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Predicting Multi-trophic Consequences of an Emerging Disease

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PREDICTING MULTI-TROPHIC CONSEQUENCES OF AN EMERGING DISEASE

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A Dissertation

Submitted in Partial Fulfillment of the Requirements for the
Doctor of Philosophy in Plant Biology

Department of Plant Biology
in the Graduate School
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PREDICTING MULTI-TROPHIC CONSEQUENCES OF AN EMERGING DISEASE

By

Adam D. Chupp

A Dissertation Submitted in Partial

Fulfillment of the Requirements

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in the field of Plant Biology

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TITLE: PREDICTING MULTI-TROPHIC CONSEQUENCES OF AN EMERGING DISEASE

MAJOR PROFESSOR: Dr. Loretta L. Battaglia

There are numerous examples of how exotic insect pests and pathogens have altered the dominance of native tree species and the ecological processes and function related to those species. While targeted species may persist in a functionally altered state via vegetative sprouting, the widespread decimation of a species can have dramatic direct and indirect consequences for organisms in multiple trophic levels. Devastation due to alien insect herbivores poses the greatest threat to native insect larvae that specialize on the impacted host species. The loss of pollinators whose larvae feed on impacted species and provide services for native plants may also be a serious but yet undocumented indirect threat of these exotic invasions. The disruption of mutualistic relationships between native species will have negative consequences for those species and could potentially benefit exotic species. In the southeastern US, laurel wilt disease (LWD) is impacting numerous species in the Lauraceae family, with the majority of cases observed on *Persea borbonia*, a common sub-canopy tree found in many Coastal Plain habitats. This species is also known to be the primary larval host of the palamedes swallowtail (*Papilio palamedes*). While infection rates and crown dieback are catastrophically high (>90%), basal resprouting is a common response in *P. borbonia*. The exotic *Cinnamomum camphora* is the only Lauraceae species that has shown resistance to LWD and could benefit from opportunities to replace *P. borbonia* and other Lauraceae species threatened by LWD. The primary objectives of this study were four fold: 1) to quantify *P. borbonia* sprouting responses in

the field and greenhouse and determine the effect of *P. borbonia* removal on the composition and abundance of woody and herbaceous plant species in the understory layer, 2) to test the relative suitability of *C. camphora* as an alternative larval host for *P. palamedes*, 3) to determine the reliance of the *Platanthera ciliaris* on *P. palamedes* for successful pollination and the relative availability of alternative long-tongued pollinators, and 4) to forecast how disease-induced shifts in the relative abundance of native (*P. borbonia*) and exotic (*C. camphora*) fruit may alter patterns of consumption and subsequent dispersal of *C. camphora* by birds. The field component (Grand Bay National Estuarine Research Reserve (GBNERR), Jackson County, MS) of chapter two involved the removal of *P. borbonia* main stems to mimic the impacts of LWD which resulted in a significant increase (~50%) in light transmission. All treated individuals produced sprouts and the size and number of sprouts was positively related to initial tree size. Following the removal of *P. borbonia* from treatment plots, *Ilex vomitoria* showed the greatest increase in basal area after two years. Both woody seedlings and herbaceous plants showed no significant trends in composition and/or abundance over time. In the greenhouse (Southern Illinois University, Carbondale, IL), the stem and leaf biomass of vegetative sprouts was significantly greater in a high-nutrient treatment. Light treatments had no effect on sprout production. Results from chapter two suggest that the loss of *P. borbonia* from the canopy layer may have little direct effect on plant community dynamics. In addition, I found that sprout production is vigorous in *P. borbonia* and the capacity to persist and tolerate future disturbances may be enhanced on more nutrient-rich sites. In chapter three, I used laboratory experiments and field observations to compare larval performance and adult female preference of *P. palamedes* between *C. camphora* and *P. borbonia* foliage. My results indicate moderate survivorship on *C. camphora* (46%) compared to *P. borbonia* (87%) and there were no differences in first and

