sweetbay (*Magnolia virginiana* L.), and redbay (Davis 1943). The hardwood forests varied in their composition from

one site to the next and included previously mentioned evergreen species, various deciduous species such as sweet gum (*Liquidambar styraciflua* L.), tulip poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), oaks (*Quercus* spp.), *Nyssa* spp. and pines. Carolina bays are elliptical shaped, isolated shallow depressions largely fed by rain and shallow groundwater found in the coastal plain (SREL 2007). Typical woody plants in a Carolina Bay are black gum (*Nyssa sylvatica* Marsh.), sweet gum, sweetbay, bald cypress (*Taxodium distichum* (L.) Rich.), red maple, gallberry (*Ilex coriacea* (Pursh) Chapm.), and redbay (SREL 2007). See Table 2.1 for study site information. The sites sampled were in different habitat types and had different community compositions, but attempts were made to standardize them as much as possible. All sites had a slope of 0-2% and soils that were poorly or very poorly drained (Table 2.2) with redbay as a dominant or co-dominant canopy species.

Only 3 control sites were selected instead of 5 because there was less variability in redbay population structure in control sites, whereas the infested sites were in various stages of decline and thus the population structure was more varied. Also, there was a limited availability of comparable infested and control sites as LWD is advancing westward into the upper coastal plain. All infested sites were in the lower coastal plain, but one control site (C2) was in the upper coastal plain.

Experimental Design

Four to seven transects at least 10 m apart were run through each study location, with points along the transects randomly selected for plot location (Figure 2.3a). Site C3 did not have transects because the area to sample was too small, but instead a compass was used to line up plots roughly parallel to the highway in a triangular section of forest. The number of plots sampled was determined by the use of species area curves for tree, shrub, and herb layers

separately. The point at which there was no increase in the number of species in the sample was determined as a sufficient sample size. The length of transects also varied based on the size and shape of the forest area containing redbay (Figure 2.3a).

A 10x10 m plot was set up to measure redbay at the tree layer at each random point selected along the transect, for a total of 8-10 plots per site (Figure 2.3a). The 10x10 m plot was sectioned into 25 2x2 m subplots, and 4 or 5 were randomly selected to sample the redbay shrub layer (Figure 2.3b) depending on species area curves. Within each of the 2x2 m subplots, a nested 1x1 m plot was set up to sample redbay seedlings at the herb layer (Figure 2.3b).

Redbay Measurements

Measurements of redbay population and size structure were conducted once per site and took place May-September 2008 and May-October 2009.

Tree layer: The diameter at breast height (DBH, 1.3 m above ground surface), diameter at ground height (DGH), number of live and dead stump sprouts, and tree status (live or dead primary stem) were recorded for all redbay trees ≥3 cm DBH at the 10x10 m plots in control and infested sites. It was not always possible to obtain a DBH measurement if the tree was topped (12 trees) or to obtain a DGH if the tree was too rotted (7 trees). DBH was obtained for fallen trees by measuring them on the ground 1.3 m from ground level, including the stump. Primary redbay stems were defined as the largest stem of an individual tree, excluding stump sprouts. Dead stems were identified to species either by the presence of stump sprouts, wilted leaves, or by its characteristic bark texture: grayish to reddish brown, with deep irregular fissures that turn into scaly ridges on older trees. Stump sprouts were defined as such by their close proximity to a larger diameter redbay, and were attached to the base of it or to its root system. Tree height was measured for all intact trees (both live and dead) using a clinometer, and standing at least 10 m away from the base

of the tree. Crown area was measured for all live redbay trees ≥3 cm DBH at control sites. Crown area was determined by measuring the width of the crown at its widest part (W_1), then measuring a second width of the crown perpendicular to the first (W_2). Crown width was estimated along the ground by lining up a pin flag directly below the edge of a tree on either end of the widest part, and the distance between flags was measured along two perpendicular axes. These values were used in the formula for the area of an ellipse:

$$\text{Crown Area} = \pi(W_1/2)(W_2/2)$$

Basal area was also determined for all trees ≥10 cm DBH in the control plots using the formula:

$$\text{Basal Area} = \pi(\text{DBH}/2)^2$$

Shrub Layer: The height and DGH of all live and dead redbay stems including shrubs, saplings, and tree stump/root sprouts <3 cm DBH and taller than 50 cm were measured. Stem diameters were taken with a digital caliper. Any presence of laurel wilt was noted.

Herb Layer: The height and stem diameter of all redbay <50 cm tall were measured at the herb layer.

A survey conducted by the Georgia Forestry Commission showed that in infested areas large redbay trees were found dead, but trees from 2.5 to 10 cm DBH were observed alive (Cameron et al. 2008). To determine redbay mortality by stem size for this study, all redbay measured were sorted into size classes based on DGH for comparison between control and infested sites. The larger individuals (>5 cm DGH) were categorized into broader scale size classes because they were more noticeably affected by LWD. Smaller individuals (<5 cm DGH) were categorized into finer scale size classes because they were less noticeably affected by LWD. The finer scale size classes aided in determination of the size at which redbay began to succumb to the disease. Note that Georgia Forestry Commission used DBH because they only observed

trees and I used DGH for analyses because I measured individuals at all life stages from seedlings to trees. The mean proportion live redbay by size class were compared in two ways. For one analysis, live redbay and redbay with symptoms of LWD (not yet dead) were combined to determine mean proportion live redbay by size class. For a separate analysis, only live redbay not symptomatic of LWD were used to determine mean proportion live redbay by size class. Considering that the majority of redbay observed with LWD symptoms eventually die and no resistant trees have yet been found (personal observation), calculations with live, healthy redbay only most accurately depicted the proportion of live redbay. Stump sprouts were included in these calculations.

To evaluate redbay regeneration in the understory, redbay density was calculated at the shrub layer as the number of live individuals per area sampled (4 m^2). The plants were categorized into 3 DGH size classes (0-1.00, 1.01-3.00, and 3.01-9.00 cm) and averaged by site. Stump sprouts were included in density calculations.

Data Analysis

This study was designed as a nested ANOVA, with treatment and sites nested within treatment (control vs. infested) as effects. However, data were not normally distributed, therefore data were averaged by site and the site averages were used in a one-way ANOVA to determine differences in control and infested sites. All data were tested for the assumptions of normality with the Shapiro Wilk W test and equal variance with the Levene test. For data that met the assumptions, a one-way ANOVA was used to analyze differences in control and infested sites for the following factors: mean tree DBH, mean height, mean shrub DGH, mean proportion live redbay by size class, mean redbay density by size class, and mean number of stump sprouts per tree. When one of the assumptions was not met, a non-parametric Mann-Whitney U test was

used. In all non-parametric tests except mean DGH of all live and dead stems and mean number of stump sprouts, sample size was <20, so a table of critical upper and lower limit values was used to determine significance of the calculated rank sum (U) at $P \leq 0.05$. The rank sum of the control sites was compared to the critical values to determine significance because it had the smallest sample size of the two treatments (control N=3, infested N=5). This test was used to analyze differences in mean percent live redbay by layer, mean DGH of all live and dead stems, shrub density, mean proportion live redbay by size class, and number of sprouts.

Simple linear regression was used to determine the relationship between crown area and basal area of trees ≥10 cm DBH in control sites to obtain the equation: crown area = -1.315 + 717.32*basal area. This equation was used to estimate the amount of crown area lost of trees ≥10 cm DBH from infested sites.

Linear regression was also used to determine and the relationship between shrub diameter and height and crown area at control and infested sites. An ANCOVA was used to test for growth patterns in shrub data with treatment as the effect, diameter as a covariate, and crown area or height as response variables. A homogeneity of slopes test (interaction of treatment and diameter) was then used to determine if there was a difference in slopes between treatments for shrub data. All statistical analyses were conducted using JMP 8.0 (SAS Institute Inc., Cary, NC, 2008).

Results

Infested and control sites differed in many of the population characters measured, suggesting that redbay population structure has been altered by laurel wilt disease in the 2-4 years since infestation. The disease has primarily killed redbay trees ≥ 3 cm DBH, while smaller individuals survived (Figure 2.4). Only 8.1 ± 2.2% of redbay trees ≥ 3 cm DBH were live in infested sites, compared to 80.4 ± 9.8% live at control sites, a 10-fold difference (Mann-Whitney

U test: U=21, N_C=3 N_I=5, P<0.05, Figure 2.4). No differences were found in mean percent live redbay for individuals <3 cm DBH at the shrub layer and of redbay seedlings <50 cm tall at the herb layer (shrub: $F_{1,6}$=0.061, P=0.8135; herb: Mann-Whitney U test, U=18, N_C=3 N_I=5, P<0.05; Figure 2.4).

Live redbay trees ≥3 cm DBH had 2.1 times greater DBH in control than infested sites but the DBH of dead trees did not differ (live trees: $F_{1,6}$=7.124, P=0.0371; dead trees: $F_{1,5}$= 0.422, P=0.5447; Figure 2.5a). In infested sites, the mean DBH of dead trees was 1.8 times higher than live trees ($F_{1,8}$=6.887, P=0.0304) but in control sites the DBH of live versus dead trees did not differ ($F_{1,3}$=0.741, P=0.4526; Figure 2.5a). These results suggest that laurel wilt disease has caused mortality of larger trees while smaller stems were unaffected.

Neither live nor dead redbay shrub stem diameter differed in control and infested sites (live shrubs: $F_{1,6}$=0.159, P=0.7038; dead shrubs: $F_{1,6}$=4.484, P=0.0786; Figure 2.5b). However, a statistical trend of larger diameter shrubs were found dead in infested sites than in control sites, suggesting LWD may have a negative impact on larger shrubs.

The mean DGH of all dead stems was almost 2 times greater in infested than the mean DGH of all dead stems in control sites (Mann-Whitney U test: U=12280, N_C= 86 N_I=264, P=0.0006; Figure). There was no difference in mean DGH of all live stems in control and infested sites (Mann-Whitney U test: U=421995.5, N_C=521 N_I=1159, P=0.0838, Figure 2.6).

Mean proportion live redbay in the 5.01-10.00 cm size class was almost 5 times greater at control than infested sites when calculated 1) with only live stems with no LWD symptoms and 2) with live stems including those with LWD symptoms (Table 2.3, Figure 2.7a-b). The proportion live redbay was 2 times greater in control than infested sites in the 1.01-3.00 cm size class when calculated with live, healthy stems only (Table 2.3; Figure 2.7b). Also, a trend of a higher

proportion live redbay in control sites was found at the 0-1.00 cm size class when calculated with live, healthy stems only (Table 2.3; Figure 2.7b). This suggests that stems as small as or smaller than 1 cm DBH are killed by the disease. Importantly, no live redbay ≥15 cm DBH were found in infested sites.

To determine if there was significant regenration of redbay in the understory, the density of redbay at the shrub layer was compared between control and infested sites. The density of redbay did not differ in control and infested sites in any size class at the shrub layer (0-1.00: Mann-Whitney U test, U=9, N_C =3 N_I=5, P=n.s.; 1.01-3.00: Mann-Whitney U test, U=9.5, N_C =3 N_I=5, P=n.s; 3.01-9.00: ANOVA, $F_{1,6}$= 0.467, P=0.5198; Figure 2.8).

Differences in growth patterns of shrubs were found in control and infested sites. A positive relationship was found between height and DGH of shrubs at infested sites (R^2=0.2473, $F_{1,495}$= 162.647, P<0.0001) and at control sites (R^2=0.3986, $F_{1,115}$=76.217, P<0.0001, Figure 2.9). A positive relationship was also found between DGH and crown area of shrubs at infested sites (R^2=0.2303, $F_{1,495}$=148.111, P<0.0001) and control sites (R^2=0.4279, $F_{1,115}$=86.014, P<0.0001; Figure 2.10). The slope of the fit line for control sites was more positive than that of infested sites for both regressions (DGH vs. height: $F_{1,610}$=19.739, P<0.0001; DGH vs. crown area: $F_{1,610}$, F=8.648, P=0.0034). This suggests that shrubs in control sites were taller with larger crowns than those in infested sites relative to their diameter.

Sprouts were found at the base of dead and live redbay trees in both infested and control sites. However, in control sites the trees classified as live with sprouts were generally injured or in infested sites showed signs of laurel wilt disease. Injuries occurred from nearby treefalls. Dead primary stems had almost 3 times more stump sprouts per tree on average in infested sites than in control sites (Mann-Whitney U test: U=18519.5 N_C= 106 N_I=348, P<0.0001) but there

was no difference in the number of stump sprouts per tree at live trees in infested and control sites (Mann-Whitney U test: U=3301.5, N_C=226 N_2=24, P=0.2039; Figure 2.11).

Mean basal area of live redbay present in control sites was 370 cm^2 ± 119 per 10x10 m plot (Table 2.4). Mean basal area of dead trees in infested sites was almost twice that of control sites, 694 cm^2 ± 464 per 10x10 m plot (Table 2.4). A positive relationship was found between basal area and crown area (crown area = -1.315 + 717.32*basal area; R^2=0.755, df = 1, 24, P<.0001) of live redbay trees (>10 cm DBH) at control sites (Figure 2.13). Average crown area of redbay trees ≥10 cm present in control sites was 13.8 m^2 ± 3.7 per 10x10 m plot (Table 2.4). For trees ≥10 cm DBH in infested sites, estimated crown area lost to LWD was 43.5 m^2 ± 31.5 per 10x10 m plot (Table 2.4). Tree plots were 100 m^2, therefore an estimated crown area exceeding this meant crowns overlapped outside of the 10x10 m plots.

Discussion

Laurel wilt disease has significantly impacted redbay population and size structure, with the greatest impact on the tree layer. Only 8% of redbay trees ≥3 cm DBH were alive in infested sites compared to 80% in control sites. On a gross scale comparison, no differences were found in percent live redbay at the herb and shrub layers, suggesting laurel wilt disease has only impacted individuals ≥3 cm DBH (Figure 2.4). However, when mean proportion live redbay was compared on a fine scale, a greater proportion of live redbay was found in shrubs within the 1.01-3.00 cm DGH size class in control sites (Figure 2.6). A trend of greater proportion live redbay was even found in control sites at the smallest size class, 0-1.00 cm DGH (Figure 2.6). This shows LWD has impacted very small individuals and not just trees. Fraedrich et al. (2008) observed redbay seedlings were less affected by laurel wilt disease compared with larger diameter trees, presumably because they are not as readily attacked by *X. glabratus*. But they also

observed aborted tunnels similar in size to those made by *X. glabratus* in stems and branches as small as 1 cm in diameter. They hypothesized that *X. glabratus* is able to infect healthy redbay with the laurel wilt fungus by tunneling even without egg laying (Fraedrich et al. 2008). The present study provides support for this hypothesis. In this study, no redbay trees >15 cm DBH were found alive in infested sites. Stump sprouts were included in my calculations, which can become infected by the laurel wilt fungus via roots and die back (personal communication, S. Fraedrich). Therefore, it is possible that the smaller individuals affected were stump sprouts reinfected with LWD from the root system and not attacked by beetles themselves.

This study provides evidence that the size structure of redbay has shifted to smaller individuals as larger live trees occurred in control sites and larger dead trees in infested sites. The mean DGH of all dead stems in infested sites was twice that of all dead stems in control sites. The largest living redbay in control sites had a DBH of 29.6 cm compared to 10.5 cm in infested sites. The largest dead redbay in control sites had a DBH of 65.5 cm. Similarly, in an area of Virginia affected by the chestnut blight, Stephenson et al. (1991) found the vast majority of living stems were <2.5 cm DBH and stems >6.3 cm were rare or uncommon. In the case of Dutch elm disease, all large elms (*Ulmus americana* L and *Ulmus rubra* Muhl.) in streamside forest stands in Illinois died as a result of Dutch elm disease and were replaced by smaller elms (Johnson and Bell 1975). In a study of American beech (*Fagus grandifolia* Ehrh.) infested with beech bark disease in the Adirondack forests in NY, Forrester et al. (2003) found mortality of American beech to be highest among larger diameter stems and over a 15 year period the smallest diameter class of beech trees increased. In New Hampshire, the number of small beech saplings (<10 cm) increased 5-fold since infestation (Latty 2001). Mize and Lea (1979) found that diameter of beech trees in an Adirondack Forest declined by 26% from pre-disease (1954) to aftermath

periods (1976). Van Leaven and Evans (2005) found similar results with beech in the Adirondacks, where 16% of dead trees were ≤13 cm DBH and 55% of dead trees were >13 cm DBH. For redbay, I found similar shifts in size structure with the majority of surviving individuals in small diameter classes.

The mean density of redbay shrubs in control and infested sites did not differ, suggesting increased regeneration of redbay has not occurred at the shrub layer in infested sites. Other studies have shown significant regeneration of species affected by fungal diseases, however. Studies of elms affected by Dutch elm disease showed red elm (*Ulmus rubra* Muhl.) regeneration was greater than any other species, and comprised 35% of seedlings (<1.5 cm) and 50% of small saplings (2.5-5 cm diameter) per acre in the stand (Root et al. 1971). If redbay is no longer capable of maturing to produce fruit in infested sites and clonal sprouts continue to become re-infected with LWD, I predict its density will actually decrease below the density of redbay in control sites over time.

Disturbances, such as the fall of a canopy tree, temporarily increase the availability of resources for plant growth (Canham and Marks 1985). The most obvious environmental change in forest gaps is in the increase in light availability (Collins et al. 1985). Nutrient availability may increase in gaps due to increased decomposition of organic matter, and increased nutrient release may increase flow of nutrients to understory plants (Collins et al. 1985). Light and nutrients are often the limiting resources for plant growth and they can have a substantial influence on how plant biomass is allocated (Meekins and McCarthy 2000). Availability of soil resources and light may, for instance, alter the root: shoot ratio (Wilson 1988, Olff et al. 1990). Plants that are nutrient limited may allocate a greater proportion of their total biomass to roots rather than to stems and leaves (Chapin 1980, Smart and Barko 1980). Plants that are light limited, however,

increase in height to avoid shading competition and will have greater stem biomass or they may increase their leaf biomass to have more surface available for light interception (Abrahamson and Gadgil 1973). Because of increased light availability in infested sites with open canopy, I might have predicted that shrubs would have been taller (faster growth) with wider crowns, resulting in lower diameter to height and diameter to crown ratios than those in control sites. The opposite pattern of growth was found, however. In control sites, shrubs had the lower diameter: height ratio (Figure 2.8), and also a lower diameter: crown ratio (Figure 2.9). These growth patterns may be a result of light as a limiting factor. Low light conditions promote stem and leaf growth to maximize photosynthesis (McConnaughay and Coleman 1999, Hirose 1987). In this study, plants put more resources into height and lateral branching under a shaded canopy to maximize photosynthetic capacity. Walters et al. (1993) found a similar pattern in early successional members of Betulaceae, which exhibited greater height per unit stem mass in low light than in high light. Further measurements such as relative growth rates would need to be determined to confirm this, however.

Water availability limits growth of redbay with shorter stems in drier, well-drained sites and taller stems in wetter, more poorly-drained sites (Coder 2007). Also, redbay are shorter farther inland and higher above sea level (Coder 2007). All of the sites in this study were in low, wet areas that were poorly drained with slopes of 0-2% (Table 2.2). Soil moisture levels were not tested, so water availability cannot be ruled out as a factor affecting the growth of plants, but it was unlikely to be the cause. Control sites were the furthest inland and had the highest elevations above sea level, ranging from 60 to 81 m, whereas infested sites had lower elevations ranging from 29 to 56 m. Elevation ranges almost overlapped so this also most likely did not contribute to the smaller stature of trees (live or dead) in control than infested sites. Approximate ages of the

forests or redbay trees at sites were unknown because dead redbay trees in infested sites were too rotted to obtain a tree core to determine their age, but younger trees in control sites may have been the reason for smaller trees.

The mean number of tree sprouts at dead trees was almost 3 times greater in infested than control sites (Figure 2.10). Fraedrich et al. (2008) also observed numerous sprouting of redbay at the ground line of dead trees. Most sprouts observed occurred at dead or injured trees and were found in both infested and control sites. It was sometimes difficult to determine whether an individual redbay was a root sprout or an individual plant if the original tree had rotted away completely. Because stump sprouts can be infected with LWD via roots, it is not likely that they will develop into new individuals to replace the primary stems. The pattern of mortality of large trees and increasing abundance of root sprouts have been seen in other cases of a species affected by a fungal disease, such as in American chestnut affected by the chestnut blight (Griffin 1989, Stephenson et al.1991), elms affected by Dutch elm disease (Root et al. 1971, Johnson and Bell 1975), and American beech affected by beech bark disease (Houston 1994, Latty 2001, Forrester et al. 2003, Van Leaven and Evans 2005). American chestnut also produces sprouts from tree roots after primary stem mortality. They eventually succumb to the fungal disease, new sprouts form, and the process starts over (Anagnostakis 2001). Griffin (1989) found that the diameter of live chestnut sprouts (0.5-2.3 cm) were smaller than that of dead sprouts (3.1-5.4 cm). I did not find differences in the diameter of live and dead sprouts of redbay in infested sites, but my sample size of dead sprouts may have been too small to accurately assess this (N_{dead}=9, N_{live}=60). More sprouts were found at larger trees in control and infested sites, which could mean that root systems were still intact and loss of primary stems increase the amount of water and nutrients available to put into new growth.

The basal area loss for trees ≥3 cm DBH and estimated canopy loss for trees ≥10 cm DBH was greatest at I1 (Table 2.6, Figure 2.14). This site was somewhat of an outlier from my other sites because it contained the largest diameter redbay and the greatest density of redbay trees. Extensive redbay regeneration had taken place here in the understory, but with the heavy infestation here it is unlikely young redbay will survive to larger sizes.

Broader Implications

Significant losses of redbay, as in site I1, may alter soil moisture and soil temperatures as has been shown in hemlock woolly adelgid infested forests (Jenkins et al. 1999, Cobb and Orwig 2002, Small et al. 2005, Orwig et al. 2008). Loss of biomass may decrease total transpiration in redbay forests and affect hydrology as Ford and Vose (2007) have shown in forests with severe decline of eastern hemlock. Inputs of leaf litter and woody debris from dead and dying trees might increase decomposition in the forest floor and alter nutrient cycling as has been shown in HWA infested forests (Jenkins et al. 1999, Yorks et al. 2003).

In its native range of Asia, the redbay ambrosia beetle exists between latitudes ~10° N and up to ~40° N. In the United States, redbay is found ~25° N in Florida to ~38°N in Virginia. This suggests it is quite possible for the redbay ambrosia beetle to spread laurel wilt disease to redbay throughout its range. It may also spread to other members of its genus and other species of Lauraceae. There are 70 members in the genus *Persea* throughout the neotropics which LWD could potentially spread to if climatic conditions are favorable. Importantly, avocado grown in Florida, California, Mexico, and tropical Americas (Morton 1987) could potentially be at risk of the disease. Other species such as sassafras, which occurs throughout the entire east coast, may also be at risk of decline. Hanula et al. (2008) found that sassafras was not more attractive than non-host species such as live oak and sweetgum, however, *X. glabratus* could successfully breed

in sassafras wood. It is possible more sassafras are being affected that currently realized, because once they are affected with LWD, their leaves drop immediately and they are harder to identify without leaves (C. Bates, personal communication). Redbay, on the other hand, retains its leaves after death for several years and is easily noticed, even from long distances.