fourth instar growth rates between treatments. Fourth instars consumed less *C. camphora* foliage than *P. borbonia*, but metabolic efficiency did not differ between treatments. In the field and laboratory, I found no oviposition preference for *C. camphora* relative to *P. borbonia*. While females laid eggs on *C. camphora* during laboratory trials, the same number of eggs was also laid on inanimate objects. I conclude that *C. camphora* is suitable for larval development but host-switching to this species by *P. palamedes* will be primarily constrained by oviposition behaviors. In chapter four, I monitored pollinator visitation and measured nectar spur lengths of *P. ciliaris* flowers and proboscis lengths of its floral visitors (at GBNERR). *Papilio palamedes* was the primary visitor (44 visits) but *Phoebis sennae* was also observed (4 visits). There were no significant differences among *P. ciliaris* nectar spurlength and the proboscis lengths of *P. palamedes* and *P. sennae*. Fruit set was $55 \pm 10.8\%$ with access to pollinators and 0% on bagged inflorescences (pollinators excluded). Although I found a positive relationship between visitation and inflorescence size, there was no such pattern in fruit set, indicating that fruit set was not limited by pollinator visitation within the range of visitation rates I observed. *Phoebis sennae* may provide supplemental pollination service but is likely constrained by habitat preferences that do not always overlap with those of *P. ciliaris*. Although additional observations are needed, my results suggest that expected LWD-induced declines of *P. palamedes* will threaten the reproductive success and persistence of *P. ciliaris* populations. In chapter five, I investigated redundancy between *C. camphora* and *P. borbonia* with respect to fruit characteristics (physical and chemical) and selectivity by frugivorous birds (at GBNERR). Across two winter survey periods I observed fruit removal from artificial infructescences. I manipulated background species upon which displays were hung (*Myrica cerifera* and *Triadica sebifera*) and the accessibility of the displays. Using motion-activated cameras I confirmed foraging bouts on both

P. borbonia and *C. camphora* fruits by three bird species (*Dumetella carolinensis*, *Turdus migratorius*, and *Catharus guttatus*). There was no significant difference in selectivity between fruit types during year one of my surveys but there was a significant preference for *C. camphora* in year two, which coincided with significantly lower mean daily temperatures. Background tree species and accessibility had no apparent effect on fruit preference. Total polyphenols and pulp:seed ratio were significantly higher in *C. camphora* fruit. I conclude that the fruits of *C. camphora* and *P. borbonia* represent nearly substitutable resources for native birds. However, native species may prefer *C. camphora* fruit in times of energetic stress. The decline of *P. borbonia* will likely increase the consumption and dispersal of *C. camphora* fruits. Additional studies are required to determine if such changes could ultimately increase the distribution and abundance of this exotic species. Combined, the chapters of this dissertation present substantial empirical evidence for the potential multi-trophic level impacts of an exotic plant disease. While it remains unclear how dramatic these impacts will be, the approach used here is vital for understanding and mitigating the long-term ecological effects of species/disease invasions.

DEDICATION

I dedicate this dissertation to my grandparents, Paul and Margaret Werth, Daniel Chupp, and Irene Troyer, and to my parents, Stephen and Linda Chupp. I love you very much. Thank you for everything.

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I am extremely grateful for the support and guidance from my advisor, Dr. Loretta Battaglia. I thank her for her hard work and patience over the last four years and the wisdom that she has imparted upon me. Her leadership and enthusiasm have been inspirational throughout my tenure at SIU. My growth as a research scientist is owed largely to her efforts and for this I am forever thankful. I would also like to thank my other committee members Dr. Sara Baer, Dr. John Reeve, Dr. Eric Schaubert, and Dr. Sedonia Sipes. Their highly valued service to this dissertation and to my development as a professional biologist is greatly appreciated. I also thank the members of the SIU department of plant biology, including former and current chairs, Dr. Dale Vitt and Dr. Stephen Ebbs.

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PREFACE

The entire contents of Chapter 3 have been published as a manuscript in the journal entitled *Biological Invasions*. The manuscript can be found on pages 2639–2651 in the December 2014 issue (Volume 16) of the journal. As lead author, I co-developed this study with co-author Dr. Loretta L. Battaglia, conducted all the research, analyzed the data and wrote the initial manuscript. Dr. Loretta Battaglia assisted with developing the project and research design, edited the manuscript, and helped prepare the paper for submission (and later required revisions) in the journal *Biological Invasions*.