Resistance to laurel wilt disease in redbay has not yet been found, but it has been found in a non-native species introduced to the U.S. In June 2007 in McIntosh County, Georgia, one camphor tree (*Cinnamomum camphora* (L.) J. Presl) was found infected with laurel wilt disease, but the majority of its crown was intact (Cameron et al. 2008). A follow up visit to the tree in April 2008 showed it had recovered, but the laurel wilt fungus was still present in its tissues (Cameron et al. 2008). Camphor trees are in the Lauraceae family and are native to southeast Asia, and this example shows possible resistance due to coevolution of exposure to the fungus in its native range (Cameron et al. 2008). Southeast Asia and Brazil are the two major centers of diversity for Lauraceae (Kopp 1966). There is also experimental evidence that North American hosts of alien insects are more susceptible than their coevolved congeners as in beech scale and North American beeches (Houston 1987) and hemlock wooly adelgid and eastern hemlocks (Havill et al. 2006).

Some dramatic changes in redbay population and size structure have occurred within the range of *X. glabratus* and will most likely occur wherever it spreads. Long-term monitoring of redbay populations are needed to determine further shifts in population structure that may occur, and if regenerating sprouts will have the ability to grow into mature trees. Redbay may face a similar fate as American chestnut, and may continually regenerate via stump sprouts that will never be able to mature enough to fruit and flower. Other species, such as sassafras, should also

be monitored for effects of laurel wilt disease. Ecosystem processes may also be affected by redbay mortality and will be an important area of future study.

CHAPTER 3

Forest Community Structure and Composition

Introduction

Invasive insects and their associated pathogens alter forest communities by causing tree mortality and subsequent biotic and abiotic disturbances. For example, they alter abiotic factors by increasing nutrient levels and soil organic matter from inputs of litter fall and woody debris (Grace 1986, Orwig and Foster 1998, Jenkins et al. 1999, McNulty and Masters 2005, Latty 2005). Defoliation of trees by gypsy moth (*Lymantria dispar* L.) caterpillars increased quantities of nitrogen, phosphorous and potassium in litter fall (Grace 1986). In forests infested with the hemlock woolly adelgid (*Adelges tsugae* Annand), inorganic nitrogen availability increased as a result of hemlock mortality (Jenkins et al. 1999). In forests infested with the hemlock woolly adelgid and beech bark disease, woody debris increased (Orwig and Foster 1998, McNulty and Masters 2005).

Invasive insects and pathogens also cause canopy gaps with increased light levels, associated with increased vegetation cover, species richness, and occurrence of invasive plant species (Orwig and Foster 1998, Jenkins et al. 1999, McNulty and Masters 2005, Small et al. 2005, Eschtruth et al. 2006). Death of hemlocks from the hemlock woolly adelgid (HWA) led to increased light, which in turn resulted in rapid understory vegetation response, an increase in herb richness and abundance, increases in densities of clonal saplings, and increases in opportunistic exotic species (Orwig and Foster 1998, Jenkins et al. 1999, Small et al. 2005). Similarly, in forests affected by beech bark disease, species richness and abundance increased in canopy gaps (McNulty and Masters 2005).

Forest composition shifts have also occurred as a result of mortality of a dominant or co-dominant tree species via invasive insects and pathogens. Mortality of American elm (*Ulmus americana* L.) by Dutch elm disease in Illinois mesic forests saw a 70% decrease of elm basal area and a 60% increase in basal area of sugar maple (*Acer saccharum* Marsh.) (Boggess and Bailey 1964). Canopy gaps created by elm mortality also decreased smaller elms that were out-competed by faster growing sugar maple (Boggess and Geis 1966). Elimination of American chestnut (*Castanea dentata* (Marsh. (Borkh.) due to chestnut blight and replacement by co-dominant tree species, especially oaks, has been well documented (Korstian and Stickel 1927, Augenbaugh 1935, Keever 1953, Nelson 1955, Good 1968). Woods and Shanks (1959) observed three processes in which openings made by American chestnut mortality were re-occupied: 1) canopy closure by adjacent dominant and co-dominant trees in mature stands, 2) rapid growth of seedlings and saplings reacting to increased amounts of light, and 3) growth of seedlings able to establish in higher light environments that otherwise would not have survived. Thus, canopy gaps, as a result of tree mortality, facilitate forest composition shifts.

Mortality of redbay (*Persea borbonia* (L.) Spreng) as a result of laurel wilt disease (LWD) may create canopy gaps and induce similar disturbances and forest community composition shifts. Redbay is fairly common, but not abundant, throughout the southeastern United States. It is generally considered a midstory tree or understory shrub (Harrar and Harrar 1946), but has the potential to reach canopy tree size and is a co-dominant species in certain habitat types. In smaller canopy gaps, adjacent dominant and co-dominant trees may respond by closing in these gaps. In larger canopy gaps, rapid growth of shrubs and seedlings may occur, as well as colonization by species adapted to higher light environments. In the forest types in which redbay is a co-dominant tree, species composition shifts are especially likely to occur.

Little research has been published on forest composition changes as a result of laurel wilt disease and redbay mortality. Goldberg and Heine (2009) compared arborescent vegetation in maritime hammock communities in Florida pre- (1983) and post- (2008) redbay mortality due to LWD. They found frequency and density of canopy species had changed and densities of understory shrubs increased (Goldberg and Heine 2009). Maritime hammocks are hardwood forest habitats of live oak associations (*Quercus virginiana* Mill.) in coastal dunes <1 km from the coast (Oosting 1954). Their study is a comparison of redbay habitats 25 years apart, whereas my research shows a real-time change as infested sites are in various stages of decline. Goldberg and Heine's (2009) study focused on s very different community type in Florida and no research has been published on changes to forest communities as a result of LWD in the Coastal Plain of Georgia. To determine whether disturbances occurred and community structure and composition changed as a result of redbay mortality, a comparison was made between five infested sites and three control sites. The objectives of this study were to: 1) determine community composition and structure at infested and control sites and 2) compare abiotic factors such as light level, litter depth, percent litter and percent woody debris between control and infested sites.

Methods

Communities With Redbay

According to the forest cover types by the Society of American Foresters, redbay is a major component in the forest cover type sweetbay-swamp tupelo-redbay (*Magnolia virginiana-Nyssa sylvatica* var. *biflora-Persea borbonia*) (Eyre 1980). It is also commonly found in the following cover types: loblolly pine-hardwood pond pine (*Pinus taeda-Pinus serotina*), baldcypress-tupelo (*Taxodium distichum-Nyssa* spp.), and water tupelo-swamp tupelo (*Nyssa aquatica- Nyssa sylvatica* var. *biflora*) (Eyre 1980). Redbay is a minor component of the following cover types: cabbage palmetto (*Sabal palmetto*), loblolly pine, Atlantic white-cedar

(*Chamaecyparis thyoides*), pondcypress (*Taxodium distichum* var. *nutans*), and baldcypress (Eyre 1980).

Numerous species may occur with redbay, depending on the geographic location, site, and stand history. Common hardwoods associated with redbay are red maple (*Acer rubrum*), sweetbay, swamp tupelo, black tupelo (*Nyssa sylvatica*), Ogeechee tupelo (*Nyssa ogeche*), loblolly-bay (*Gordonia lasianthus*), sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), laurel oak (*Quercus laurifolia*), yellow-poplar (*Liriodendron tulipifera*), and southern magnolia (*Magnolia grandiflora*) (Eyre 1980). Common conifers associated with redbay include slash pine (*Pinus elliottii*), longleaf pine (*Pinus palustris*), loblolly pine, pond pine, baldcypress, pondcypress, and Atlantic white-cedar (Eyre 1980). Some of the small trees and shrubs associated with redbay are buckwheat-tree (*Cliftonia monophylla*), swamp cyrilla (*Cyrilla racemiflora*), Virginia sweetspire (*Itea virginica*), large gallberry (*Ilex coriacea*), dahoon (*Ilex cassine*), yaupon (*Ilex vomitoria*), inkberry (*Ilex glabra*), blueberries (*Vaccinium* spp.), lyonia fetterbush (*Lyonia lucida*), staggerbush lyonia (*Lyonia mariana*), summersweet clethra (*Clethra alnifolia*), bayberry (*Morella* spp.), poison-sumac (*Toxicodendron vernix*), and switchcane (*Arundinaria* spp.) (Eyre 1980).

Forest Community Measurements

The same study sites, study design, and plots were used for this portion of the research as were in the redbay population structure portion (Chapter 2). Measurements of forest communities were conducted once per site from May-September 2008 and May-October 2009 (same sampling dates as Chapter 2).

Tree layer: The diameter at breast height (DBH) and tree status (live or dead) were recorded for all stems of all species ≥3 cm DBH at the 10x10 m plots in three control sites and five infested

sites. For trees with multiple stems, each was counted separately because comparisons were of stems and not genotypes. Frequency and density of all live trees were calculated as well as basal area of all live trees using the formula:

$$\text{Basal Area} = \pi(\text{DBH}/2)^2$$

Shrub layer: The crown area and height of all live stems <3 cm DBH and taller than 50 cm were measured. Crown area was determined by measuring the width of the crown at its widest part (W_1), then measuring a second width of the crown perpendicular to the first (W_2), and these values were used in the formula for the area of an ellipse:

$$\text{Crown Area} = \pi(W_1/2)(W_2/2)$$

Frequency and density of all live shrubs were also calculated.

Herb layer: Ocular estimates were made of the percent cover of each species, litter, and woody debris and standardized with a 10x10 cm square covering 1% of the 1x1 m plot. Any percent cover of a species <1% was rounded up to 1%. The frequency of all species was calculated.

Importance values were calculated for each species at tree, shrub, and herb layers for each site. Relative frequency, relative density, and relative dominance using basal area of all live stems ≥3 cm DBH were summed to determine importance value of a species at the tree layer. The same values were also calculated for live and dead stems ≥3 cm DBH combined to compare importance values of redbay before and after the occurrence of laurel wilt disease. The relative frequency, relative density, and relative dominance using crown area of all live shrubs <3 cm DBH and taller than 50 cm were summed to determine the importance value of a species at the shrub layer. Relative frequency and relative dominance using percent cover were calculated for all live stems <50 cm tall, and summed to determine importance values of each at the herb layer.

The following formulas were used to calculate relative frequency, density, and dominance:

$$\text{Relative Frequency} = \frac{\text{Absolute frequency of species i}}{\sum \text{ of frequency values for all species}} \times 100$$

$$\text{Relative Density} = \frac{\text{Absolute density for species i}}{\sum \text{ of density for all species}} \times 100$$

$$\text{Relative Dominance} = \frac{\text{Absolute dominance for species i}}{\sum \text{ of dominance for all species}} \times 100$$

The maximum importance value for tree and shrub layer was 300 and was calculated as:

IV = Relative frequency + Relative density + Relative dominance

The maximum importance value for herb layer was 200 and was calculated as:

IV = Relative frequency + Relative dominance

Species richness was determined at all sites for tree, shrub, and herb layers separately as the number of species per plot or subplot averaged by site. Plot size was 10x10 m for tree layer, 2x2 m for shrub layer, and 1x1 m for herb layer.

Abiotic Factors

To determine light availability below the canopy in control and infested sites, photosynthetically active radiation (PAR) measurements were taken with a Model PAR-80 AccuPAR ceptometer (Decagon Devices, Inc., Pullman, WA). The AccuPAR ceptometer has a linear array of 80 adjacent 1 cm^2 PAR sensors along a ~1 m long bar for more accurate measurements in variable light environments. Measurements were taken between August 8, 2009 and September 4, 2009 during the time of day when the sun is most directly overhead, 11 AM – 1:30 PM, with clear skies. If clouds passed overhead, I waited until they were clear of the sun before continuing measurements. Measurements were taken in all 2x2 m subplots along two

perpendicular axes approximately 1 m above ground level. Three measurements were taken at each axis and all measurements at each subplot were averaged.

Litter depth was haphazardly measured in one location in each 2x2 m subplot as the depth of leaf litter above the organic matter layer.

Data Analysis

All data were tested for the assumptions of normality with the Shapiro Wilk W test and equal variance with the Levene test. Mean importance value for individual species at tree, shrub, and herb layers in infested and control sites were compared using t-tests for parametric data and a Mann-Whitney U test for nonparametric data. Importance values calculated with live stems and calculated with live plus dead stems for trees were compared by treatment (control, infested) using t-tests for parametric data and a Mann-Whitney U test for nonparametric data. If sample sizes were <20, a table of critical upper and lower limit values was used to determine significance of the calculated rank sum (T) at $P \leq 0.05$. Light level, litter depth, and percent cover of woody debris and leaf litter were log transformed to obtain a normal distribution, then tested with a nested ANOVA. Species richness was compared for each layer with a nested ANOVA. For each nested ANOVA, treatment (control, infested) and sites nested within treatment were the effects tested. All statistical analyses were conducted using JMP 8.0 (SAS Institute Inc., Cary, NC, 2008).

Results

Twenty-four different species were recorded in 66 10x10 m plots across all study sites at the tree layer (≥3 cm DBH). Eighteen species were recorded from control sites and 20 species were present in infested sites. Species richness did not differ at the tree layer in infested and control sites, but varied by site (Table 3.1, Figure 3.1, Appendix A; Refer to Table 2.1 for detailed

study site information). The total number of tree species per site ranged from 5 (I1 and I4) to 14 (I2) (Appendix B).

Persea borbonia had the greatest mean importance value (IV) of tree species at control sites, followed by *Magnolia virginiana, Gordonia lasianthus* and *Acer rubrum* (Table 3.3). In the infested sites, *M. virginiana* had the highest mean IV, followed by *G. lasianthus*, *Pinus taeda* and *Nyssa* sp. (*N. sylvatica* or *N. biflora*) (Table 3.3). When IVs were calculated with live stems only, *P. borbonia* had the 8th highest mean IV in infested sites (10.2 ± 3.2) compared to the highest mean IV in control sites (52.4 ± 20.3), and was significantly greater in control sites (Table 3.3, Figure 3.2). When all stems (live and dead) were counted in IV calculations for infested sites, *P. borbonia* had the greatest mean IV (70.8 ± 28.1) and was significantly greater than that of the mean IV for live stems only (10.2 ± 3.2) (Table 3.4). There was no difference in IVs of live stems versus live and dead stems of *P. borbonia* in control sites (Table 3.3). Also, there was no difference in IV of live and dead stems of *P. borbonia* in control and infested sites ($t_{(6)}$=0.267, P=0.7985). This suggests there were no preexisting differences in importance of redbay in infested sites before the onset of LWD.

Variation in community composition at the tree layer is apparent across sites when the top 4 IVs are compared by site (Appendix B). *Persea borbonia* was present in all 8 sites and was in the top 4 highest IVs at 4 of these (2 infested, 2 control), and ranked 1st only at C2. *Magnolia virginiana* was present in all sites but one (C2), and was always in the top 3 highest IVs. *Gordonia lasianthus* was present in all sites but two (C2 and I2), and was always in the top 4 highest IVs. *Acer rubrum* was present in 6 sites and was among the top 4 highest IVs at 5 of these. *Nyssa* sp. (either *N. sylvatica* or *N. biflora*) was present in 7 sites but only had a high IV at sites I2 and I3. *Pinus taeda* was present in 5 sites and was in the top 4 greatest IV at 4 of these.

Other species present in the top 4 highest IVs at only 1 site include *Cliftonia monophylla*, *Liriodendron tulipifera, Liquidambar styraciflua, Quercus nigra*, and *Vaccinium corymbosum*.

Fifty-two different species were found across 298 2x2 m plots across all study sites at the shrub layer (<3 cm DBH, ≥50 cm tall). Thirty-one different species were present in control sites compared to 43 in the infested sites, yet species richness did not differ statistically (Table 3.1, Figure 3.1, Appendix A). The total number of species per site ranged from 11 species (C3, I3) to 28 species (I2) and differed among sites (Table 3.1, Appendix C).

At the shrub layer in control sites, *Ilex coriacea* (large gallberry) had the highest mean IV, followed by *P. borbonia, Vaccinium elliottii* (Elliott's blueberry), and *Lyonia lucida* (Lyonia fetterbush) (Table 3.4). At infested sites, *P. borbonia* had the highest IV followed by *Lyonia lucida, I. coriacea,* and *Vaccinium corymbosum* (Table 3.4). *Persea borbonia* was present in all 8 sites, was among the top 4 highest IVs at all, and had the greatest IV at 5 sites (Appendix C). *Vaccinium corymbosum* was the only other species present in all 8 sites and was among the 4 highest IVs at 4 sites. *Vaccinium corymbosum* had a greater mean IV in infested sites than in control sites (Table 3.4). *Ilex coriacea* was found in 6 study sites and was among the top 4 highest IVs at all, and the highest at 2 sites. *Magnolia virginiana* was present in 6 out of the 8 sites but was not among the top 4 highest IVs in the shrub layer. Other species in the top 4 greatest IVs were *G. lasianthus* (2 sites), and each of the following were in the top 4 at only 1 site: *Morella caroliniensis*, *Morella cerifera, Nyssa* sp., *Quercus nigra*, *Symplocos tinctoria*, *Vaccinium arboreum*, and *Vaccinium elliottii* (Appendix C).

Fifty-eight different species were recorded in the herb layer across 298 1x1 m plots across all study sites. Forty-two species occurred in control sites and 45 in infested sites, however, mean species richness was 1.3 times greater in control sites at the herb layer (Table 3.1, Figure 3.1,

Appendix A). The total number of species per site at the herb layer ranged from 37 (C1) to 11 (I3) (Appendix D).

In control sites at the herb layer, *Ilex coriacea* had the greatest mean IV, followed by *P. borbonia*, *Lyonia lucida*, and *Lyonia ligustrina* (Table 3.4). In infested sites, *Lyonia lucida* had the highest mean IV, followed by *P. borbonia*, *I. coriacea*, and *Vitis rotundifolia* (Table 3.4). *Persea borbonia* was found at all 8 sites and was among the top 4 highest IVs at 6 of them (Appendix D). *Lyonia lucida* was present in 7 sites and was in the top 4 highest IVs at all 7. *Quercus* sp. seedlings were present in 7 sites but did not have high IVs. *Ilex coriacea* was present in 5 sites and was in the top highest IV at 4 of them. Other species among the top highest 4 IVs were several sedges (*Carex* spp.), vines (*Smilax glauca, Smilax laurifolia, Vitis rotundifolia*), ferns (*Osmunda cinnamomea, Woodwardia areolata),* ericaceous shrubs (*Vaccinium arboreum, Vaccinium elliottii, Lyonia ligustrina*), and several woody shrubs and trees (*Cliftonia monophylla*, *Gordonia lasianthus, Itea virginica*) (Appendix D).

Percent cover of woody debris and percent cover of litter did not differ between control and infested sites, but did differ by site (Table 3.5, Appendix E). Light levels were 4.8 times greater in infested sites than in control sites and this also differed by site (Table 3.5, Appendix F). Litter depth did not differ by treatment, but did by site (Table 3.5, Appendix F).

Discussion

Mortality of redbay as a result of the introduction of laurel wilt disease has opened canopy gaps in only 2-4 years since infestation, which has facilitated alterations in community composition and structure. Of the dead trees in control sites, 68.8% (53/77) of them were redbay. In infested sites, 32.5% (226/696) of all trees sampled were dead, of which 77% (174/226) were redbay. At site C1, no dead redbay was observed in study plots. At site C2, 33% of redbay trees were dead, and at site C3 35% of redbay trees were dead. It is not clear what other factors caused

this high percentage of mortality of larger redbay in control sites. Other species of bark or ambrosia beetles may have played a role because beetle entry holes were evident in trees that were obviously not infected with the laurel wilt fungus (personal observation).

Inclusion of data on standing dead redbay trees gives some insight into the effects of their mortality on overall stand composition. Redbay ranked 8th in mean importance value out of 20 species in infested sites when only live trees were included, but ranked 1st in mean IV when live and dead trees were counted. Redbay had the highest mean IV at control sites out of 18 species and was statistically more important than redbay at infested sites. *Magnolia virginiana* and *Gordonia lasianthus* were the 2nd and 3rd most important species at control sites after redbay, and were the 1st and 2nd most important species in infested sites. These results suggest that in infested sites, redbay mortality has altered community composition and contributed to greater IVs of the co-dominant species *M. virginiana* and *G. lasianthus*. These two co-dominant tree species may respond to redbay mortality by closing in canopy gaps in time. I surveyed at sites 2-4 years after LWD was first detected, which was too soon for new trees of co-dominant species to fill in the canopy gaps.

At the shrub layer, redbay had the greatest mean IV in infested sites and the 2nd greatest mean IV at control sites. The IVs were not statistically different, but these results may suggest that some amount of regeneration of redbay has occurred in the understory in infested sites. Regeneration of redbay could have been a response to increased light from open canopy gaps left by the death of primary stems or increases in abundance of stump sprouts. Seedling regeneration and increases in clonal saplings occurred in forests affected by HWA (Jenkins et al. 1999, Small et al. 2005). At the herb layer, redbay had the second highest mean IV at both control and infested sites, which were not statistically different.

Species richness did not differ between treatments at the tree or shrub layer, but it was 1.3 times greater in control sites at the herb layer. Over time, greater species richness in infested sites may occur as a response to the increased light availability to the forest floor. As other studies have shown, new species may become established that survive only in higher light conditions that would not have been present under a shaded canopy. In forests affected by HWA, Eschruth et al. (2006) found increases in species richness, which was positively correlated with change in understory light availability. Others have also found increases in light availability corresponding to increases in herb richness and abundance in forests affected by HWA (Orwig and Foster 1998, Small et al. 2005).

As a result of redbay mortality, light levels were almost 5 times higher in infested sites than in control sites. For example, at site I1 which was infested in 2006, significant canopy loss has occurred (Figure 3.3), where 74% of all trees were dead, 97% of which were redbay. PAR readings here averaged very high at 935.1μmol $m^{-2}s^{-1}$, for comparison the highest average PAR reading in a control site was 86.11μmol $m^{-2}s^{-1}$ (Appendix F). I visited this site both in 2008 and 2009 and observed changes including an increase in opportunistic early successional species which require high light for establishment such as *Erechtites hieracifolia* (American burnweed) and *Phytolacca americana* (American pokeweed). *Phytolacca americana* was also present at study site I4. Orwig and Foster (1998) also found *P. americana* and *E. hieracifolia* had become established as a forest response to hemlock mortality from HWA. Both species exhibit a buried seed strategy and can rapidly increase in abundance following disturbance (Del Tredici 1977, Peterson and Pickett 1990). *Parthenocissus quinquefolia*, also a higher-light demanding species (Eschruth et al. 2006), was present at the herb layer in infested sites I1, I2, and I4. Similarly, *P. quinquefolia* was found in plots after death of hemlocks from HWA (Eschruth et al. 2006).

Both Small et al. (2005) and Eschtruth et al. (2006) found non-native plant species in their sites following disturbance by HWA. However, only one non-native species was observed in one plot of one study site (I4), *Ligsutrum sinense*, (Chinese privet), and thus was not a major factor in community composition shifts as of yet but could potentially become so.

There was no difference in amount of woody debris or litter depth between control and infested sites. The earliest infestation was in 2005 at I3 and I1-I5 were infested in 2006. There was still a great amount of standing dead biomass of redbay in infested sites and the 2008-2009 study may be too soon for trees to have rotted and fallen to add significant amounts of debris at study sites. Also, leaves are retained for several years on trees and thus inputs of woody debris and litter would be gradual, unlike other types of disturbance such as hurricanes which produce an immediate pulse of leaf litter and biomass (Pascarella 1998). Future studies of LWD infested forests may show increases in woody debris, leaf litter, and thus alterations in nutrient cycling.