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CHAPTER 1

INTRODUCTION

Biodiversity and Biological Invasions

In biologically diverse systems, multiple species may have functionally redundant contributions to the same ecological processes (*i.e.*, effect trait redundancy; Lawton & Brown 1993, Naeem 1998, Walker 1992). As a result, the ecosystem services provided by those processes may be more stable and resilient to perturbation. However, effect trait redundancy between two species is of little consequence when they respond similarly to disturbance (Chapin et al. 1997, Elmqvist et al. 2003). Thus, the value of biodiversity may be largely driven by the combined effects of functional redundancy and response diversity which together provide resilience against the loss of ecological function (Hooper et al. 2005, Naeem 1998, Walker 1999, Yachi and Loreau 1999). This logic provides an excellent framework for understanding the impacts of disturbances that threaten the persistence of species.

Arguably the greatest threat to biodiversity is the disturbance produced by biological invasions which have been increasing world-wide due to the intensification and expansion of global trade and movement (Hulme 2009). As a result, the field of invasion biology has grown substantially over the last two decades. Unfortunately, it is now quite clear how invasions of exotic organisms can be responsible for large scale decreases in the abundance of indigenous species (Blackburn et al. 2004; Gaertner et al. 2009; Hejda et al. 2009; Richardson and Ricciardi 2013); the most profound impacts occur when exotic species are directly responsible for the local or regional extinction of native species.

In North America, several well-documented cases of disease invasion, *e.g.*, Dutch elm disease (Dunn 1986), hemlock woolly adelgid (Orwig and Foster 1998), and emerald ash borer

(Haack et al. 2002), have resulted in dramatic declines in formerly dominant native tree species. In all three cases, an alien insect either vectors a pathogen or directly damages a native species. Determining the ecological role of the target species will be vital to understanding the impacts of these biological invasions; some key features worth considering include the host's importance, uniqueness (*e.g.*, symbiotic relationships), and phytosociology (Lovett et al. 2006). In addition, identifying the redundancy of these key features within the community will help to define potential resiliency and forecast the consequences of these disturbances. Although we can describe with great certainty the direct effects of emerald ash borer and other invading organisms, detailed accounts of invaders and their effects on less conspicuous ecological processes are scarce. Such studies should focus on how invasions alter ecosystem function at multiple scales and levels of biological organization (Parker et al. 1999).

Plant Regeneration and Persistence

Tree death and subsequent canopy gap formation may have dramatic consequences for community dynamics. By altering light availability, temperature, and moisture, canopy gaps modify conditions for survival and recruitment which may shift local species composition (Case and Bengtsson 2010). In North America, widespread tree mortality due to Dutch elm disease (Dunn 1986), beech bark disease (Houston et al. 1979), and chestnut blight (Anagnostakis 1987) has resulted in local and regional shifts in the structure and dominance of native species. However, in response to these disturbances, the target tree species (American chestnut, American elm, and American beech) are all known to vigorously produce sprouts and persist in canopy gaps (Barnes 1976; Griffin 1989; Forrester et al. 2003). Although these diseases have largely prevented the maturation and regeneration (seed production) of these afflicted species

(Anagnostakis 1987, Ellison et al. 2005), persistence through resprouting may heavily influence the dynamics of associated understory plant communities.

Historically, studies of plant demographics and community composition have focused on the life history strategies that affect recruitment. Seed and seedling ecology have been central to this theme, and there is a large body of literature suggesting the factors that may influence seed production, dispersal, germination, and ultimately seedling establishment (*i.e.*, recruitment). This research focus is perhaps best illustrated by Grubb (1977) which has been cited 3261 times. In the article Grubb states that for plants, the niche is largely defined by the set of environmental and biotic circumstances that allow for optimal regeneration from seed (*i.e.*, “regeneration niche”). More recently, studies have addressed the ecophysiology of seed production/germination (*e.g.*, Baskin & Baskin 1988) and others have used the characteristics of seeds to define functional groups of species (*e.g.*, Westoby 1998) that may influence ecosystem processes and the resilience of ecosystems following disturbance (*e.g.*, Tilman et al. 1997).