Long-term studies of these forest communities will show what species will replace *P. borbonia* in the future. Based on current importance values at infested sites, it is likely *M. virginiana* and *G. lasianthus* will continue to increase in importance. I observed no seedlings of *M. virginiana*, however, and numerous seedlings of *G. lasianthus*, so this suggests that *G. lasianthus* will become the most important tree species over time. At the shrub layer, it is unlikely that *P. borbonia* will continue to be the most important species at infested sites as they grow and become reinfected with LWD and when all the seeds from the seed bed are exhausted. I predict *Lyonia lucida* and *Ilex coriacea* will increase in importance as *P. borbonia* decreases. Shifts in species compositions are likely to affect nutrient cycling as well.

Redbay mortality could ramify through the food web and affect the overall community by changes in wildlife species. Reduction in the amount of redbay might mean significant declines

for the Palamedes swallowtail caterpillar (*Papilio palamedes* Drury), whose primary food plant is redbay (Minno et al. 2005), especially if it has a preference for older leaves. Also, populations of psyllid leaf gallers, *Trioza magnoliae* (Ashmeade), that feed on redbay (Leege 2006) may be altered. Loss of trees might reduce the amount of fruit production of redbay as a food source to birds and other wildlife as has reductions in beech nuts (Lovett et al. 2006) and seeds of elms (Waldron 2003). Mortality of redbay might also reduce habitat for wildlife and nesting sites for birds as declines in elms in England have shown (Osbourne 1985).

Finally, if control sites used in this study become infested with LWD, data gathered here can be useful for pre- and post-infestation community studies.

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Table 2.1 Study site information, for site codes: I = infested and C = control.

Site	County	Date of Infestation in County	Site Description	Community Type	Area† (m^2)	Latitude (N)	Longitude (W)	N Transects	N ($10m^2$ plots)	N ($2m^2$ and $1m^2$ plots)
I1	Evans	2006	private property off GA 169	bay swamp	50,000	32°12′06″	81°56′54″	7	8	32
I2	Evans	2006	Evans County Public Fishing Area	hardwood forest	10,000	32°07′56″	81°47′28″	6	10	50
I3	Bulloch	2005	Bulloch Bay, private property	bay swamp	16,000	32°10′52″	81°44′02″	4	8	40
I4	Tattnall	2006	private property off GA 56	hardwood forest	12,000	32°04′44″	82°08′33″	5	8	40
I5	Tattnall	2006	private property off GA 147	hardwood forest	12,000	32°00′54″	82°09′10″	4	8	40
C1	Emanuel	—	Ohoopee Dunes Natural Area, Halls Bridge Tract	hardwood forest	15,000	32°31′42″	82°27′18″	6	8	32
C2	Jenkins	*	Big Dukes Pond Natural Area	Carolina bay	17,000	32°52′03″	82°02′24″	4	8	32
C3	Emanuel	—	Private property off Highway 80	bay swamp	12,000	32°33′56″	82°27′03″	—	8	32

*Infestation was noted by Georgia Forestry Commission in Jenkins County in 2007, but was not found in the northwestern part of the county during sampling.

†The area selected for transect locations, and not necessarily the entire habitat containing redbay.

Table 2.2 Soil data for study sites: I = infested and C = control. Data from Web Soil Survey (2010).

Site	Soil Type	Land Form	Slope (%)	Drainage Class	Depth to Water Table (cm)	Flooding Frequency	Typical Profile (cm)
I1	Ru: Rutledge sand	bays, depressions	0-2	very poorly drained	0-15	none	0-178: sand
I2	OS: Osier soils	floodplains	0-2	poorly drained	0-30	frequent	0-15: loamy fine sand 15-167: sand
I3	RkA: Rutledge sand	bays, depressions, drainageways	0-2	very poorly drained	0	frequent	0-69: loamy fine sand 69-183: sandy clay loam
I4	OS: Osier soils	floodplains	0-2	poorly drained	0-30	frequent	0-15: loamy fine sand 15-168: sand
I5	Ru: Rutledge sand	bays, depressions	0-2	very poorly drained	0-15	none	0-178: sand
C1	Me: Meggett loam	floodplains	0-2	poorly drained	0-30	frequent	0-10: loam 10-66: sandy clay 66-132: clay 132-160: sandy clay loam
C2	PeA: Plummer sand	flats, stream terraces, shallow depressions	0-2	poorly drained	0-30	none	0-127: sand 127-183: sandy clay loam
C3	KFA: Kinston and Bibb soils	floodplains	0-2	poorly drained	0-30	frequent	0-15: loam 15-160: sandy clay loam

Table 2.3 Statistics for mean proportion live and LWD infested redbay and mean proportion of live redbay only within each diameter size class. Five infested sites were compared to three control sites.

DGH Size Class (cm)	Test	F/U†	df	P
		Live and LWD infested redbay		
0-1.00	ANOVA	0.6566	1, 6	n.s.
1.01-3.00	ANOVA	3.5843	1, 6	n.s.
3.01-5.00	Mann-Whitney U test	10†		n.s.
5.01-10.00	ANOVA	12.4511	1, 5	0.0168*
10.01-15.00	Mann-Whitney U test	18†		n.s.
>15				
		Live, healthy redbay		
0-1.00	ANOVA	5.2760	1, 6	0.0614+
1.01-3.00	Mann-Whitney U test	21†		<0.05*
3.01-5.00	ANOVA	0.8595	1, 5	n.s.
5.01-10.00	ANOVA	12.4511	1, 5	0.0168*
10.01-15.00	Mann-Whitney U test	18†		n.s.
>15				

* Significance at P≤0.05

+ Indicates a trend

† U is the rank sum of mean proportion redbay for the control sites, which was compared to critical values of U to determine significance, where N_C=3, N_I=5, U_L=6, U_U=21.

Table 2.4 Average basal area of live redbay ± standard error in control sites compared to average basal area of dead redbay ± SEM in infested sites. Also average crown area of live redbay present ± SEM in control sites and estimated average crown area of redbay lost ± SEM.

Site	Sum of basal area of live redbay† (cm^2)	Number of plots	Redbay basal area/plot (cm^2/100 m^2)	Site	Sum of basal area of dead redbay†(cm^2)	Number of plots	Basal area lost/plot (cm^2/100 m^2)
C1	1232	8	1.54	I1	20284	8	25.36
C2	4514	8	5.64	I2	2606	10	2.61
C3	3147	8	3.93	I3	1202	8	1.50
				I4	3435	8	4.29
				I5	745	8	0.93
Average			3.70 ± 1.19	Average			6.94 ± 4.64

Site	Sum of crown area (m^2)‡	Number of plots	Crown area present/plot (m^2/100 m^2)	Site	Estimated sum of crown area‡ from basal area* (m^2)	Number of plots	Estimated crown area lost/plot (m^2/100 m^2)
C1	65.7	8	0.08	I1	1347.7	8	1.69
C2	100.5	8	0.13	I2	152.1	10	0.15
C3	165.9	8	0.21	I3	24.3	8	0.03
				I4	203.9	8	0.26
				I5	42.0	8	0.05
Average			0.14 ± 0.37	Average			0.44 ± 0.32

*Estimated crown loss calculated per tree from the equation: crown area = -1.315 + 717.32*basal area. Tree plots were 100 m^2, therefore an estimated crown area exceeding this meant crowns overlapped outside of the 10x10 m plots.

†Basal areas calculated for all trees ≥3 cm DBH.

‡Crown areas calculated for all trees ≥10 cm DBH.

Table 3.1 Nested ANOVA table for species richness at tree, shrub, and herb layers.

Layer and Effect	df	F	P
Tree			
Treatment (control, infested)	1,6	0.2486	n.s.
Site[Treatment]	6, 58	6.9887	<0.0001*
Shrub			
Treatment (control, infested)	1,6	3.1865	0.0752
Site[Treatment]	6, 58	3.1084	0.0057*
Herb			
Treatment (control, infested)	1,6	17.3388	<0.0001*
Site[Treatment]	6, 58	15.2950	<0.0001*

* Significance at $P \leq 0.05$

Table 3.2 Mean importance values ± standard error (SE) at the tree layer calculated with live stems only and with live and dead stems for control and infested sites. The top 4 greatest mean IVs are bolded. Maximum mean IV was 300 for live and live + dead for each treatment.

	Control			Infested			Control vs. Infested
Species	Live Mean IV ¥ ± SE	Live + Dead Mean IV ± SE	t-ratio/ T‡	Live Mean IV ± SE	Live + Dead Mean IV ± SE	t-ratio/ T‡	t-ratio/T‡ for live stems
Acer rubrum	**32.2 ± 16.1**	**31.4 ± 15.7**	9.5	27.1 ± 10.3	23.3 ± 9.6	-0.269†	-0.271†
Cliftonia monophylla	—	—	—	20.0 ± 13.1	17.2 ± 10.7	27	—
Cyrilla racemiflora	—	—	—	2.3 ± 2.3	2.0 ± 2.0	27	—
Gordonia lasianthus	**38.5 ± 19.6**	**37.2 ± 18.8**	9.5	**59.4 ± 35.1**	**34.2 ± 16.1**	-0.653†	0.519†
Ilex coriacea	4.2 ± 4.2	4.6 ± 4.6	11	1.4 ± 1.4	1.2 ± 1.2	27	15
Ilex opaca	7.1 ± 5.1	6.8 ± 4.8	-0.044†	0.8 ± 0.8	0.7 ± 0.7	27	18
Liquidambar styraciflua	14.9 ± 14.9	14.1 ± 14.1	10	3.1 ± 2.4	2.9 ± 2.1	26.5	14
Liriodendron tulipifera	18.1 ± 13.5	17.7 ± 13.2	9.5	—	—	—	—
Lyonia lucida	—	—	—	0.8 ± 0.8	0.7 ± 0.7	27	—
Magnolia virginiana	**51.6 ± 26.0**	**49.7 ± 25.1**	9.5	**60.8 ± 16.9**	**50.6 ± 14.9**	24	0.296†
Nyssa ogeche	—	—	—	1.9 ± 1.9	1.9 ± 1.9	27	—
Nyssa sp.	18.6 ± 9.8	17.8 ± 9.3	9	**39.3 ± 20.0**	33.9 ± 17.2	24.5	13
Osmanthus americanus	3.3 ± 1.7	3.2 ± 1.7	-0.040†	—	—	—	—
Persea borbonia	**52.4 ± 20.3**	**59.8 ± 23.4**	0.240†	10.2 ± 3.2	**70.8 ± 28.1**	40*	21*
Pinus elliottii	—	—	—	11.9 ± 9.4	1.8 ± 1.8	24	—
Pinus palustris	3.1 ± 3.1	3.0 ± 3.0	10	—	—	—	—
Pinus sp.	1.5 ± 1.5	1.5 ± 1.5	10	—	—	—	11
Pinus taeda	11.9 ± 7.1	13.0 ± 8.3	10.5	**45.0 ± 22.2**	**44.2 ± 21.5**	27	—
Quercus laevis	1.2 ± 1.2	1.2 ± 1.2	10	—	—	—	—
Quercus laurifolia	3.0 ± 1.7	3.0 ± 1.7	-0.026†	3.8 ± 3.8	3.4 ± 3.4	27	16
Quercus nigra	31.4 ± 25.7	29.5 ± 23.9	9.5	2.7 ± 1.7	2.3 ± 1.5	26.5	17.5
Quercus sp.	4.9 ± 2.6	4.8 ± 2.6	-0.037†	3.9 ± 2.5	3.5 ± 2.3	26.5	-0.276†
Rhododendron sp.	—	—	—	0.6 ± 0.6	0.5 ± 0.5	27	—
Symplocos tinctoria	1.8 ± 1.8	1.7 ± 1.7	10	0.8 ± 0.8	0.7 ± 0.7	27	15
Vaccinium corymbosum	—	—	—	4.3 ± 4.3	8.3 ± 5.1	29	—

* Significance at $P \leq 0.05$

‡T-tests used for parametric data, Mann-Whitney U test used for nonparametric data. T is the rank sum of IVs which was compared to critical values of T to determine significance, where $N_1=3$, $N_2=3$, $T_L=5$, $T_U=16$ for control sites and $N_1=5$, $N_2=5$, $T_L=18$, $T_U=37$ for infested sites.

†Value represents t-ratio for parametric data. All others represent rank sums (T)

Table 3.3 Mean importance values ± standard error (SE) and test statistics for species at shrub layer by treatment. The top 4 greatest mean IVs for each treatment are bolded.

Species	Control Mean IV ¥ ± SE	Infested Mean IV ¥ ± SE	t-ratio/T‡
Acer rubrum	2.1 ± 2.1	0.3 ± 0.3	15
Arundinaria gigantea	0.9 ± 0.9	—	—
Callicarpa americana	—	0.2 ± 0.2	—
Clethra alnifolia	—	4.2 ± 3.1	—
Cliftonia monophylla	0.9 ± 0.9	1.4 ± 1.4	14
Cornus foemina	1.1 ± 1.1	0.5 ± 0.5	15
Cyrilla racemiflora	—	0.3 ± 0.3	—
Erechtites hieracifolia	—	0.2 ± 0.2	—
Gordonia lasianthus	1.8 ± 1.8	7.9 ± 5.0	12
Hamamelis virginiana	0.8 ± 0.8	1.1 ± 0.7	13
Hypericum hypericoides	—	0.3 ± 0.3	—
Ilex coriacea	**131.0 ± 67.8**	**38.3 ± 16.7**	17
Ilex glabra	—	0.7 ± 0.7	—
Ilex opaca	5.3 ± 5.3	—	—
Itea virginica	—	3.2 ± 2.4	—
Liquidambar styraciflua	3.8 ± 2.5	—	—
Lyonia ligustrina	5.4 ± 2.8	0.8 ± 0.8	18
Lyonia lucida	**18.5 ± 14.6**	**69.1 ± 23.4**	8
Magnolia grandiflora	1.1 ± 1.1	—	—
Magnolia virginiana	2.4 ± 2.4	9.2 ± 2.5	1.992†
Morella caroliniensis	0.7 ± 0.7	8.5 ± 7.9	12
Morella cerifera	10.5 ± 10.5	1.4 ± 1.4	15
Nyssa sp.	5.5 ± 5.5	2.1 ± 2.1	15
Osmanthus americanus	9.0 ± 9.0	—	—
Osmunda cinnamomea	—	0.8 ± 0.8	—
Persea borbonia	**57.1 ± 25.0**	**116.5 ± 31.7**	1.468†
Photinia pyrifolia	0.6 ± 0.6	—	—
Pinus sp.	—	0.2 ± 0.2	—
Pteridium aquilinum	—	0.4 ± 0.4	—
Quercus nigra	3.7 ± 2.2	1.2 ± 0.8	-1.107†
Symplocos tinctoria	6.0 ± 4.0	1.5 ± 1.5	1.025†
Rhododendron sp.	—	1.2 ± 1.2	—
Rhododendron viscosum	—	1.5 ± 1.5	—
Rubus sp.	—	3.7 ± 3.7	—
Serenoa repens	—	0.5 ± 0.5	—
Toxicodendron radicans	—	0.3 ± 0.3	—
Toxicodendron vernix	—	1.5 ± 1.5	—
Vaccinium arboreum	6.7 ± 6.7	0.4 ± 0.4	0.390†
Vaccinium corymbosum	10.4 ± 2.3	**19.7 ± 1.4**	0.350†*
Vaccinium elliottii	**22.3 ± 22.3**	—	—
Viburnum nudum	—	0.4 ± 0.4	—
Woodwardia virginica	0.6 ± 0.6	—	—

* Significant difference at $P \leq 0.05$

¥ Maximum mean IV was 300 for each treatment.

†Value represents t-ratio for parametric data. All others represent rank sums (T)

‡ T-tests used for parametric data, Mann-Whitney U test for nonparametric data. T is the rank sum of the IV for the control sites, which was compared to critical values of T to determine significance, where $N_1=3$, $N_2=5$, $T_L=6$, $T_U=21$.

Table 3.4 Mean importance values ± standard error (SE) and test statistics for species at herb layer by treatment. The top 4 greatest mean IVs for each treatment are bolded.

Species	Control Mean IV ¥ ± SE	Infested Mean IV ¥ ± SE	t-ratio/T‡
Acer rubrum	3.3 ± 2.2	2.7 ± 1.4	-0.213†
Arundinaria gigantea	1.0 ± 0.6	0.1 ± 0.1	-1.535†
Berchemia scandens	0.8 ± 0.7	—	—
Bignonia capreolata	1.3 ± 0.9	—	—
Botrychium sp.	0.3 ± 0.3	—	—
Callicarpa americana	—	0.1 ± 0.1	—
Carex spp.	8.1 ± 8.1	1.0 ± 1.0	15
Chasmanthium laxum	1.6 ± 1.6	—	—
Clethra alnifolia	0.9 ± 0.5	1.5 ± 1.1	13.5
Cliftonia monophylla	—	3.1 ± 1.9	—
Cyrilla racemiflora	—	0.4 ± 0.4	—
Dichanthelium sp.	0.9 ± 0.9	—	—
Dioscorea villosa	0.9 ± 0.9	—	—
Erechtites hieracifolia	—	0.4 ± 0.4	—
Gelsemium sempervirens	2.9 ± 1.0	0.4 ± 0.4	-2.429†
Gordonia lasianthus	0.3 ± 0.3	6.6 ± 4.8	12
Hamamelis virginiana	0.3 ± 0.3	0.1 ± 0.1	15
Hexastylis arifolia	—	0.4 ± 0.4	—
Hypericum hypericoides	0.6 ± 0.6	—	—
Ilex coriacea	**43.8 ± 30.0**	**13.6 ± 8.6**	-0.966†
Ilex opaca	1.9 ± 1.5	0.1 ± 0.1	18
Itea virginica	0.9 ± 0.5	3.5 ± 2.0	1.268†
Liquidambar styraciflua	2.8 ± 2.5	—	—
Liriodendron tulipifera	0.3 ± 0.3	—	—
Lyonia ligustrina	**12.8 ± 7.0**	3.1 ± 3.1	-1.283†
Lyonia lucida	**13.1 ± 7.0**	**56.6± 25.7**	10
Magnolia virginiana	2.0 ± 1.4	1.5 ± 0.7	-0.282†
Mitchella repens	4.2 ± 2.2	1.2 ± 0.9	-1.286†
Morella caroliniensis	0.3 ± 0.3	2.2 ± 2.0	12
Morella cerifera	1.8 ± 1.8	—	—
Moss	—	1.6 ± 1.2	—
Nyssa sp.	1.1 ± 0.7	1.3 ± 0.9	0.1733†
Osmanthus americanus	0.6 ± 0.6	—	—
Osmunda cinnamomea	4.4 ± 2.4	4.1 ± 2.5	14
Parthenocissus quinquefolia	—	1.9 ± 1.3	—
Peltandra virginica	—	0.6 ± 0.6	—
Persea borbonia	**26.8 ± 11.2**	**43.6 ± 26.4**	14

Table 3.4 continued

Species	Control Mean IV ¥ ± SE	Infested Mean IV ¥ ± SE	t-ratio/ T‡
Pinus sp.	0.8 ± 0.8	0.4 ± 0.4	0.683†
Pteridium aquilinum	0.4 ± 0.4	2.6 ± 1.6	-0.342†
Quercus sp.	3.5 ± 0.6	1.4 ± 0.9	18
Quercus laurifolia	2.2 ± 1.1	0.3 ± 0.3	18
Quercus nigra	5.0 ± 4.6	0.4 ± 0.4	17
Rhododendron sp.	0.5 ± 0.5	0.4 ± 0.4	14
Rhododendron viscosum	—	0.2 ± 0.2	—
Rubus sp.	—	4.3 ± 2.6	—
Smilax glauca	9.5 ± 9.1	1.9 ± 0.9	14
Smilax laurifolia	3.1 ± 1.7	6.2 ± 4.3	13
Smilax rotundifolia	—	0.2 ± 0.2	—
Sphagnum sp.	0.3 ± 0.3	2.1 ± 2.1	14
Symplocos tinctoria	3.8 ± 1.6	1.1 ± 1.1	1.589†
Toxicodendron radicans	—	1.6 ± 1.0	—
Toxicodendron vernix	—	0.5 ± 0.5	—
Vaccinium arboreum	8.0 ± 8.0	0.3 ± 0.3	15
Vaccinium corymbosum	6.6 ± 5.3	3.1 ± 2.1	-0.621†
Vaccinium elliottii	5.9 ± 5.9	—	—
Viburnum nudum	—	0.8 ± 0.6	—
Vitis rotundifolia	5.5 ± 2.5	**11.3± 5.8**	0.915†
Woodwardia areolata	2.1 ± 2.1	9.1 ± 7.6	12
Woodwardia virginica	2.6 ± 2.6	0.3 ± 0.3	15

†Value represents t-ratio for parametric data. All others represent rank sums (T)

¥ Maximum mean IV was 200 for each treatment

‡T-tests used for parametric data, Mann-Whitney U test used for nonparametric data. T is the rank sum of the IV for the control sites, which was compared to critical values of T to determine significance, where N_1=3, N_2=5, T_L=6, T_U=21.

Table 3.5 Nested ANOVA for abiotic factors tested where treatment and site nested within treatment were the effects.

Factor Tested	df	F	P
% Cover Woody Debris			
Treatment (control, infested)	1, 6	0.0557	0.8135
Site[Treatment]	6, 58	5.6383	<0.0001*
% Cover Litter			
Treatment (control, infested)	1, 6	0.7500	0.3871
Site[Treatment]	6, 58	6.8510	<0.0001*
PAR			
Treatment (control, infested)	1, 6	52.0595	<0.0001*
Site[Treatment]	6, 58	26.4309	<0.0001*
Litter depth			
Treatment (control, infested)	1, 6	1.3748	0.2420
Site[Treatment]	6, 58	11.1467	<0.0001*

* Significance at $P \leq 0.05$

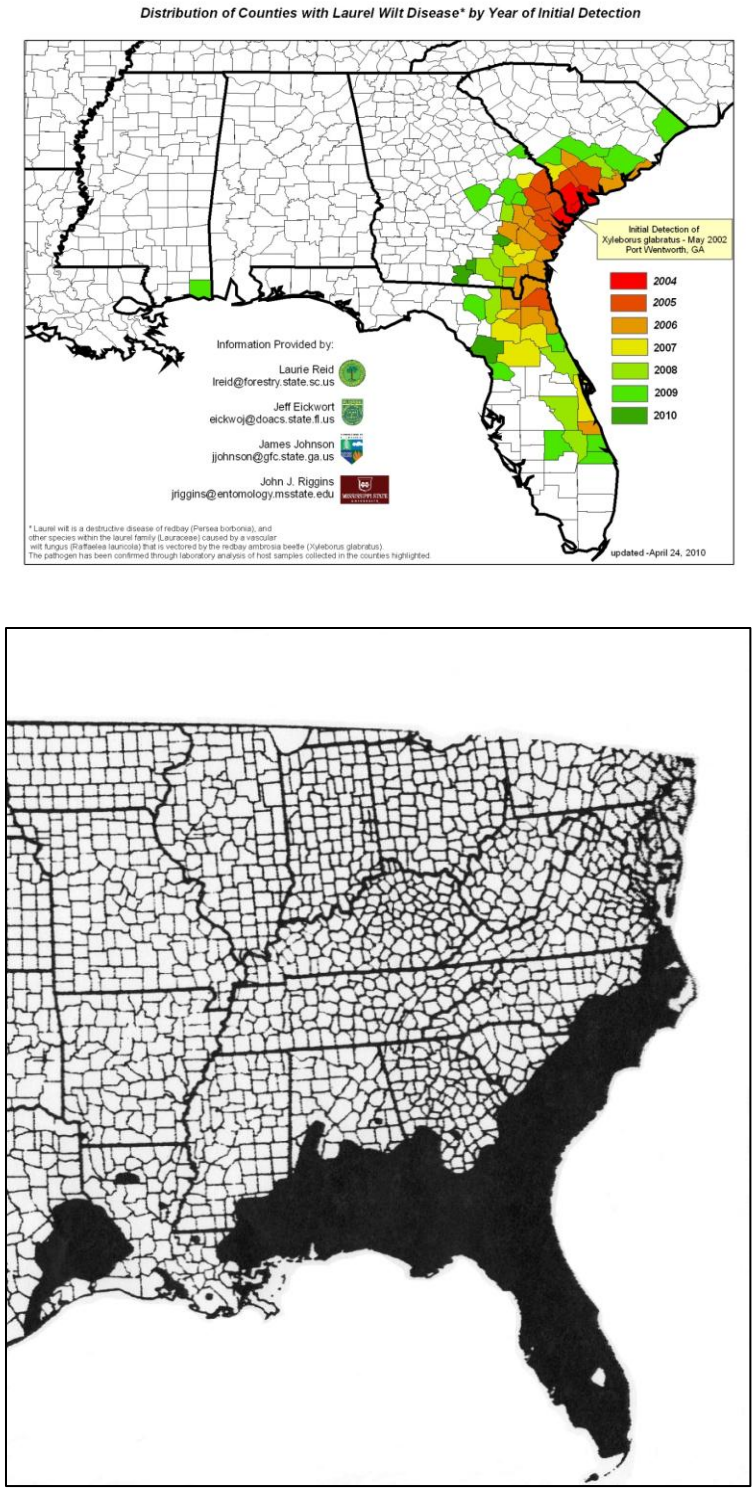


Figure 1.1 Map of a) spread of laurel wilt disease by county and year of initial detection (Reid et al. 2010) and b) redbay range (Brown and Kirkman 1990).

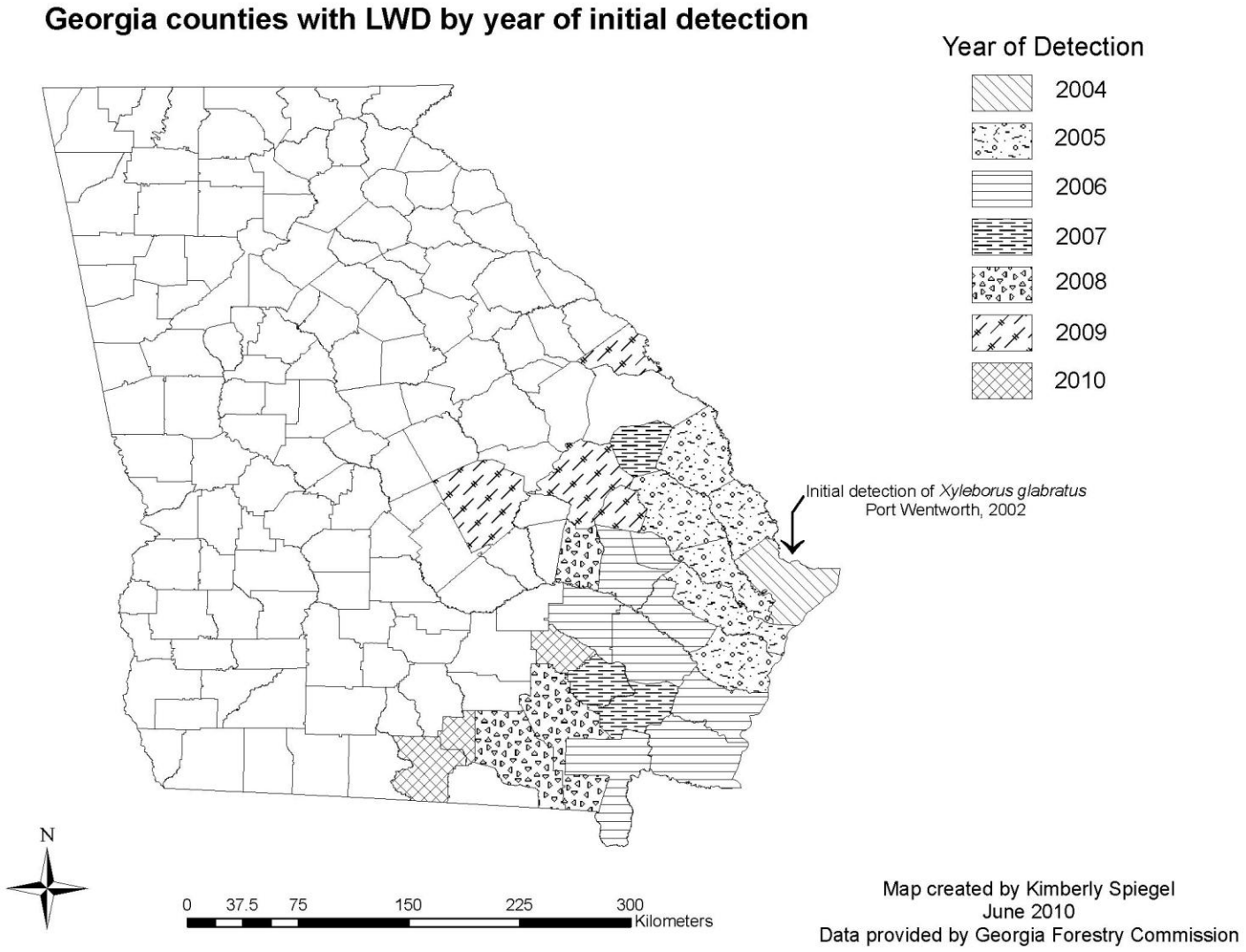


Figure 2.1 Laurel wilt disease spread in Georgia by initial year of detection.

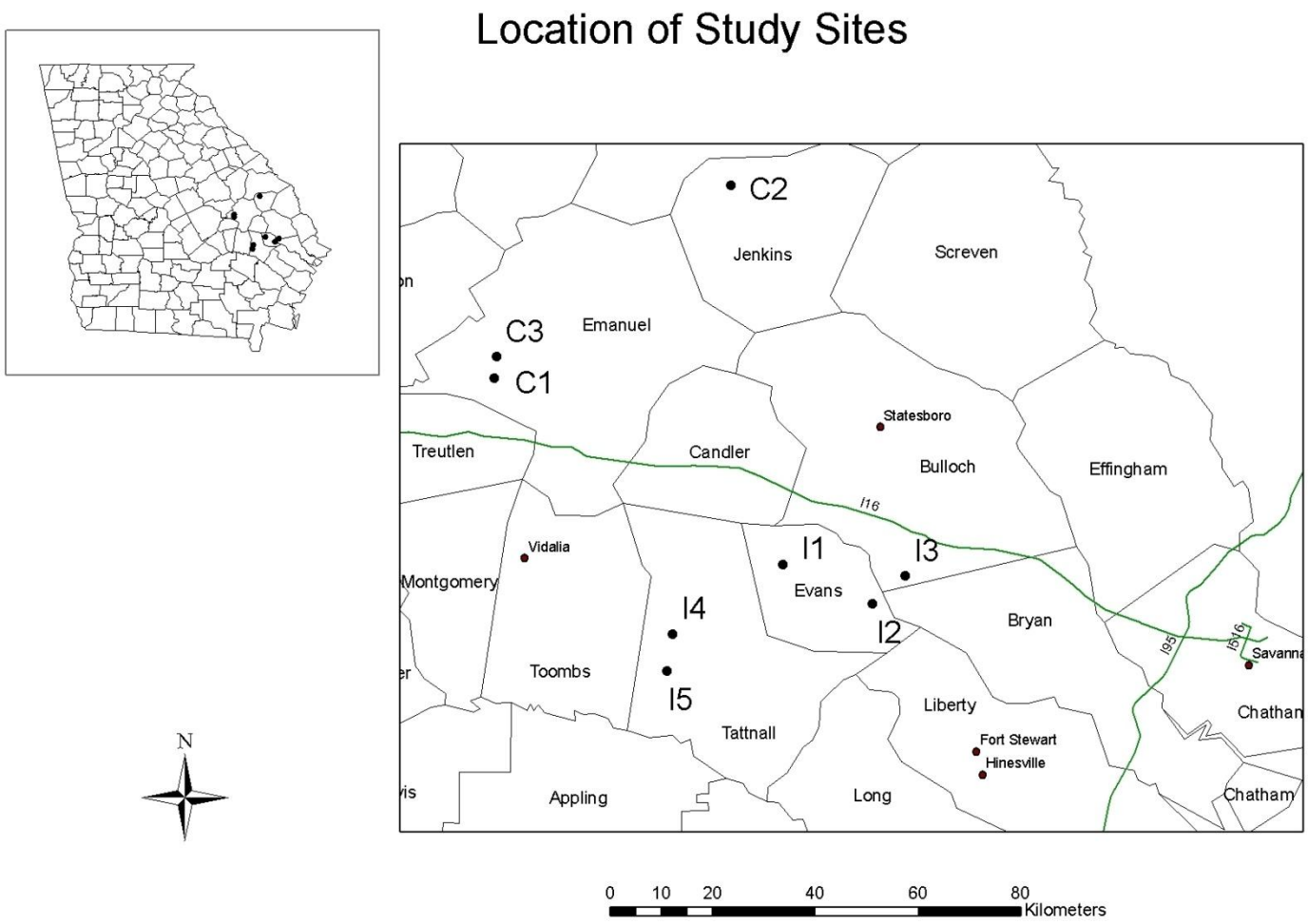
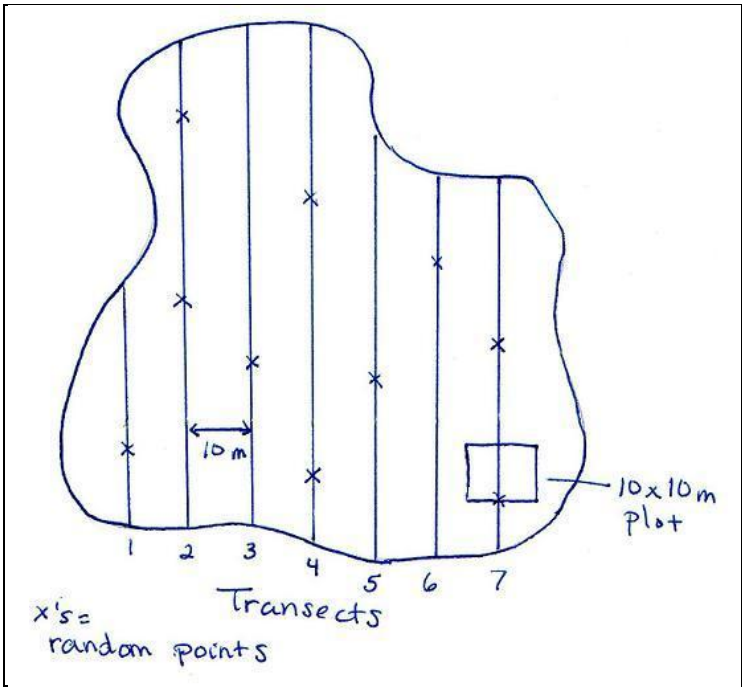


Figure 2.2 Location of study sites. C1-C3 are control sites in Emanuel and Jenkins counties, I1-I5 are infested sites in Bulloch, Evans, and Tattnall counties.

a)



b)

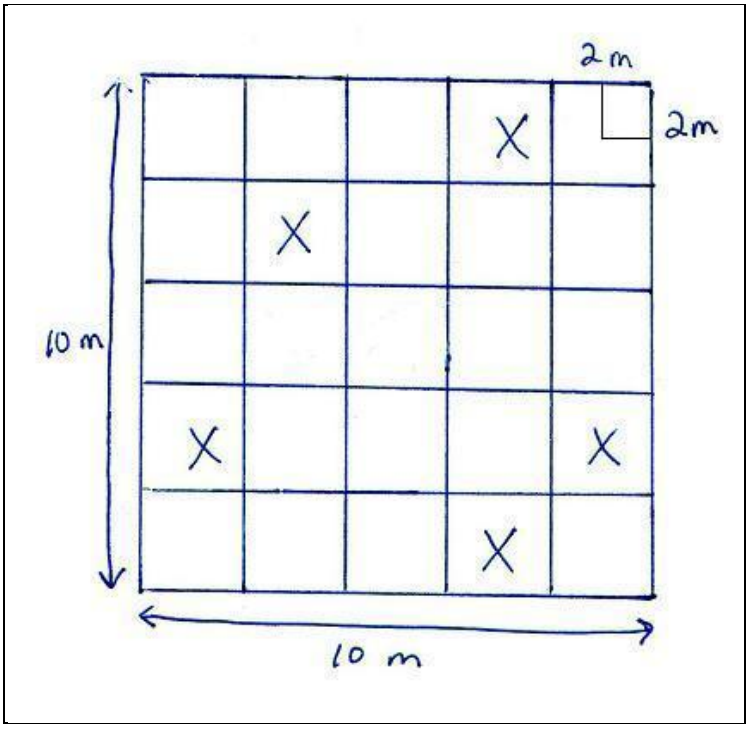


Figure 2.3 a) Study design set up with random transects at least 10 m apart within study area and random points selected along transects for a total of 8-10 10x10 m tree layer plots and b) 4-5 randomly selected 2x2 m shrub layer plots within 10x10 m plots, and nested 1x1 m herb layer plots.

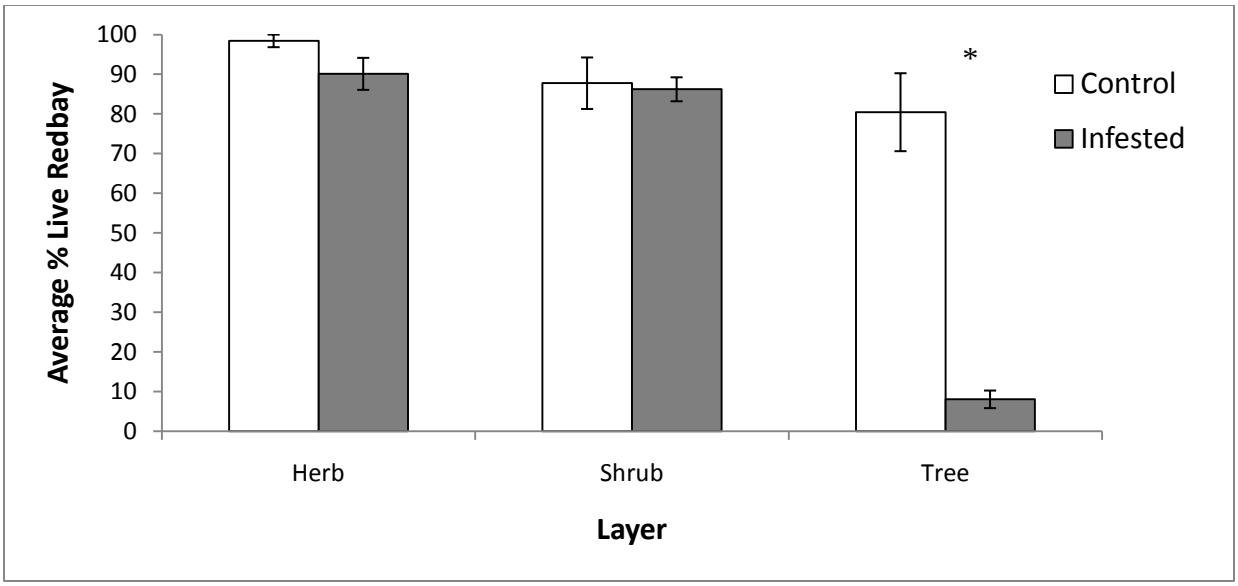


Figure 2.4 Mean percent live redbay stems ± SE by layer. Five infested sites were compared to three control sites. Starred bars show a significant difference in control and infested sites at P ≤0.05.

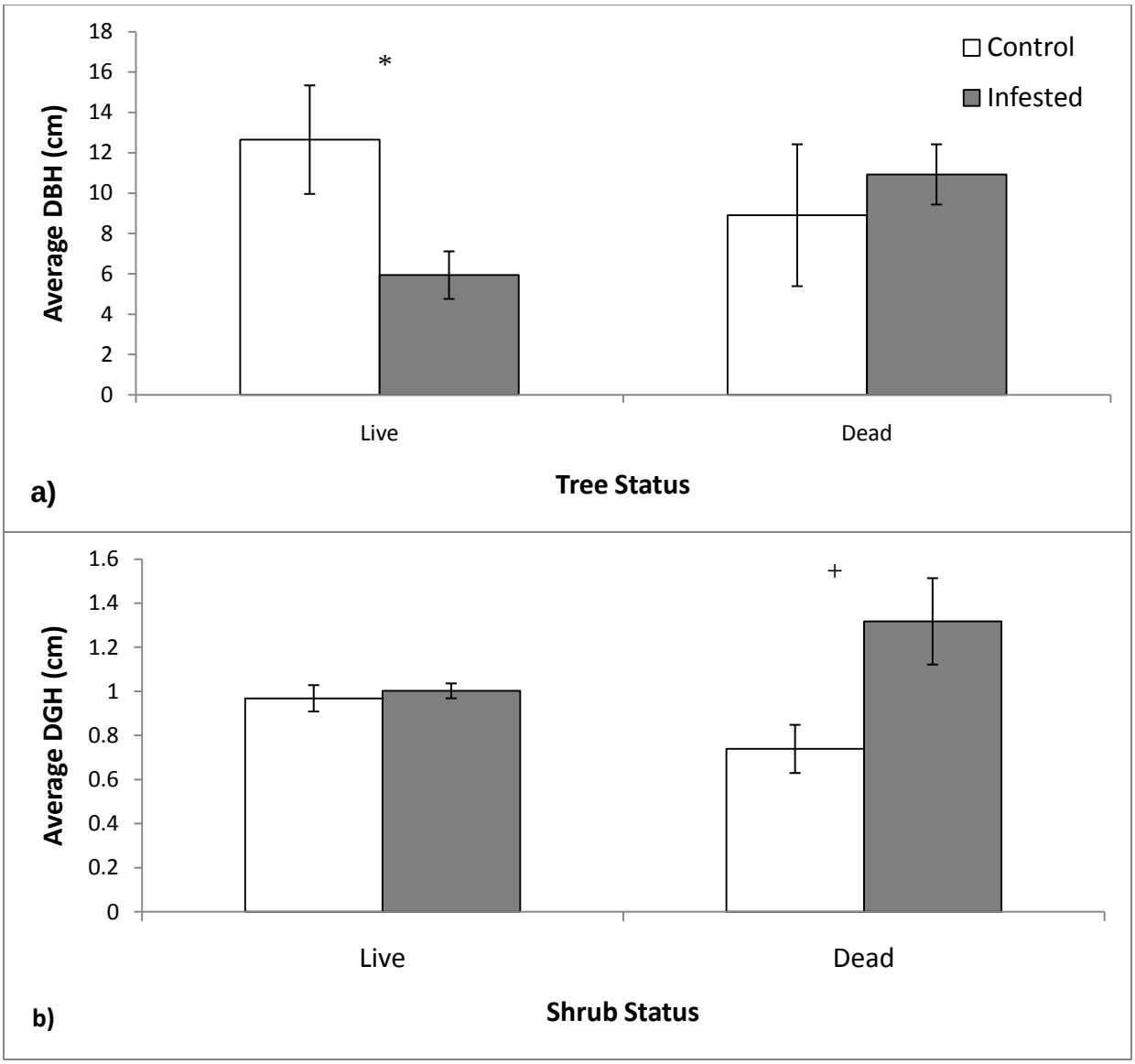


Figure 2.5 Mean a) DBH of all redbay stems (≥3 cm DBH) ± SE and b) DGH of all redbay stems (<3 cm DBH, ≥50 cm high) ± SE in control and infested sites. Five infested sites were compared to three control sites. Starred bars show a significant difference at P ≤0.05, plus sign indicates a trend (P=0.07) between control and infested sites.

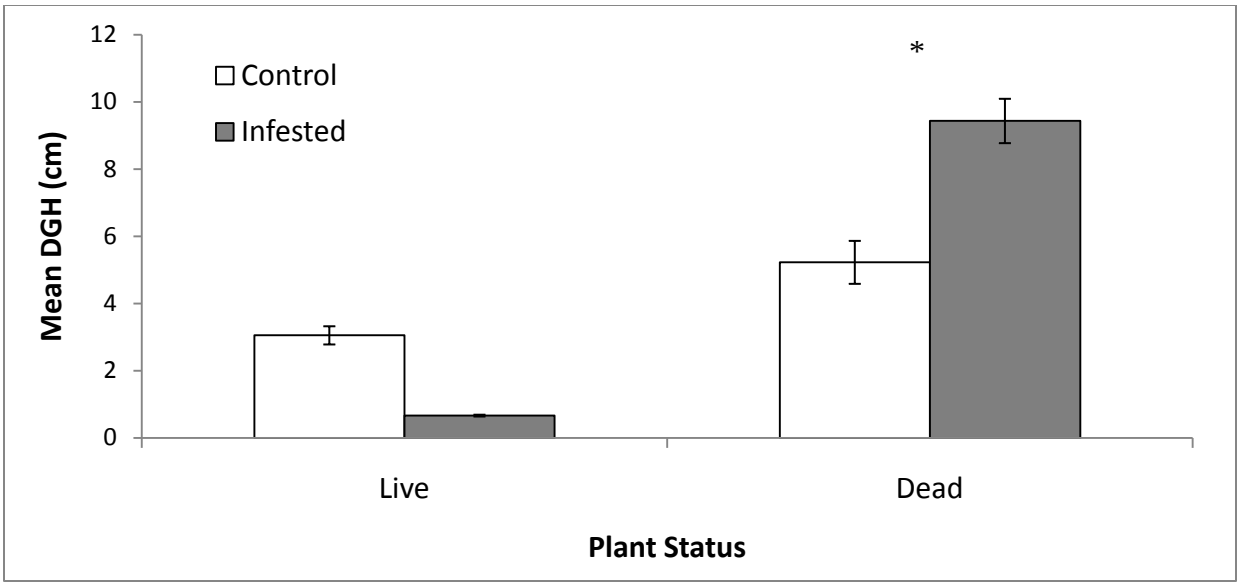


Figure 2.6 Mean DGH of live and dead redbay stems ± SE in control and infested sites. Five infested sites were compared to three control sites. Starred bars show a significant difference between control and infested sites at $P \leq 0.05$.