While studies of recruitment and regeneration from seed and seedling have been central to traditional theories of gap dynamics, the role of non-seed regeneration (*i.e.*, resprouting) had been largely overlooked until the last decade (Bellingham and Sparrow 2000; Bond and Midgley 2001; Garcia and Zamora 2003; Knox and Clarke 2005; Keith et al. 2007; Clarke et al. 2010). Asexual sprouting is common among woody angiosperms and is very likely the ancestral mode of reproduction (Wells 1969). Resprouting is generally induced by a disturbance resulting in crown dieback or broken stems, with new sprouts (resprouts) emerging from below the point of damage (Paciorek 2000). Unlike the regeneration of individuals from seed or seedling, resprouting represents the persistence of an already established individual in the population. Resprouting may have significant impacts on demographics by decreasing the rates of

popoulation turnover, increasing resilience to disturbance, and shifting away from seed dependence. Paciorek et al. (2000) suggested that the importance of resprouting for community dynamics is a function of 1) the amount of physical damage, 2) the amount of resprouting, and 3) the performance of resprouts; where the long term importance of resprouting is likely determined by the ability of resprouts to reproduce sexually. The type and magnitude of the resprouting response is highly variable among closely related species and levels of disturbance (Bond & Midgley 2001). The ability of species to resprout appears to be an important functional characteristic that determines the persistence of individuals and the resilience of community structure following disturbance.

Laurel Wilt Disease

The beetle-vectored pathogen causing laurel wilt disease (LWD) is now widespread in Atlantic and Gulf Coast ecosystems (Fraedrich et al 2008) and could have long-term ecological consequences. Laurel wilt disease is vectored by an exotic ambrosia beetle (*Xyleborus glabratus*) which carries the disease-causing fungus (*Raffaelea lauricola*) in specialized structures called mycangia (Kendra et al. 2010). The symbiotic fungus is introduced to the host tree's xylem during the excavation of galleries by female beetles (Fraedrich et al 2008). The fungus apparently blocks water transport in the host tree causing wilting and crown dieback (Mayfield 2008). The first detection of *X. glabratus* in North America was in 2002 near Port Wentworth, Georgia and as of March 2015, mortality of *P. borbonia* due to LWD has been observed in more than 100 counties in Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, and South Carolina (USDA Forest Service 2015a).

The primary target of LWD (*P. borbonia*) is a highly aromatic, shade-tolerant member of the Lauraceae and is a dominant sub-canopy species in many Gulf and Atlantic Coastal Plain forests in the southeastern US (Van Deelan 1991). In Duval County, Florida, Fraedrich et al. (2008) reported LWD-induced dieback in 92% of *P. borbonia* trees over a 16-month period (July 2005 – Dec. 2006). On Cumberland Island, South Carolina, the main stems and crowns of more than 95% of *P. borbonia* trees have wilted and died over a two-year period (Paul Merten pers. comm.). Following crown dieback, it is common for individual trees to vigorously produce basal resprouts (Evans et al. 2013; Spiegel and Legee 2013; Adam Chupp pers obs). The long-term persistence of *P. borbonia* to LWD will depend on the performance, survival, and reproductive success of those sprouts. Furthermore, ecosystem resilience to LWD may be largely influenced by this response and the redundancy of *P. borbonia* functional traits within the community; redundancies that maintain symbiotic interactions with herbivorous species may be especially influential (Lundberg and Moberg 2003).

Host Shifting by Herbivorous Insects

Specialist insect herbivores are greatly threatened by diseases that target their primary host plants (Ghandi and Herms 2010). The plasticity of host selection behaviors and host chemistry is important for determining the suitability of host plants and the likelihood of host shifts (*e.g.*, Ehrlich and Raven 1964, Bowers 1983, Miller 1987, Murphy and Feeny 2006, Baur et al. 1993). Regardless of their taxonomic definitions, insects prefer hosts that share chemical profiles and may switch to novel hosts that are chemically similar. Therefore, host shifting is only initiated when the novel and ancestral hosts share some type of chemical signature. Three hypotheses have been proposed to explain how secondary compounds facilitate host shifts in

herbivorous insects: 1) similarities between chemical stimulants/attractants produced by ancestral and novel host (behavioral-facilitation hypothesis) (*e.g.*, Dethier 1941; Feeny 1991), 2) insect overcomes a chemical constraint (toxic compound) that is shared by ancestral and novel hosts (metabolic-preadaptation hypothesis) (*e.g.*, Ehrlich and Raven 1964; Feeny 1991), and 3) general similarities of a large number of secondary compounds between ancestral and novel host (*e.g.*, Ehrlich and Raven 1964; Feeny 1991). In addition to the influences of chemical compounds, host shifts can be facilitated by ecological processes.