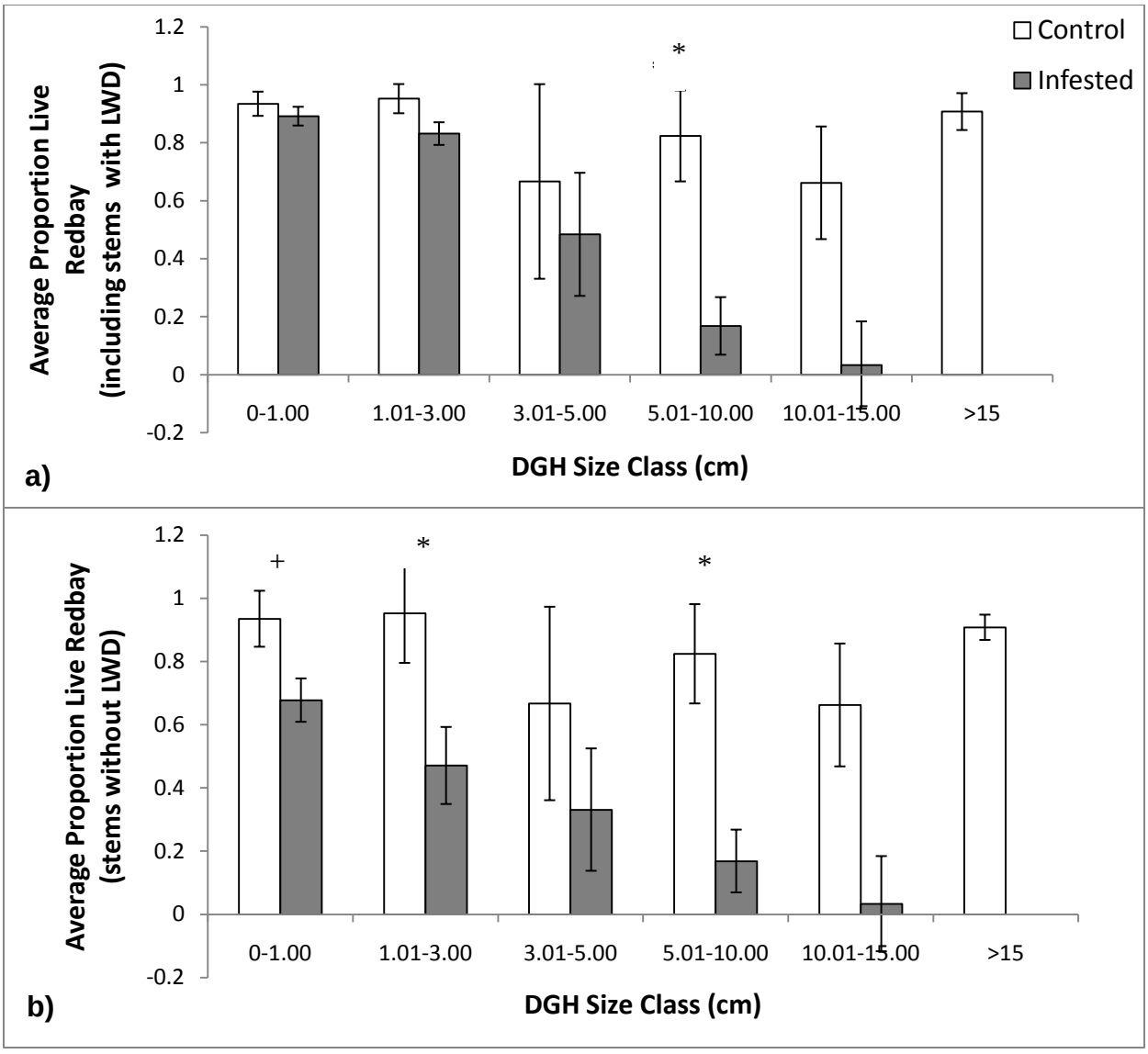


Figure 2.7 Mean proportion a) live and LWD infested redbay stems ± SE and b) healthy live redbay stems ± SE by DGH size class. Five infested sites were compared to three control sites. Starred bars indicate a significant difference between control and infested sites at P≤0.05, a plus sign indicates a trend (P=0.0614).

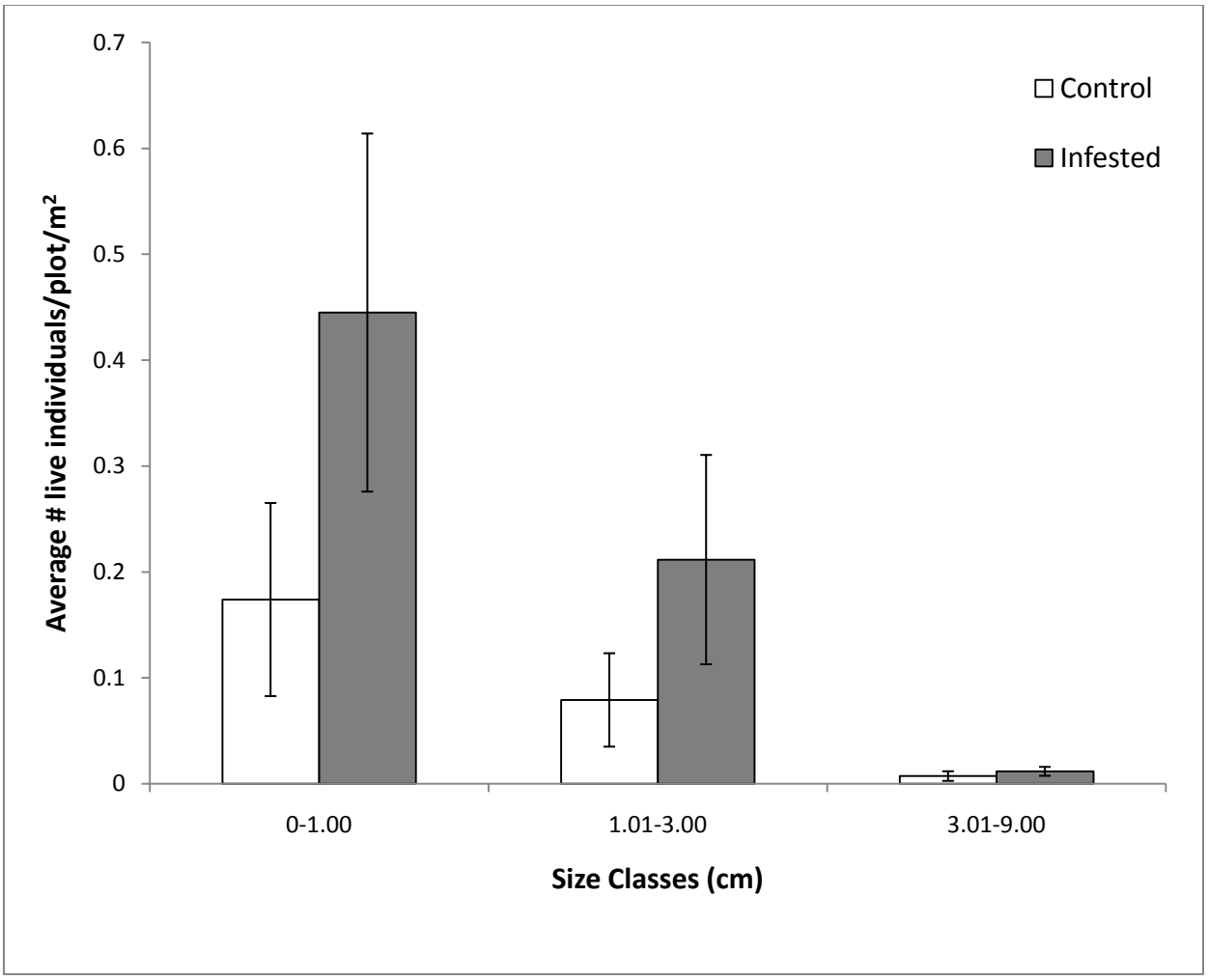


Figure 2.8 Mean density ± SE of live redbay at the shrub layer in control and infested sites. Five infested sites were compared to three control sites. No significant differences were found at any size class.

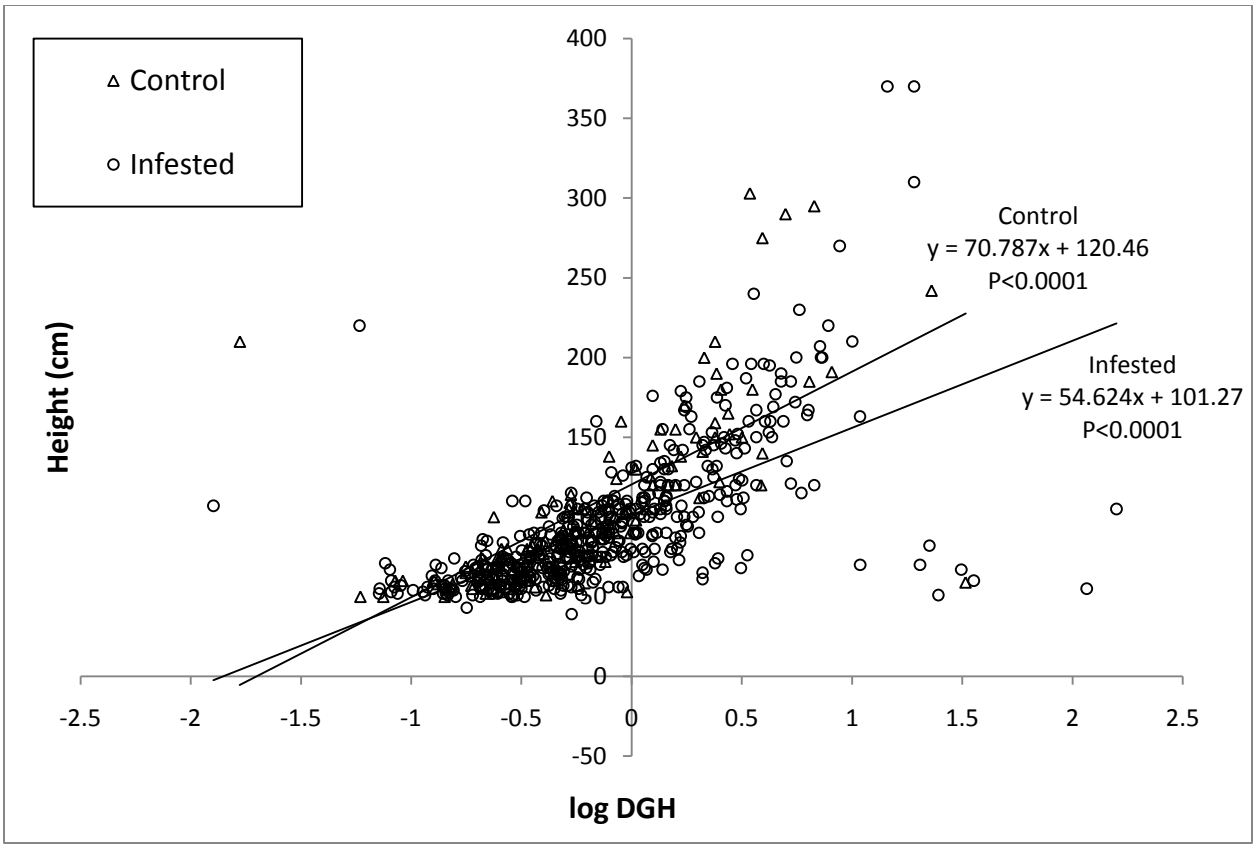


Figure 2.9 Regression of log diameter at ground height and height of shrubs for infested and control sites. Five infested sites were compared to three control sites. DGH was plotted on a log scale to better show data points clustered in range 0-2 cm DGH, though log values were not used in data analyses.

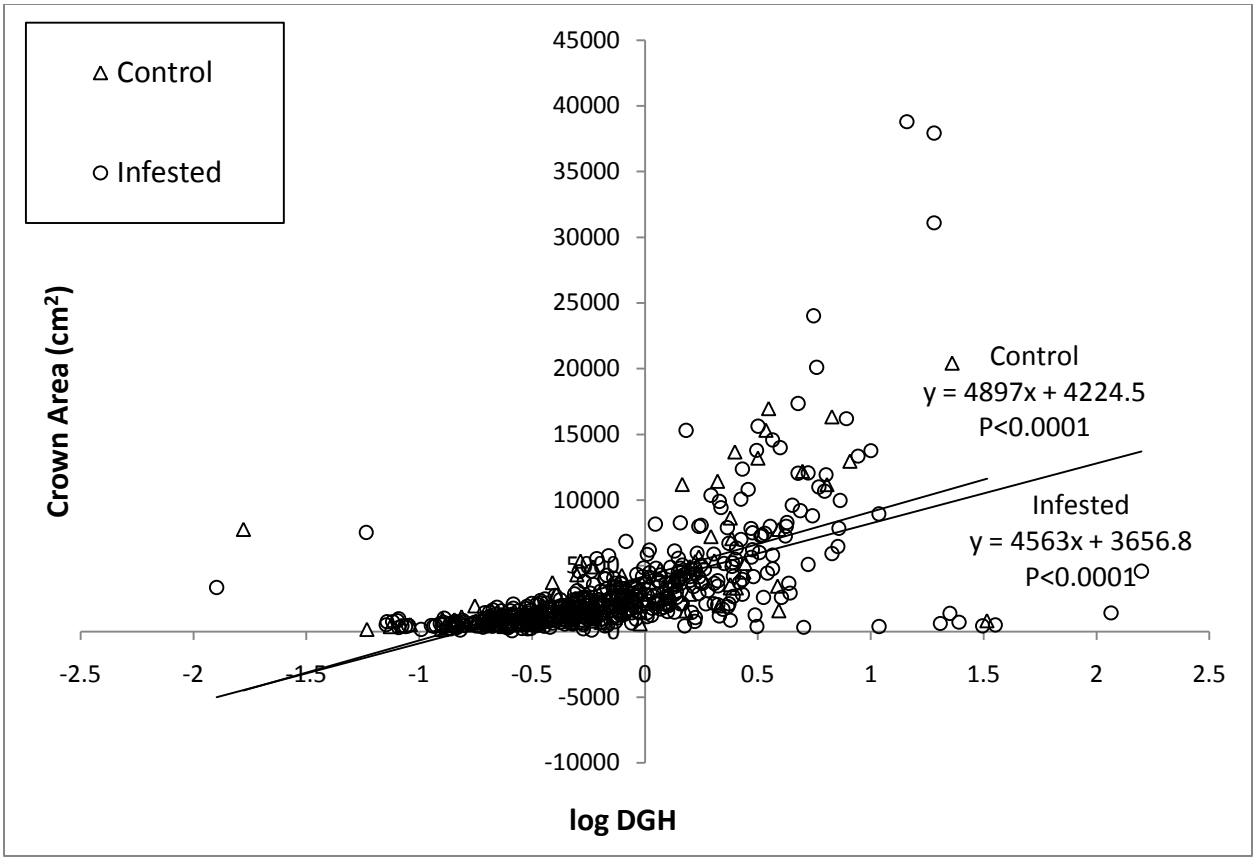


Figure 2.10 Regression of log diameter at ground height and crown area of shrubs for infested and control sites. Five infested sites were compared to three control sites. DGH was plotted on a log scale to better show data points clustered in range 0-2 cm DGH, though log values were not used in data analyses.

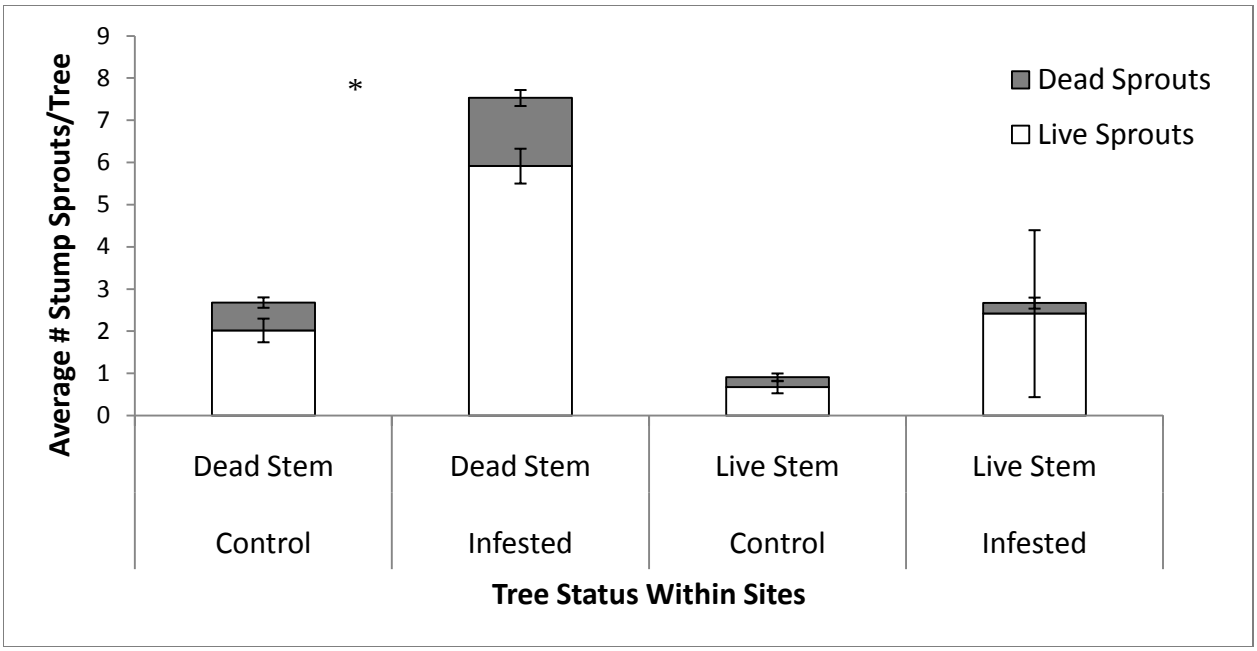


Figure 2.11 The mean number of stump sprouts (live and dead) per stem ± SE for live and dead primary stems (≥3 cm DBH) at control and infested sites. Five infested sites were compared to three control sites. Star indicates a significant difference in total number of sprouts at dead trees in control vs. infested sites at $P \leq 0.05$.

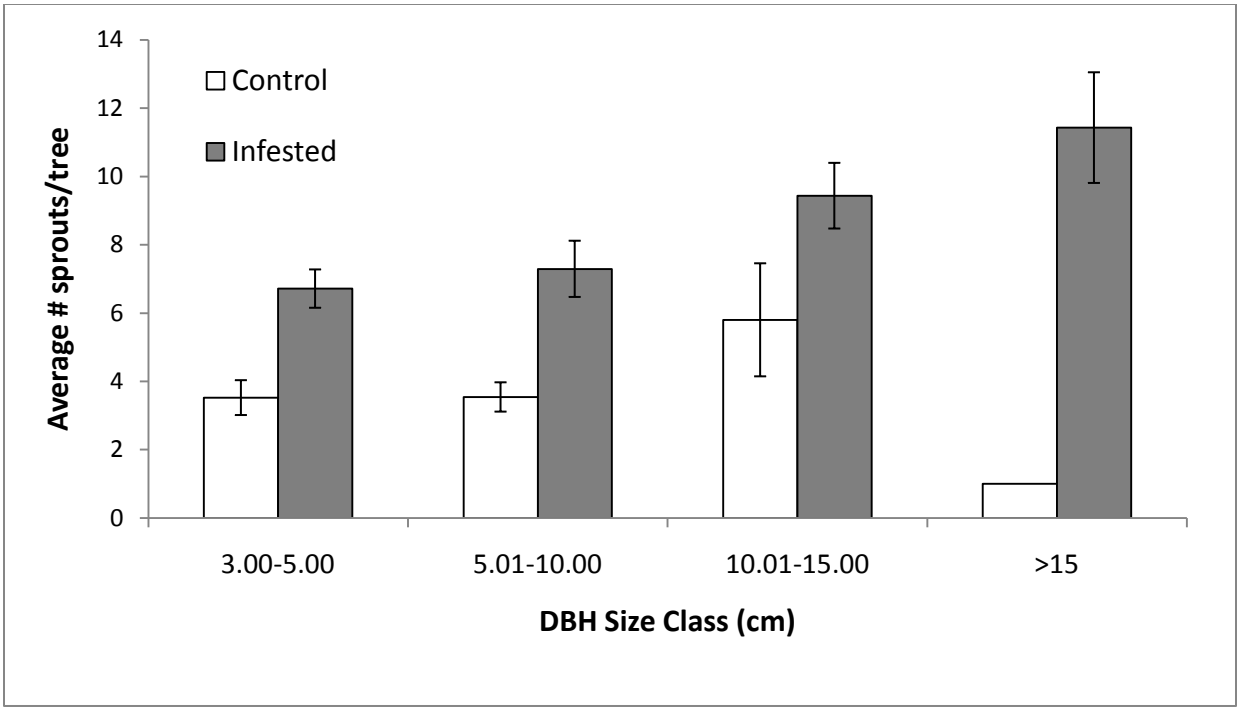


Figure 2.12 Mean number of clonal sprouts per tree ± SE by DBH size class for control and infested sites. Five infested sites were compared to three control sites.

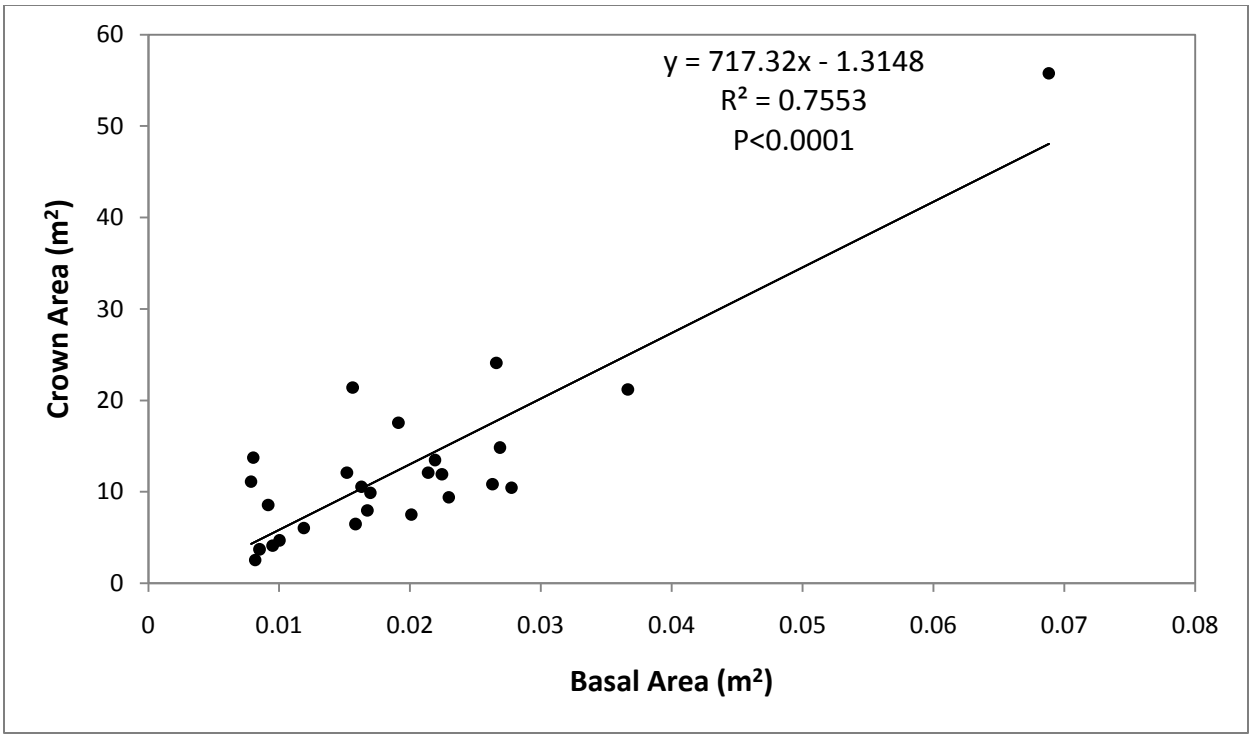


Figure 2.13 The relationship between basal area and crown area of live redbay trees ≥10 cm DBH. Data taken from three control sites. N=26.

a)

b)

Figure 2.14 Aerial photographs of study location I1 in Evans County a) pre- (2005) and b) post- (2009) laurel wilt disease. Note near total loss of redbay in canopy due to laurel wilt disease.

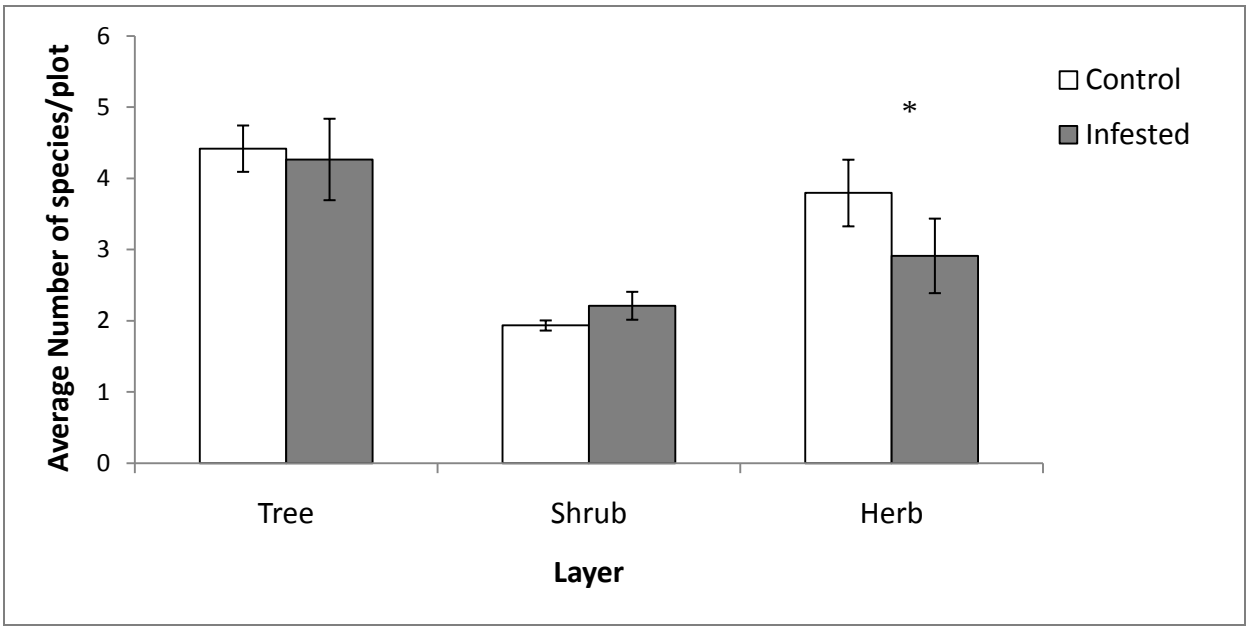


Figure 3.1 Mean number of species per plot ± SE at tree, shrub, and herb layers between control and infested sites. Three control sites were compared to five infested sites. Starred bars indiciate a significant difference between control and infested sites at $P \leq 0.05$. Plot sizes were as follows: tree 10x10 m, shrub 2x2 m, herb 1x1 m.

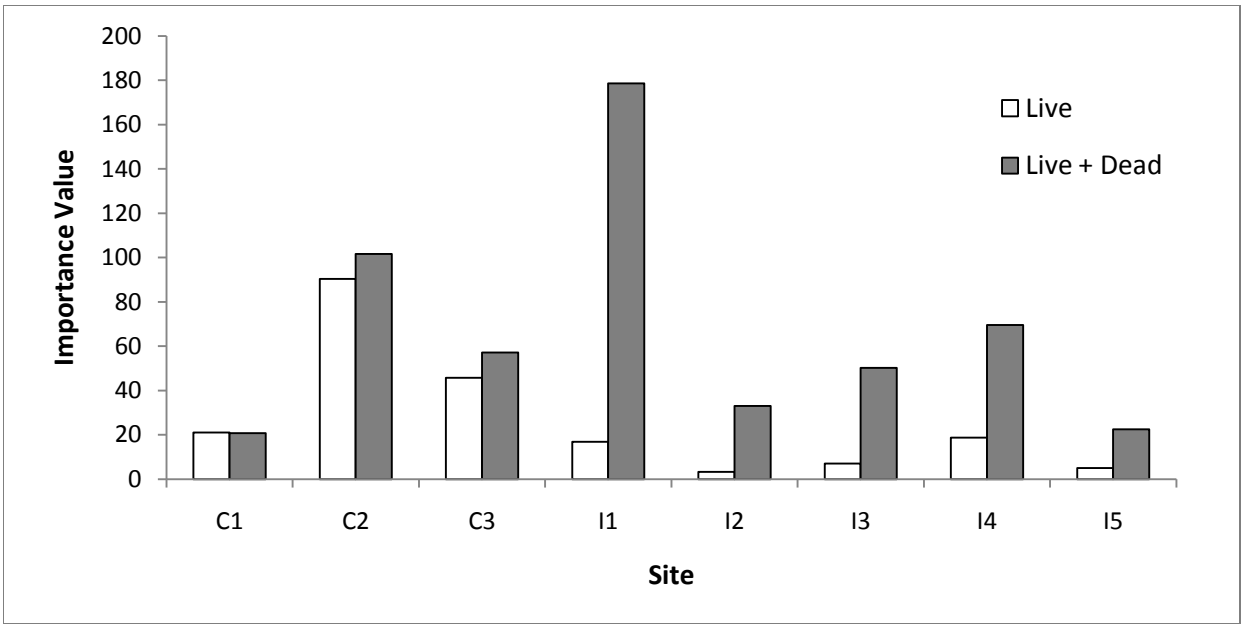


Figure 3.2 Comparison of redbay importance values at the tree layer calculated with live redbay stems only and with live and dead redbay stems combined. IVs were calculated by summing relative frequency, relative density, and relative dominance using crown area. Maximum IV was 300.

APPENDIX A

Mean number of species per plot ± standard error for tree, shrub, and herb layers. At tree layer, plots were 10x10 m, at shrub layer plots were 2x2 m, at herb layer plots were 1x1 m.

Site	Tree	Shrub	Herb
C1	3.88 ± 0.40	1.88 ± 0.25	4.41 ± 0.44
C2	5.00 ± 0.38	2.08 ± 0.20	4.10 ± 0.22
C3	4.38 ± 0.46	1.85 ± 0.15	2.88 ± 0.29
I1	2.25 ± 0.37	1.70 ± 0.13	3.10 ± 0.27
I2	5.20 ± 0.44	2.68 ± 0.28	4.54 ± 0.33
I3	5.25 ± 0.45	2.28 ± 0.16	1.48 ± 0.11
I4	3.75 ± 0.16	2.28 ± 0.19	3.30 ± 0.24
I5	4.88 ± 0.52	1.83 ± 0.21	2.15 ± 0.28

APPENDIX B

Importance values of live tree species ≥3 cm DBH at 10x10 m plots by site. IVs were calculated using relative frequency, relative density, and relative dominance calculated with basal area. Maximum possible IV per site was 300. The top 4 greatest IVs for each site are bolded.

	Control Sites			Infested Sites					# of sites
Species	C1	C2	C3	I1	I2	I3	I4	I5	present
Acer rubrum	**49.3**	**47.4**	—	13.9	**55.3**	**19.9**	—	**46.2**	6
Cliftonia monophylla	—	—	—	—	10.3	19.2	**70.6**	—	3
Cyrilla racemiflora	—	—	—	—	—	11.4	—	—	1
Gordonia lasianthus	**52.0**	—	**63.6**	**188.4**	—	4.3	**78.1**	**26.1**	6
Ilex coriacea	12.7	—	—	—	6.9	—	—	—	2
Ilex opaca	4.4	16.9	—	—	4.0	—	—	—	3
Liriodendron tulipifera	9.9	—	**44.5**	—	—	—	—	—	2
Liquidambar styraciflua	—	**44.7**	—	—	—	3.5	—	12.2	3
Lyonia lucida	—	—	—	—	3.9	—	—	—	1
Magnolia virginiana	**82.4**	—	**72.6**	**32.1**	**47.1**	**52.9**	**126.8**	**45.1**	7
Nyssa ogeche	—	—	—	—	—	9.4	—	—	1
Nyssa sp.	10.9	6.8	38.1	—	**85.9**	**90.4**	5.7	14.8	7
Osmanthus americanus	5.8	—	4.1	—	—	—	—	—	2
Persea borbonia	21.1	**90.4**	**45.7**	**16.9**	3.3	7.1	**18.8**	5.0	8
Pinus elliottii	—	—	—	—	10.6	—	—	—	1
Pinus palustris	—	—	9.3	—	—	—	—	—	1
Pinus taeda	**24.7**	—	10.9	—	**32.4**	**81.8**	—	**110.6**	5
Pinus sp.	—	4.6	—	—	—	—	—	—	1
Quercus sp.	9.1	—	5.7	—	7.4	—	—	12.2	4
Quercus laevis	—	3.7	—	—	—	—	—	—	1
Quercus laurifolia	5.9	3.1	—	—	—	—	—	18.9	3
Quercus nigra	11.9	**82.4**	—	—	8.2	—	—	5.1	4
Symplocos tinctoria	—	—	5.5	—	—	—	—	4.0	2
Rhododendron sp.	—	—	—	—	3.1	—	—	—	1
Vaccinium corymbosum	—	—	—	**48.7**	21.6	—	—	—	2
Number of species	13	9	10	5	14	10	5	11	

APPENDIX C

Importance values (IVs) of live shrub species <3 cm DBH and ≥50 cm in height at 2x2 m plots per site. IVs were calculated using relative frequency, relative density, and relative dominance calculated with crown area. Maximum possible IV was 300. The top 4 greatest mean IVs for each site are bolded.

	Control Sites			Infested Sites					# sites
Species	C1	C2	C3	I1	I2	I3	I4	I5	found
Acer rubrum	—	6.2	—	P	—	1.6	—	—	3
Arundinaria gigantea	—	—	2.7	—	—	—	—	—	1
Callicarpa americana	—	—	—	—	1.2	—	—	—	1
Clethra alnifolia	2.8	—	—	—	16.2	4.8	—	—	3
Cliftonia monophylla	3.4	—	—	—	—	—	6.8	—	2
Cornus foemina	—	—	—	—	2.3	—	—	—	1
Cyrilla racemiflora	—	—	—	—	—	1.5	—	—	1
Ditrysinia fruticosa	P	—	—	—	—	—	—	—	1
Erechtites hieracifolia	—	—	—	—	1.1	—	—	—	1
Gordonia lasianthus	5.5	—	—	**15.9**	—	—	23.8	—	3
Hamamelis virginiana	—	—	2.3	—	3.4	—	—	2.2	3
Hypericum hypericoides	—	—	—	—	1.3	—	—	—	1
Ilex coriacea	**166.2**	—	**226.8**	P	**49.3**	—	**57.2**	**85.1**	6
Ilex glabra	—	—	—	—	3.5	—	—	—	1
Ilex opaca	—	15.8	—	P	—	—	—	—	2
Itea virginica	—	—	—	—	1.4	12.7	—	2.0	3
Ligustrum sinense	—	—	—	—	—	—	P	—	1
Liquidambar styraciflua	2.7	8.6	—	—	—	—	—	—	2
Lyonia ligustrina	7.2	—	9.1	—	—	—	—	4.0	3
Lyonia lucida	**47.2**	—	8.2	**16.4**	**42.3**	**155.3**	**64.7**	**66.8**	**7**
Magnolia grandiflora	—	3.2	—	—	—	—	—	—	1
Magnolia virginiana	7.1	—	—	7.0	14.6	4.1	15.8	4.6	6
Morella caroliniensis	—	—	2.0	—	**40.1**	—	—	2.5	3
Morella cerifera	—	**31.4**	—	—	7.0	—	—	—	2
Nyssa sp.	—	16.5	—	—	—	10.4	—	—	2
Osmanthus americanus	2.7	—	—	—	—	—	—	—	1
Osmunda cinnamomea	—	—	—	—	4.0	—	—	—	1
Persea borbonia	**41.7**	**106.1**	**23.6**	**239.5**	**58.8**	**84.4**	**93.5**	**106.1**	8
Photinia pyrifolia	—	1.8	—	—	—	—	—	—	1
Phytolacca americana	—	—	—	P	—	—	P	—	2
Pinus sp.	—	—	—	—	1.2	—	—	—	1
Pteridium aquilinum	—	—	—	—	2.0	—	—	—	2
Quercus sp.	—	—	—	—	P	—	—	—	1
Quercus nigra	**7.6**	3.6	—	—	3.8	—	—	2.0	4
Symplocos tinctoria	—	4.3	**13.6**	—	—	—	—	7.5	3
Rhododendron sp.	—	—	—	—	6.2	—	—	—	1
Rhododendron viscosum	—	—	—	—	—	—	7.7	—	1
Rubus sp.	P	—	—	—	18.3	—	—	—	2
Serenoa repens	—	—	—	—	2.4	—	—	—	1
Toxicodendron radicans	—	—	—	—	1.5	—	—	—	1

APPENDIX C continued

Species	Control Sites			Infested Sites					# sites found
	C1	C2	C3	I1	I2	I3	I4	I5	
Toxicodendron vernix	—	—	—	—	—	—	7.5	—	1
Vaccinium arboreum	—	**20.2**	—	—	—	—	—	2.1	2
Vaccinium corymbosum	6.0	13.5	**11.7**	**21.2**	18.3	20.9	22.9	15.0	8
Vaccinium elliottii	—	**67.0**	—	—	—	—	—	—	1
Viburnum nudum	—	—	—	—	—	2.0	—	—	1
Woodwardia virginica	—	1.8	—	—	—	—	—	—	1
Vines									
Gelsemium sempervirens	P	P	—	P	P	—	—	—	4
Smilax glauca	—	P	—	P	—	—	—	—	2
Smilax laurifolia	P	—	P	P	P	P	P	—	6
Smilax rotundifolia	—	—	—	—	—	—	P	—	1
Tillandsia usneoides	—	—	—	P	P	—	—	—	2
Vitis rotundifolia	P	P	P	P	P	—	P	P	7
Number of Species	17	17	11	14	28	11	14	13	

Note: Vine species and species present in 10x10 m plot but not found in any 2x2 m subplot were only noted as present (P).

APPENDIX D

Importance values of species at the herb layer (< 50 cm tall) at 1x1 m plots per site. IVs were calculated using relative frequency and relative dominance calculated with percent cover. Maximum possible IV was 200. The top 4 greatest mean IVs for each site are bolded.

	Control Sites			Infested Sites					# sites
Species	C1	C2	C3	I1	I2	I3	I4	I5	found
Acer rubrum	7.5	2.4	—	1.9	5.1	—	—	6.7	5
Arundinaria gigantea	—	2.0	1.0	—	0.5	—	—	—	3
Berchemia scandens	2.2	—	—	—	—	—	—	—	1
Bignonia capreolata	1.1	—	3.0	—	P	—	—	—	3
Botrychium sp.	0.8	—	—	—	—	—	—	—	1
Callicarpa americana	—	—	—	—	0.7	—	—	—	1
Carex spp.	**24.4**	—	—	—	5.1	—	—	—	2
Chasmanthium laxum	4.7	—	—	—	—	—	—	—	1
Clethra alnifolia	1.8	—	1.0	—	5.6	2.0	—	—	4
Cliftonia monophylla	—	—	—	—	—	**8.3**	7.4	—	2
Cyrilla racemiflora	—	—	—	—	—	1.9	—	—	1
Dichanthelium sp.	2.7	P	—	—	P	—	—	—	3
Dioscorea villosa	2.6	—	—	—	—	—	—	—	1
Erechtites hieracifolia	—	—	—	1.9	—	—	—	—	1
Gelsemium sempervirens	3.5	4.3	1.0	1.9	—	—	—	—	4
Gordonia lasianthus	0.8	—	—	**24.9**	—	—	8.0	—	3
Hamamelis virginiana	—	—	1.0	—	0.5	—	—	—	2
Hexastylis arifolia	—	—	—	—	2.1	—	—	—	1
Hypericum hypericoides	1.8	—	—	—	—	—	—	—	1
Ilex coriacea	**30.1**	—	**101.2**	—	13.4	—	8.1	**46.5**	**5**
Ilex opaca	0.8	4.9	—	—	0.5	—	—	—	3
Itea virginica	1.8	—	1.0	—	1.7	**10.3**	—	5.5	5
Liquidambar styraciflua	7.8	0.7	—	—	—	—	—	—	2
Liriodendron tulipifera	—	—	1.0	—	—	—	—	—	1
Lyonia ligustrina	**14.5**	—	**24.0**	—	—	—	—	**15.3**	**3**
Lyonia lucida	**24.0**	—	**15.3**	**13.6**	**15.1**	**154.3**	**51.4**	**48.5**	**7**
Magnolia virginiana	4.8	—	1.1	—	3.0	—	1.9	2.7	5
Mitchella repens	7.2	5.4	—	—	4.6	—	—	1.3	4
Morella caroliniensis	—	—	1.0	—	10.0	—	1.1	—	3
Morella cerifera	—	5.5	—	—	—	—	—	—	1
Moss	—	—	—	**6.0**	1.9	—	—	—	2
Nyssa sp.	0.8	2.4	—	—	—	1.9	4.4	—	4
Osmanthus americanus	1.7	—	—	—	P	—	—	—	2
Osmunda cinnamomea	3.5	0.7	9.0	1.9	**14.0**	3.8	1.0	—	7
Parthenocissus quinquefolia	—	—	—	P	3.1	—	6.5	—	3
Peltandra virginica	—	—	—	—	—	—	2.9	—	1
Persea borbonia	11.5	**48.5**	**20.3**	**148.1**	7.9	**9.0**	**26.9**	**26.2**	**8**
Pinus sp.	1.7	0.7	—	P	2.0	—	—	—	4
Pteridium aquilinum	P	—	1.2	—	7.2	—	—	5.7	4

APPENDIX D continued

	Control			Infested					# sites
Species	C1	C2	C3	I1	I2	I3	I4	I5	found
Quercus sp.	4.3	2.4	3.9	P	P	—	3.0	4.2	7
Quercus laurifolia	3.7	3.0	—	—	—	—	—	1.3	3
Quercus nigra	0.9	14.2	—	—	—	1.9	—	—	3
Rhododendron sp.	—	1.5	—	—	2.0	—	—	—	3
Rhododendron viscosum	—	—	—	—	—	—	1.0	—	1
Rubus sp.	—	—	—	P	10.1	—	11.3	—	3
Smilax glauca	0.8	**27.6**	—	—	4.1	3.8	—	1.3	5
Smilax laurifolia	3.3	—	6.0	—	4.1	—	**22.8**	4.0	5
Smilax rotundifolia	—	—	—	—	1.0	—	—	—	1
Sphagnum sp.	0.9	—	—	—	10.4	—	—	—	2
Symplocos tinctoria	3.1	1.5	6.8	—	—	—	—	5.6	4
Toxicodendron radicans	P	—	—	P	4.1	—	—	4.0	4
Toxicodendron vernix	—	—	—	—	—	—	2.3	—	1
Vaccinium arboreum	—	**24.1**	—	—	—	—	—	1.5	2
Vaccinium corymbosum	2.7	17.1	—	—	2.2	—	1.9	11.2	5
Vaccinium elliottii	—	**17.7**	—	—	—	—	—	—	1
Viburnum nudum	—	—	—	—	—	2.9	1.0	—	2
Viola sp.	—	—	—	—	P	—	—	—	1
Vitis rotundifolia	9.7	5.8	1.0	—	**17.2**	—	**30.9**	8.4	6
Woodwardia areolata	6.4	7.7	—	—	**39.1**	—	6.4	—	4
Woodwardia virginica	—	—	—	—	1.5	—	—	—	1
Number of Species	37	23	19	13	36	11	20	18	

Note: Species present in 10x10 m plot but not found in any 1x1 m subplot were only noted as present (P).

APPENDIX E

Mean percent cover of litter and woody debris ± standard error (SE) measured at 1x1 m subplots.

Site	Mean % Cover Litter ± SE	Mean % Cover Woody Debris ± SE
C1	61.6 ± 4.1	8.3 ± 1.4
C2	76.3 ± 2.4	4.8 ± 0.6
C3	69.7 ± 3.3	7.4 ± 1.8
I1	54.7 ± 4.2	11.4 ± 2.0
I2	58.3 ± 3.6	10.6 ± 2.3
I3	74.0 ± 3.3	6.4 ± 1.2
I4	78.7 ± 2.5	7.2 ± 1.0
I5	77.3 ± 3.7	4.1 ± 0.8

APPENDIX F

Mean PAR and mean litter depth ± standard error (SE) measured at 2x2 m subplots.

Site	Mean PAR (μmol $m^{-2}s^{-1}$) ± SE	Mean Litter Depth (cm) ± SE
C1	50.5 ± 8.6	5.4 ± 0.6
C2	86.1 ± 11.1	3.4 ± 0.2
C3	50.4 ± 13.3	3.0 ± 0.1
I1	935.1 ± 98.9	6.2 ± 0.4
I2	102.3 ± 17.0	5.6 ± 0.5
I3	128.0 ± 37.0	4.5 ± 0.3
I4	200.6 ± 47.0	3.4 ± 0.2
I5	133.1 ± 36.0	3.4 ± 0.2

APPENDIX G

Growth and Resource Allocation in Redbay and Loblolly Bay Seedlings in Response to Light and Nutrients in a Greenhouse Experiment

Introduction

The death of a forest tree creates a canopy gap which temporarily increases the availability of light to the understory (Chazdon and Fetcher 1984, Platt and Strong 1989). Tree death may slowly increase the availability of nutrients to other organisms via inputs of leaf litter and woody debris (Vitousek and Denslow 1986, Franklin et al. 1987). This type of disturbance presents an opportunity for other individuals to establish and take advantage of the increase in resources (Canham 1988, Schnitzer and Carson 2001). Small gaps may be colonized by seedlings already established in the shade (non-pioneer or shade-tolerant species) and large canopy gaps are colonized by species with seeds that germinate only in the open (pioneer or shade-intolerant species) (Brokaw 1985, Brokaw 1987, Canham 1988, Whitmore 1989, Dalling 1998, Kneeshaw and Bergeron 1998, Schnitzer and Carson 2001).

It is widely assumed that plants are capable of adjusting the distribution of biomass to their different organs in response to such changes in resources (Johnson 1985, Robinson 1986, Johnson and Thornley 1987, Van der Werf et al. 1993). For example, when nutrients are abundant, plants allocate a high proportion of biomass to leaves and plants often have a low root:shoot ratio (Tilman 1988). Under low nutrient conditions, root growth is optimized while leaf growth is minimized to increase nutrient capture below-ground, hence plants maintain a high root: shoot ratio (Hirose 1987, McConnaughay and Coleman 1999). Low light conditions promote stem and leaf growth to maximize photosynthesis and minimize root growth (Hirose 1987, McConnaughay and Coleman 1999). These observations have led to the development of

the optimal partitioning theory, which predicts that plants respond to environmental variations by partitioning biomass to plant organs that optimize acquisition of either above-ground (e.g. light, CO_2) or below-ground (e.g. water, nutrients) resources in a manner that maximizes growth rates (McConnaughay and Coleman 1999). New colonizers of canopy gaps may alter their allocation of resources with increases in light and nutrients based on this theory.

The loss of canopy from laurel wilt disease-induced mortality of redbay (*Persea borbonia* (L.) Spreng.) increased the availability of light in infested sites (see Chapter 3). This presented an opportunity for gap colonization in forests infected with laurel wilt disease. Loblolly bay (*Gordonia lasianthus* (L.) Ellis) is a shade-tolerant species (Coladonato 1992) commonly found in forest types where redbay, also a shade tolerant species (Gilman and Watson 1993), occurs (Eyre 1980). Both species are small to medium-sized evergreen trees with similar maximum sizes in stem diameter, height, and leaf length (Brown and Kirkman 1990). Loblolly bay may benefit from redbay mortality and the resulting increase in light in canopy gaps. It was present as a canopy tree in 6 of my 8 study sites (I1, I3, I4, I5, C1, and C3) and held the 2nd greatest average importance value at the tree layer in the four infested sites where it was found when dead redbay were excluded. Loblolly bay is a strong competitor in bays and wet flats where tree cover is relatively light and early tree growth (5 to 15 years) is relatively rapid (Gresham and Lipscomb 1990). As a co-dominant species to redbay, loblolly bay may increase in numbers as a result of an increase in light in canopy gaps.

I conducted a greenhouse experiment to measure growth response of loblolly bay along with redbay to determine how they responded to increases in light and nutrients. Two light levels and three nutrient levels were used to simulate control and infested forests. I also evaluated how redbay and loblolly bay partition resources to their roots, stems, and leaves under

variations of light and nutrients as would possibly occur in infested forests with canopy gaps. The specific objectives were: 1) to determine survivorship, 2) measure growth rates and 3) determine root:shoot ratios in seedlings of both species under variable light and nutrient levels.

Methods

Study Species

Loblolly bay (*Gordonia lasianthus* (L.) Ellis) is an evergreen tree that occurs in North Carolina, South Carolina, Georgia, Florida, Alabama, and Mississippi (Coladonato 1992). It grows in wet areas in flat woodlands or shallow depressions with poor to very poor drainage (Gresham and Lipscomb 1990). It can grow up to 20 m in height (Coladonato 1992) and 45 cm in diameter according to Harrar and Harrar (1946), but an individual with a DBH of 70.7 cm was measured in a bay swamp at study site I1. Its leaves are 10-20 cm in length (Gilman and Watson 1993). It has perfect, showy, white flowers about 7 cm across (Brown and Kirkman 1990). Its fruit is a capsule that splits along 5 sutures with winged seeds and matures in autumn (Brown and Kirkman 1990).

For information on redbay see Chapter 2.

Experimental Design

The greenhouse experiment was a randomized factorial design with 3 nutrient levels, 2 plant species, 2 growing media, and 2 light levels. The experiment took place from October 2008 to October 2009 in a research greenhouse on Georgia Southern University.

One hundred and twenty seedlings each of redbay and loblolly bay were collected from study site I1 located in Evans County, GA (32°12′06″N, 81°56′54″ W) in October 2008. To standardize initial size, seedlings collected were from 5-15 cm in height. Seedlings were potted in 10 x 10 x 10 cm pots in playground sand and placed in the greenhouse on Georgia Southern

University campus with greenhouse shades drawn. The plants were allowed to acclimate to greenhouse conditions and watered every several days as needed. In May 2009 shades on the roof of the greenhouse were opened, and almost all of the redbay seedlings and some of the loblolly bay seedlings became sunburned.

Initially, only a sand treatment was planned for this study, but concerns of nutrient-stressed plants led to a second treatment in low nutrient potting soil. In March 2009, another 120 seedlings 5-15 cm in height of redbay and loblolly bay were collected from study site I1. These were potted in 10 x 10 x 10 cm square pots in Sta-Green® All Purpose Potting Mix With Fertilizer (0.14-0.11-0.08: 0.06% NH_4-N, 0.04% NO_3-N, 0.04% urea, 0.11% P_2O_5, 0.08% K_2O). Fertilizer components N-P-K are percentages by weight. The plants were allowed to acclimate to greenhouse conditions for several months and watered every several days as needed.

All pots were spread out on 8 tables 90 cm x 150 cm. Each table contained one species in one medium type, under all nutrient levels, and exposed to either high or low light. The design was pseudoreplicated because of limited materials and funds. Initial measurements of height, stem diameter, leaf count, and average crown width were taken for each plant in June 2009 before application of shade cloth and nutrients. Height was measured from the base of the plant at the sand or soil surface to the tip of the apical meristem. Average crown width was an average of widths measured along two perpendicular axes. For plants with multiple stems, stem diameter and number of leaves were summed and height was measured for the tallest stem. Crown width was included across both stems. The same measurements were made 5 more times, every 3 weeks after application of treatments for a total of 15 weeks. For redbay, 18 replicate plants each received one different nutrient treatment (high, medium, or low) of a granular slow-release fertilizer, Osmocote® Smart- Release® Plant Food (14-14-14: 8.2% NH_4-N, 5.8% NO_3-N, 14%

P_2O_5-P, 14% K_2O-K), and either shade cloth (low light) or no shade cloth (high light) (Table 4.1). For loblolly bay, 16 plants each received the treatments (Table 4.1). There were different sample sizes for loblolly bay and redbay because less loblolly bay survived from collection to the beginning of the experiment. Low nutrient was 43 mL of fertilizer granules per pot, medium was 215 mL (5x low) of fertilizer per pot, and high was 430 mL (10x low) of fertilizer per pot. Nutrients were applied once at the beginning of the experiment. A calculation error was made in determining proper amount of nutrients to apply, which resulted in levels 40 times higher than the recommended amount. This error was not realized until the writing of this paper. Four frames of PVC piping covered with 80% black knitted shade cloth (DeWitt Company, Sikeston, MO) were installed 1 m above the tables for the low light treatment. The percent shade cloth needed was determined by measuring PAR in the understory of control sites and in full sun inside the greenhouse to simulate understory light levels. PAR measurements were made with a Model PAR-80 AccuPAR ceptometer (Decagon Devices Inc., Pullman, WA).

Weekly growth rate was calculated for each plant at the end of the experiment as the difference in height from the 1st to the last measurement divided by the amount of time elapsed, 15 weeks. At the end of 15 weeks, all surviving plants were removed from sand or soil to measure their dry biomass. The stem, leaves, and roots were separated from each plant and dried separately in a drying oven at 105°C for 48 hours and then weighed using an electronic balance. After 48 hours, a subset of plants was weighed and dried for another 8 hours (total 56 hours) to confirm they were fully dried.

Baseline nutrient data of soil for 2 control sites (C1 and C2) and 2 infested sites (I1 and I2) was determined (Table 1). The organic layer was removed before collecting soil samples in the top 12 cm of soil with a soil corer. Several cores were taken throughout the study site and

were homogenized. Soil samples were collected in November 2008 and sent for analysis to the University of Georgia Soil, Plant, and Water Laboratory, Athens, Georgia, USA. Results were reported in lbs/acre and converted to ppm by dividing the value by 2. Monk (1968) showed concentrations of potassium of 122 ppm and phosphorous of 68 ppm in bayheads in Florida. Nutrient levels were lower in southern mixed hardwoods in Florida in which potassium was present as 11 ppm and phosphorous as 6.4 ppm (Monk 1968). Nutrient levels for my sites were in between the two reported by Monk (1968). Nutrient content of soil was not extremely different in control and infested sites, but were slightly higher at infested sites. However, not enough replicate samples were taken to determine statistical difference.

Data Analysis

A full factorial 4-way ANOVA with species, nutrient level, growth medium, and light level as effects were used to analyze biomass data (root, stem, and leaves), root to shoot ratio and weekly growth rate. The four way interaction caused a loss of degrees of freedom and was dropped from analyses. All data were tested for the assumptions of normality with the Shapiro Wilk W test and equal variance with the Levene test. Only plants that survived until the end of the experiment were included in growth analyses. Thirteen plants with negative growth rates were excluded from analyses. Negative growth rates occurred as a result of dieback of one stem when more than one was present. Stem diameter did not increase significantly throughout the experiment, therefore this measurement was not analyzed. Leaf count and crown width were not consistent measurements of plant growth because some plants were affected by sunburn and leaves died, so they were also not used in analyses. A chi-squared test was used to analyze survivorship of each species for each of the variables: medium, light, and nutrients. A chi-

squared test was also used to test for a difference in survivorship between redbay and loblolly bay. All statistical analyses were conducted using JMP 8.0 (SAS Institute Inc., Cary, NC, 2008).

Results

Survival

Not all plants survived until the end of the experiment (Table G.2). Of 192 loblolly bay plants, only 98 survived in the 15 week period, a 51% survival rate. For redbay, 135 out of 216 plants survived, a 62.5% survival. Percent survival did not differ statistically between the two species (df=14, χ^2=23.0, P=0.0603). All loblolly bay grown in soil under shade cloth at high nutrient levels died. Only loblolly bay grown in sand at high light and low nutrients had 100% survival (Table G.2). Loblolly bay also had high survival (93.75%) in sand at high light and medium nutrients, in sand at low light and low nutrients, and in soil at high light and low nutrients (Table G.2). Redbay survival was greatest (94.4%) in soil at low light and low nutrients (Table G.2). The next highest percent survivals were 88.9% for redbay in sand at low light and medium nutrients, 83.3% survival in sand at low light and low nutrients, and 77.8% at sand, high light and medium nutrients (Table G.2). For loblolly bay, there were differences in percent survival for all of the effects tested (Table G.3). Survival was 2 times greater at high light than low light, 2 times greater in sand than in soil, and greatest at low nutrient levels (Figure G.2). For redbay, however, percent survival only differed by medium and nutrients (Table G.3) and was 1.2 times greater in sand and greatest with low nutrients (Figure G.2).

Height and Growth Rates

Height over the 15 week period increased more rapidly for loblolly bay in sand and soil and redbay in soil under high light rather than under low light (Figure G.3a-c). Under low light, height increased only slightly over the 15 week period (Figure G.3a-c). The set of redbay grown

under low light conditions in sand had more rapid height gain than those under high light (Figure G.2d) because the plants under high light became sunburned when greenhouse shades were lifted. The sunburn affected redbay height and is presumably what led to an opposite pattern from the other plant treatments of greater height under low light conditions. The sunburned plants recovered, however, because height at week 9 began to steadily increase, and from weeks 12-15 their mean height was comparable with that of plants under low light (Figure G.2d).

Overall growth rates were 1.1 times greater in soil rather than sand ($P=0.0092$), more than 2 times greater in high light than low light ($P<0.0001$), and greatest at medium nutrient levels ($P=0.0005$; Table 4.4; Figure G.3a-d). Growth rates varied with light and soil ($P=0.0014$), light and nutrient level ($P=0.0049$), and growth medium and nutrient level ($P=0.0008$; Table G.4; Figure G.3a-d).

Loblolly bay grew 1.3 times faster than redbay ($P=0.05$), suggesting it may be a better competitor under the conditions tested. Loblolly bay had greater growth rate under high light than redbay under high light ($P=0.0089$; Table G.4; Figure G.3a-d). Alternatively, redbay had 1.4 times greater growth rate under low light, possibly because of the sunburn that appeared to reduce growth in redbay under high light (Mann-Whitney U test: U=, $N_{GOLA}=35$ $N_{PEBO}=74$, $P=0.0319$). Loblolly bay had an almost 2.5 times greater growth rate in soil, while redbay had 1.8 times greater growth rate in sand ($P<0.0001$; Table G.4; Figure G.3a-d). Growth rates were 3 times greater in loblolly bay when all plants grown in sand were excluded (Mann-Whitney U test: U=, $N_{GOLA}=33$ $N_{PEBO}=63$, $P<0.0001$).

Biomass and Root:Shoot Ratio

Redbay and loblolly bay were able to utilize light and nutrients effectively, and had the greatest biomass at high light and medium nutrient level. Roots, stem, and leaves of plants all

had greater biomass when grown in high light rather than low light (roots: P=0.0008; stem: P<0.0001; leaves: P<0.0001; Table G.4, Figures G.4a-d). Stem biomass was greater at medium nutrient levels than at low or high (P=0.0472; Table G.4; Figure G.4a-d). Stem and leaf biomass varied with light and nutrient level (stem: P=0.0112, leaf: 0.0150) and with medium type and nutrient level (P<0.0160; Table G.4; Figure G.4a-d). Root biomass was greater in sand (P=0.0001), but this varied with nutrient level (P=0.05). Leaf biomass was greater in soil (P=0.0028; Table G.4; Figure G.4a-d).

Loblolly bay may be a more successful colonizer of light gaps with the potential to utilize resources more efficiently and grow faster than redbay. Root and stem biomass of loblolly bay was 1.7 times greater than redbay, while loblolly bay leaf biomass was 3.2 times greater than redbay (roots: P=0.0092; stem: P=<0.0001; leaves: P<0.0001; Table G.4, Figure G.4). Loblolly bay had greater root, stem, and leaf biomass under high light (root: P=0.05; stem: P=0.0002, leaves: P<0.0001), but there was no difference in biomass allocation for redbay between light levels. Loblolly bay had greater biomass in soil than in sand (F=33.999, P<0.0001; Figure G.4a-b).

The root to shoot ratio of plants only differed by medium and was 2 times greater in sand, showing that plants allocate more biomass into their roots when grown in sand than soil (F=27.822, P<0.0001; Table 4.4; Figure G.6a-d). The root:shoot ratio of loblolly bay was 3x greater in sand than soil (F=97.9923, P<0.0001; Figures G.5, G.6a-b) and that of redbay was 2x greater in sand than soil (F=42.7131, P<0.0001; Figure G.5, Figure G.6c-d).

Discussion

The excessive amount of nutrients given to seedlings due to miscalculation in this experiment caused high mortality in seedlings, however, enough seedlings survived to produce

some interesting results. Survival did not differ between the species. Survival was greatest at low nutrients for both species and both had higher survival in sand, suggesting soil with fertilizer and the addition of more nutrients in excess of the recommended amount was detrimental. Among surviving plants, however, the greatest growth rates occurred at medium nutrient levels and at high light levels, showing that plants maximize growth at high availability of these resources. This suggests some individuals of both species are able to effectively utilize resources that may increase as a result of canopy gaps. Similarly, in seedlings of American beech (*Fagus sylvatica* L.), greatest survival rates were found at high light levels (Minotta and Pinzauti 1996).

Loblolly bay grew 1.3 times faster than redbay, suggesting that it is a better competitor. Because highest growth occurred for surviving plants at medium nutrients, but greatest survival was at low nutrients, other factors may have affected plant survival. The sunburn that occurred when greenhouse shades were lifted was most likely a factor. Loblolly bay also had greatest growth rate under light. Similarly, in American beech seedlings, the greatest growth occurred at high fertility and high light (Minotta and Pinzauti 1996). In growth experiments, quaking aspen (*Populus tremuloides* Michx.) showed increased growth in response to both the direct and interactive effects of light and nutrient availability (Hemming and Lindroth 1999).

The findings of this research support the theory of optimal partitioning. Root biomass was greater in sand, in which nutrients were more limiting than in low nutrient potting soil. The root: shoot ratio in sand was 2 times greater than in soil, which provides evidence that plants allocate more biomass into below ground organs to optimize nutrient uptake. Plants grown in soil, which were likely not nutrient limited, put more resources into their above-ground biomass to optimize photosynthesis. McKee (1995) also found a high root:shoot ratio at low nutrients in woody mangrove seedlings in a growth experiment. Low light conditions also promoted stem

and leaf growth and a low root: shoot ratio (McKee 1995), but light did not significantly affect the root:shoot ratio in this experiment. In a field experiment of Neotropical woody seedlings, sites with the lowest nutrient availability resulted in the highest allocation of biomass to roots (Paz 2003).

Because loblolly bay had higher growth rates and biomass in roots, stems, and leaves than redbay, it appears to be a better colonizer with the ability to use resources more effectively. The findings of this research show it is possible for loblolly bay to benefit from open canopy gaps created by the death of redbay at small life stages. Loblolly bay also partitions more resources into its above-ground tissues in higher nutrient inputs, making it more effective at photosynthesizing and growing taller. These findings, combined with the findings in Chapter 3, present evidence that increases in loblolly bay may contribute to community changes as a result of redbay mortality. Both species are shade tolerant but also appear to do well in high light.

Because of redbay mortality and open canopy gaps, there is a potential for influxes of nutrients and light into communities infested with laurel wilt disease. The increase in these resources may cause community composition shifts. Shade intolerant species might establish and increase in large gaps, and shade tolerant species might grow faster in small gaps. Redbay and loblolly bay are shade tolerant species I have observed in field sites responding to these gaps. The results of this experiment suggest that in the field, loblolly bay may replace redbay as they grow taller because redbay will continue to dieback from laurel wilt.

Table G.1 Amount of nutrients (ppm) in soil taken from 2 control sites and 2 infested sites in November 2008.

Site	Phosphorous	Potassium	NH_4-N	NO_3-N
C1	5.3	48.6	33.6	2.1
C2	10.8	38.0	10.6	1.6
Control Average	8.1	43.3	22.1	1.8
I1	14.0	51.1	36.7	3.3
I2	7.6	36.9	21.9	1.4
Infested Average	10.8	44	29.3	2.4

Table G.2 Percent survival over 15 weeks for redbay and loblolly bay grown in 2 media, under 2 different light levels and 3 nutrient levels. GOLA= loblolly bay, PEBO = redbay.

Species	Medium	Light	Nutrient	N	Survival (%)
GOLA	Sand	High	High	16	43.75
GOLA	Sand	Low	High	16	6.25
GOLA	Sand	High	Medium	16	93.75
GOLA	Sand	Low	Medium	16	68.75
GOLA	Sand	High	Low	16	100
GOLA	Sand	Low	Low	16	93.75
GOLA	Soil	High	High	16	6.25
GOLA	Soil	Low	High	16	0
GOLA	Soil	High	Medium	16	56.25
GOLA	Soil	Low	Medium	16	6.25
GOLA	Soil	High	Low	16	93.75
GOLA	Soil	Low	Low	16	43.75
PEBO	Sand	High	High	18	33.3
PEBO	Sand	Low	High	18	44.4
PEBO	Sand	High	Medium	18	77.8
PEBO	Sand	Low	Medium	18	88.9
PEBO	Sand	High	Low	18	72.2
PEBO	Sand	Low	Low	18	83.3
PEBO	Soil	High	High	18	16.7
PEBO	Soil	Low	High	18	27.8
PEBO	Soil	High	Medium	18	66.7
PEBO	Soil	Low	Medium	18	72.2
PEBO	Soil	High	Low	18	72.2
PEBO	Soil	Low	Low	18	94.4

Table G.3 Results of chi-squared test of percent survival of each species by effect.

	loblolly bay			redbay		
Effect	χ^2	df	P	χ^2	df	P
Medium	24.125	1	<0.0001*	7.688	1	0.0056*
Light	18.783	1	<0.0001*	1.725	1	0.1891
Nutrient	55.889	2	<0.0001*	47.531	2	<0.0001*

*Significant difference at P

Table G.4 Results of full factorial 4-way ANOVA for biomass of root, stem, and leaves, root to shoot (stem + leaves) ratio of biomass, and weekly growth rate of plants.

	Root		Stem		Leaves		Root: Shoot Ratio		Growth Rate	
Effect Test	F	df	F	df	F	df	F	df	F	df
Species	6.90	1, 241*	30.18	1, 241*	20.82	1, 241*	3.59	1, 241	3.73	1, 232*
Medium	15.05	1, 241*	1.32	1, 241	9.15	1, 241*	27.82	1, 241*	6.91	1, 232*
Light	11.48	1, 241*	36.24	1, 241*	50.14	1, 241*	2.30	1, 241	42.72	1, 232*
Nutrient	0.27	2, 482	3.10	2, 482*	1.61	2, 482	0.15	2, 482	7.82	2, 464*
Species*Medium	0.03	2, 240	1.21	2, 240	5.87	2, 240*	0.98	2, 240	21.18	2, 231*
Species*Light	3.74	2, 240*	14.21	2, 240*	24.86	2, 240*	2.38	2, 240	6.97	2, 231*
Species*Nutrient	0.38	2, 240	2.99	2, 240*	1.46	2, 240	0.30	2, 240	0.93	2, 231
Medium*Light	1.70	2, 240	19.90	2, 240*	9.86	2, 240*	0.37	2, 240	10.48	2, 231*
Medium*Nutrient	2.99	2, 240*	4.22	2, 240*	2.88	2, 240	0.77	2, 240	7.31	2, 231*
Light*Nutrient	0.02	2, 240	4.58	2, 240*	4.28	2, 240*	1.58	2, 240	5.45	2, 231*
Species*Medium*Light	1.61	3, 239	11.84	3, 239*	5.30	3, 239*	0.96	3, 239	1.71	3, 230
Species*Medium*Nutrient	1.80	3, 239	3.17	3, 239*	4.10	3, 239*	0.85	3, 239	0.16	3, 230
Species*Light*Nutrient	0.02	3, 239	1.07	3, 239	0.48	3, 239	0.26	3, 239	0.08	3, 230
Medium*Light*Nutrient	0.26	3, 239	2.12	3, 239	1.66	3, 239	0.03	3, 239	1.55	3, 230

* Significant difference at $P \leq 0.05$

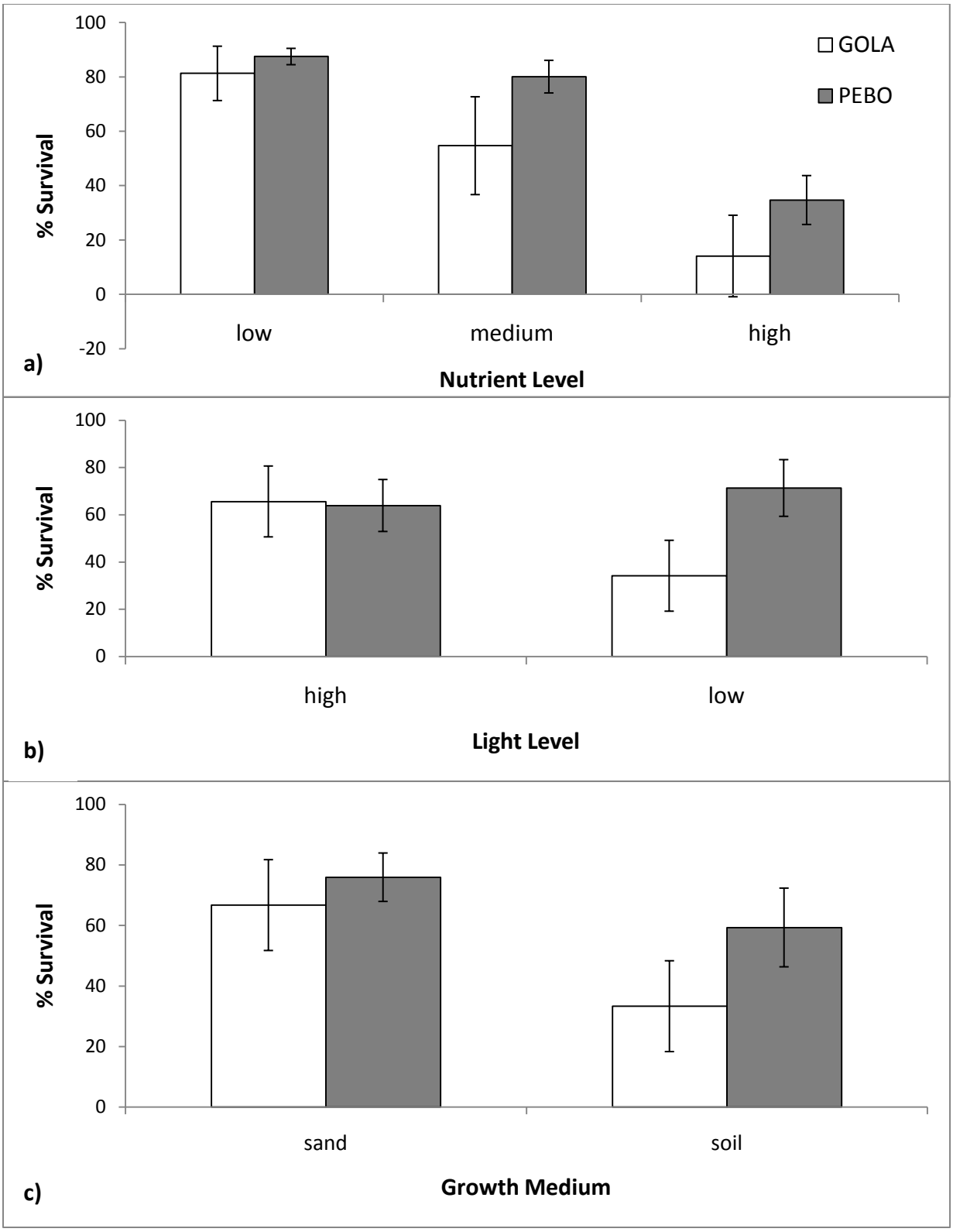


Figure G.1 Percent survivorship ± SE of redbay and loblolly bay by a) nutrient level, b) light level, and c) growth medium. GOLA=loblolly bay, PEBO=redbay.

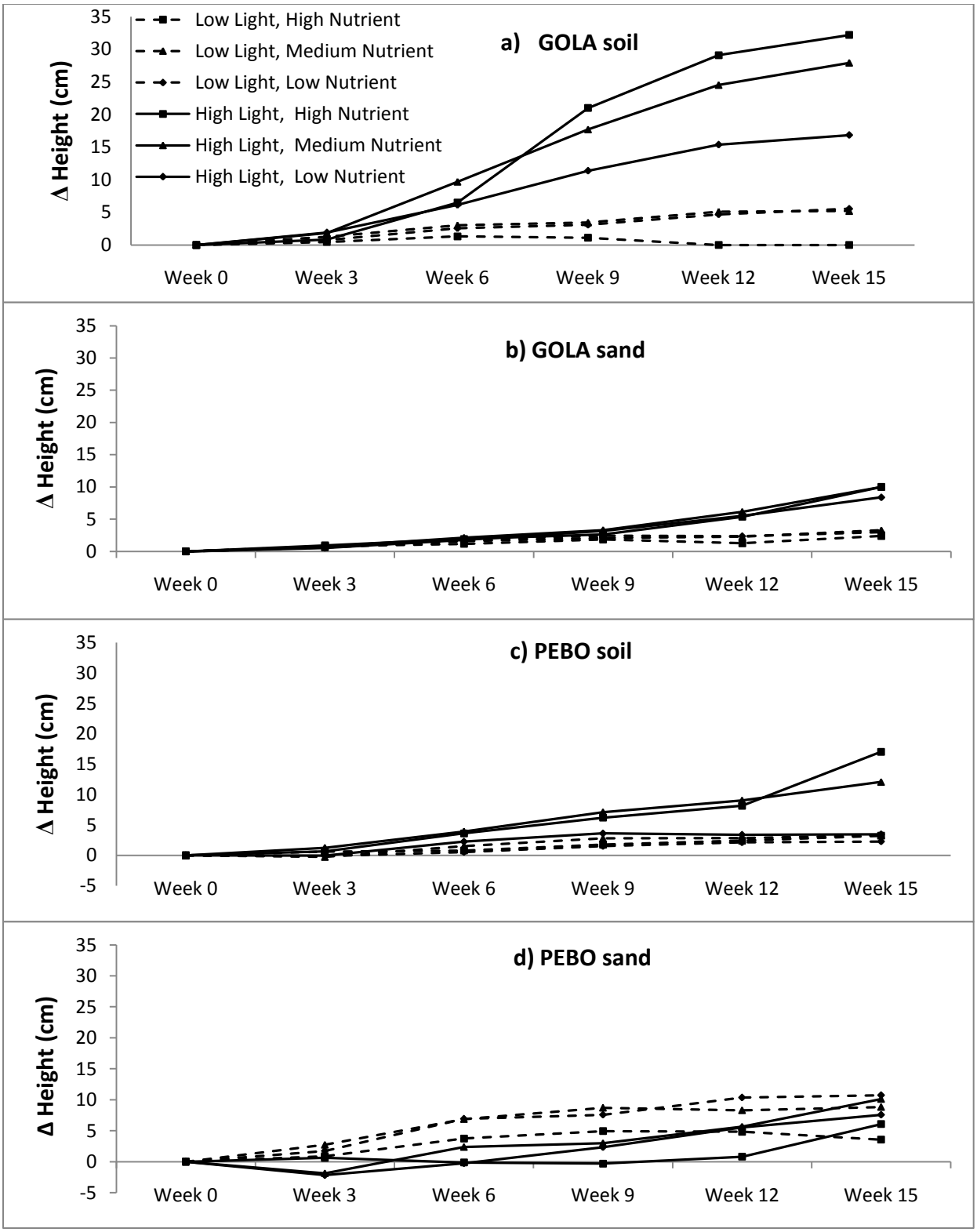


Figure G.2 Change in height from initial height at week 0 over a 15 week period in a) GOLA in soil b) GOLA in sand c) PEBO in soil d) PEBO in sand. GOLA= loblolly bay, PEBO = redbay.

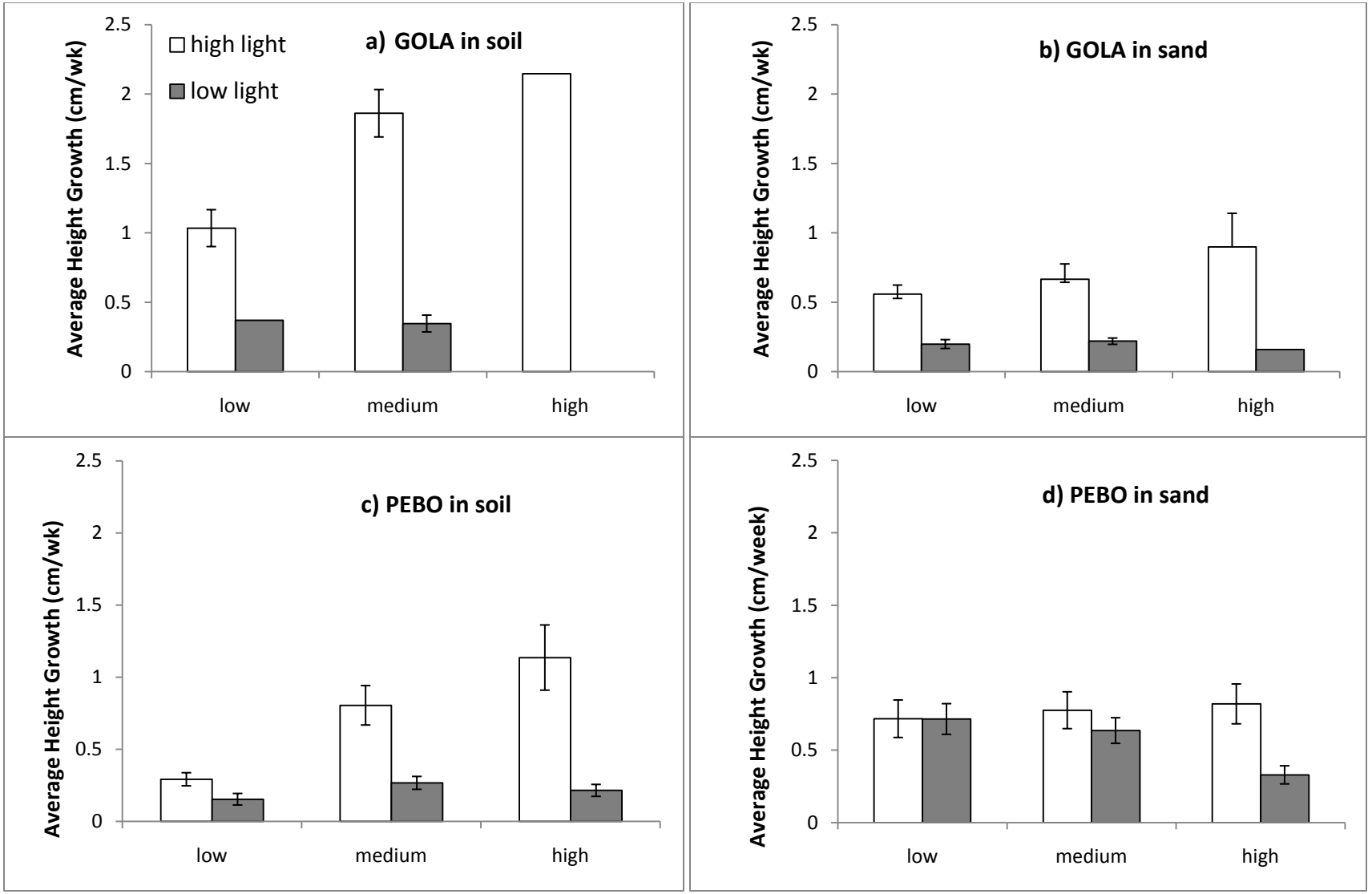


Figure G.3 Average weekly growth (Δ height from week 0/15 weeks) ± SE by nutrient level with and without shade cloth for a) GOLA in soil b) GOLA in sand c) PEBO in soil d) PEBO in sand. GOLA= loblolly bay, PEBO = redbay.

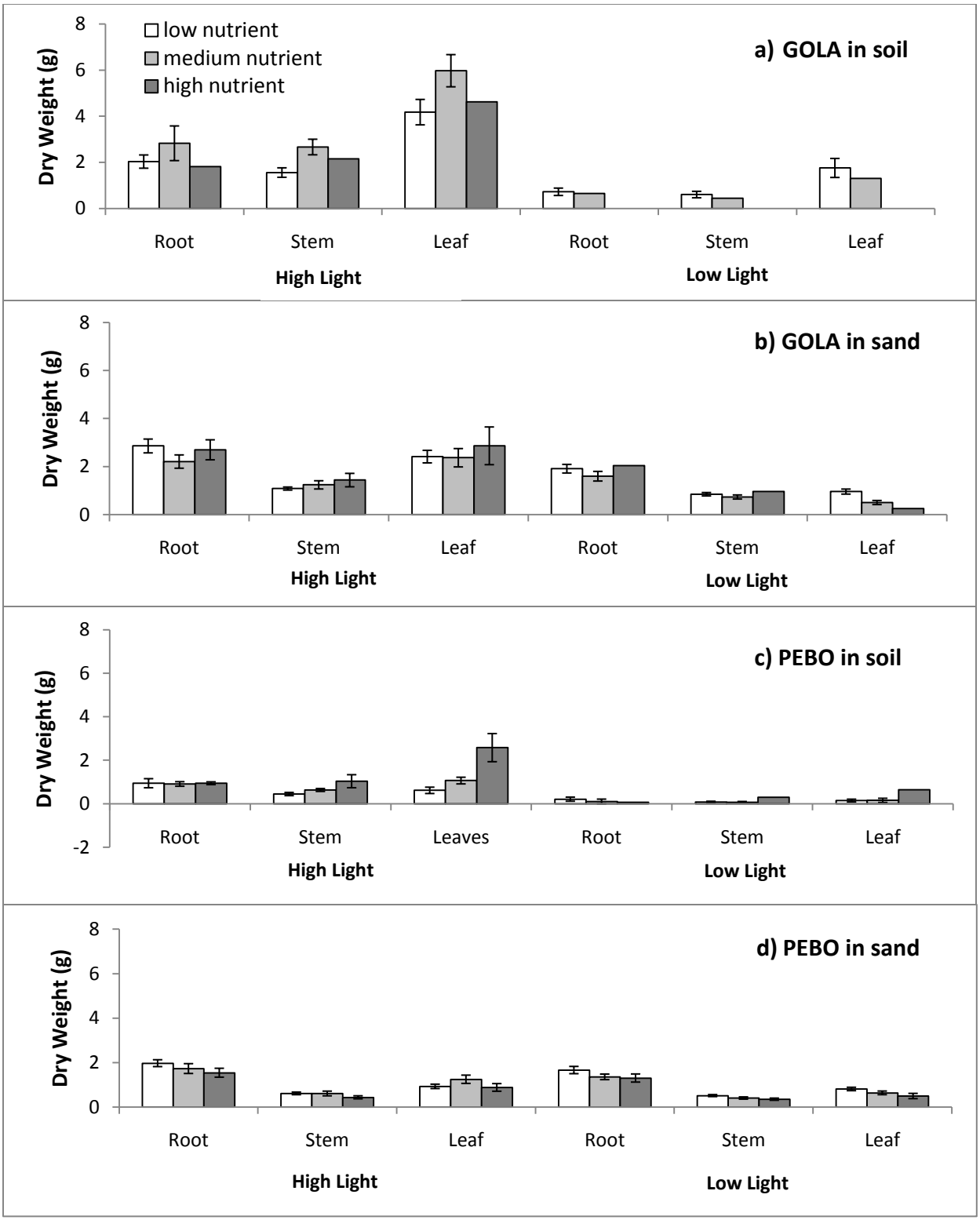


Figure G.4 Average dry biomass ± SE of root, stem and leaves at high and low light and at low, medium, and high nutrient levels for a) GOLA in soil b) GOLA in sand c) PEBO in soil d) PEBO in sand. GOLA= loblolly bay, PEBO = redbay

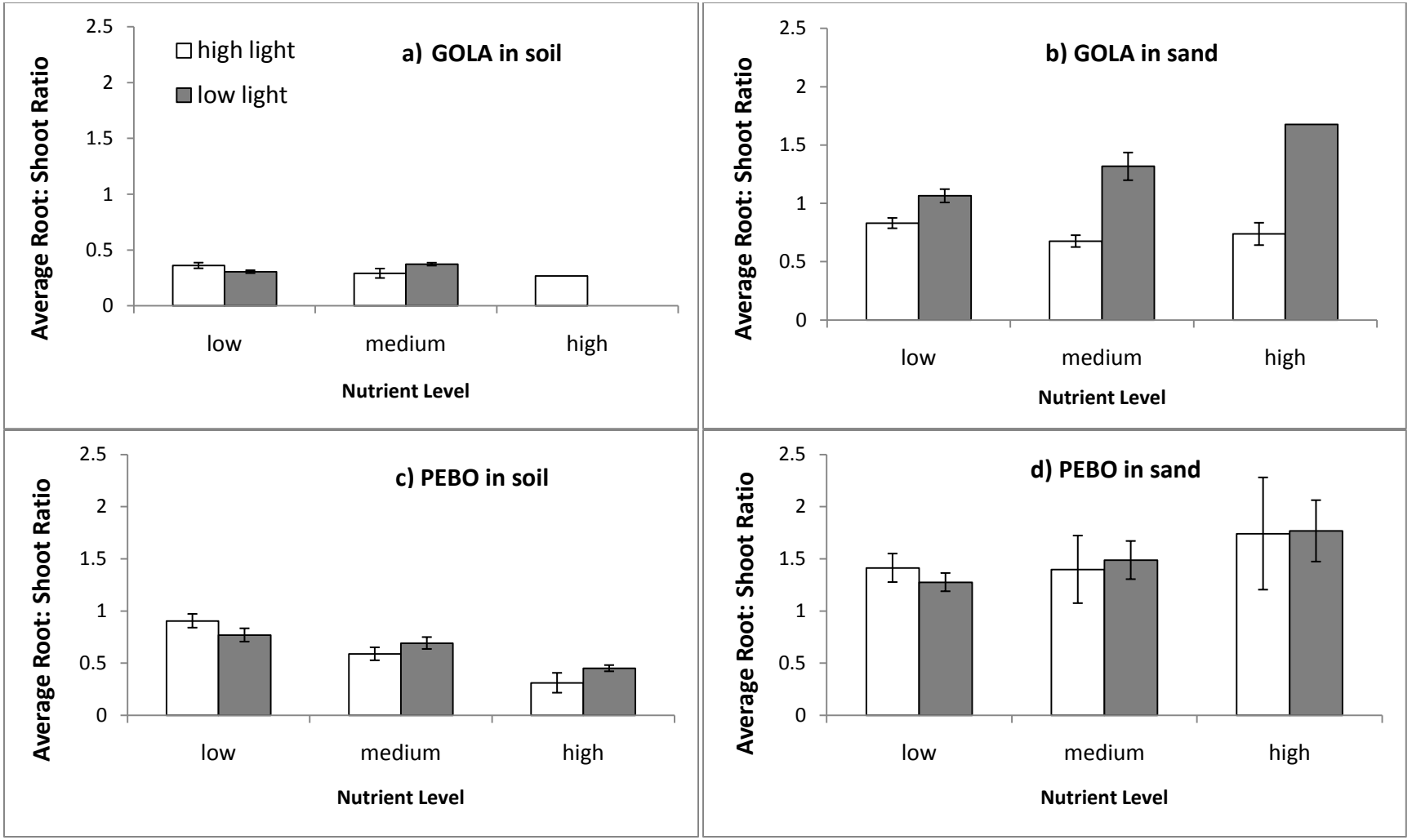


Figure G.5 Average root: shoot ratio ± SE by nutrient level with and without shade cloth for a) GOLA in soil b) GOLA in sand c) PEBO in soil d) PEBO in sand. GOLA= loblolly bay, PEBO = redbay.

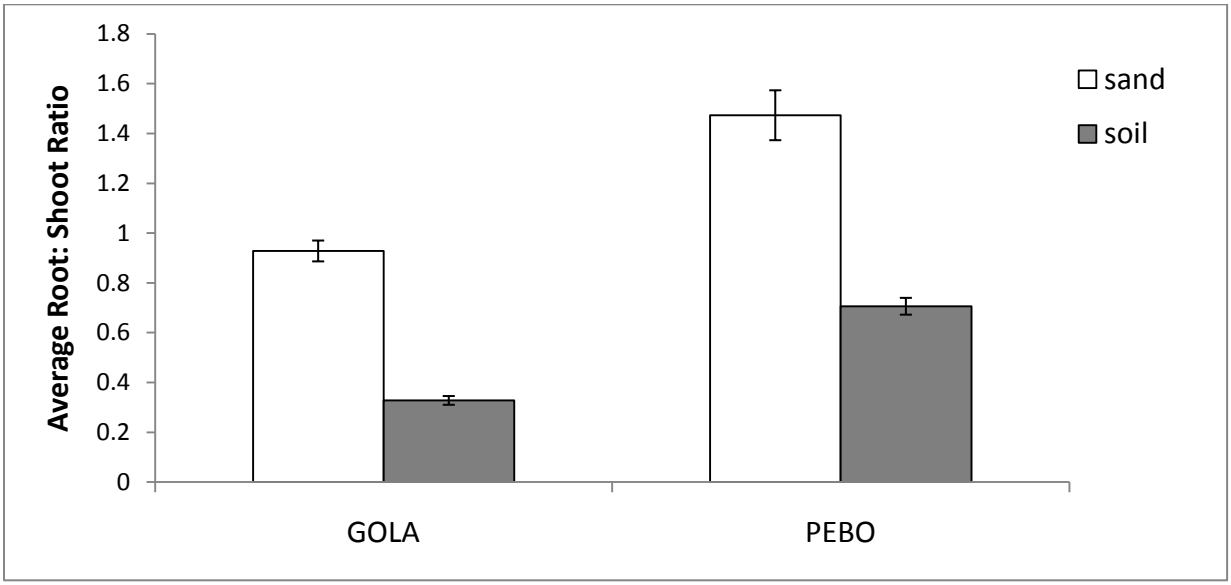


Figure G.6 Mean root:shoot ratio ± SE for loblolly bay (GOLA) and redbay (PEBO) in sand and soil. Both were significantly higher in sand.

APPENDIX H

Directions to study sites

From Statesboro:

C1: Ohoopee Dunes, Halls Bridge Tract

Take Route 80/26 west to Swainsboro. Go through Swainsboro, turn left onto Halls Bridge Road ~1 km after you pass Route 1. Travel ~5.8 miles on Halls Bridge Road, site is before Little Ohoopee River on left right after sand dunes.

C2: Big Dukes Natural Area

Travel north on Northside Dr. W/US-25 N/US-80 N/GA-67 N to Millen. In Millen, turn left on 17/West Winthrope Ave. In 0.9 miles, turn right onto Old Louisville Rd. In 7.1 miles, turn left at Big Dukes Natural Area sign. Follow dirt road to parking area, park. Walk past gate toward the bay, turn left down trail and after ~200 m, turn right into sandy area. Follow small trail past the small dunes into the bay for ~ 140 m. Site is on the right. 35° 52’ 02” N, 82° 02’ 24” W.

C3: private property off Route 80

Take Route 80/26 west to Swainsboro. Go through Swainsboro and site is ~5.1 miles past Route 1 on the left.

I1: private property off GA 169

Follow 301/25 south past I-16, turn right onto 169. Follow 169 for ~5.3 miles, turn left before the Oconee River onto 441/Macphillips Rd. Follow for 0.3 km, site on left.

I2: Evans County Public Fishing Area

Follow 301/25 south to Claxton. Turn left to travel east on 280/30 out of Claxton. Travel ~6.5 miles and turn right onto Sunbury Road. Follow Sunbury Road for 0.8 miles, then turn left onto Sand Pond Road. Site is off Sand Pond Road ~0.4 miles on the right. Or turn into the Fishing Area and park near the boardwalk, follow the boardwalk and the site is most of the area to the right of the boardwalk.

I3: Bulloch Bay

Travel south on Fair Road (GA-67), turn right onto Horace Mitchell Road 0.7 miles after I-16. Road turns into Mill Branch Club Road (County Road 282). Follow for 4.9 miles, site on left (before Backwood Road). 32° 10 52 N, 82° 02' 24" W. *Get permission from Frank Hewitt of Bradley Plywood Corporation

3960 Mill Branch Club Road

Nevils, GA 31321-3416

(912) 839-9161

I4:

Follow 301/25 south to Claxton. Turn right onto 280/30 and follow to Reidsville. Turn left onto 56/Shepards Bridge Road. Site is ~0.6 miles on the right. Park at Beauty Salon (trailer) and walk into site from road.

I5:

Follow directions as I4 to Reidsville, but turn left onto 147 S/Tattnall Street. Travel on 147 for ~5.1 miles, park in dirt area on right. Will be before the Altamaha River. Park near road and walk ~150 m down dirt road, site on the right. *Must get permission from Timberland Investments LLC for Tickanetley Timbers tract #2602.

Contact info.:

http://www.tirllc.com/contact.php

115 Perimeter Center Place, Suite 940

Atlanta, GA 30346

(877) 755-4330