For *Papilio machaon* (a species closely related to the focal species of this dissertation (*Papilio Palamedes*)), S. M. Murphy and colleagues have compiled empirical evidence for the physiological and ecological factors contributing to a naturally occurring host shift (*e.g.*, Murphy 2004, 2005, Murphy and Feeny 2006). Their evidence suggests the colonization of a new host by *P. machaon* butterflies was facilitated by similarities in plant chemical stimulants between ancestral and novel host (Murphy and Feeny 2006). Although plant chemistry was likely an important cue for initiation of the *P. machaon* host shift, Murphy and Feeny (2006) also suggest the shift was reinforced by top-down controls (*i.e.*, enemy free space) (after Murphy 2004).

The abundance of potential host plants may also affect patterns of host selection. One elegantly constructed model of this relationship was based on empirical evidence of the behavioral ecology and developmental biology of phytophagous insects (Cunningham et al. 2001). Assuming that 1) fitness is reduced when larvae feed on more than one host plant and 2) larvae searching for a second host plant will stop only when they find the same species that was previously fed upon, the resulting model predicted that larval survival will benefit from oviposition on the most abundant host. As such, host shifting may therefore be encouraged and subsequently maintained when the abundance of potential host species is permanently altered.

Papilio palamedes larvae primarily feed on the foliage of *P. borbonia* and perform poorly on other closely related species (Lederhouse et al. 1992). A better understanding of larval performance and adult oviposition preferences for alternative hosts will be crucial for predicting the future persistence of *P. palamedes* populations. While chapter three investigates the direct effects that the loss of *P. borbonia* may have on *P. palamedes*, chapter four considers its role as a mobile link organism.

Mobile Link Organisms

Herbivorous animals that consume, transport and deposit propagules may enhance seedling establishment and survival and function as “mobile link organisms” by providing a mechanism for connecting the resources, genetic material, and trophic processes of distant patches (Lundberg and Moberg 2003). Animals that transport propagules (seeds and pollen) large distances may therefore have important functional roles in maintaining plant species richness and diversity across the landscape (Howe and Smallwood 1982, Olff and Ritchie 1998).

Pollinators

Pollinators may be the most important type of mobile link organism. It is estimated that 87.5% of all flowering plants are pollinated by animals (Ollerton et al. 2011). The degree to which this service regulates plant reproductive success has been a popular subject over the last several decades. Although Bateman’s principle of sexual selection suggests that the reproductive output of female plants (seed set and maturation) is limited by resource availability rather than access to mates (pollen receipt) (Bateman 1948; Janzen 1977; Wilson et al. 1994), reviews of empirical data indicate that reproductive success is commonly (and often severely) limited by pollen/pollinator availability (Burd 1994; Ashman et al. 2004).

Insect pollinators are among the most threatened by disturbances from alien insect herbivores who share a host species with native insect larvae (Gandhi and Herms 2010). Accordingly, the pollination services provided by the adult stages of these native insects are also threatened. While a range of Lepidopteran species are imperiled by the loss of their larval hosts due to invasive insects such as the emerald ash borer (*Agrilus planipennis*), gypsy moth (*Lymantria dispar*), balsam wooly adelgid (*Adelges piceae*), and cottony cushion scale (*Icerya purchase*) (Work and McCullough 2000; Roque-Albelo 2003; Wagner 2007; Scholtens and Wagner 2007), there have been no studies of how these losses may affect the plants they pollinate. Two recent reviews of world-wide pollinator declines corroborate this gap in our understanding of these disturbances; whereas numerous exotic plant invasions have been linked to reductions in pollinators, impacts from exotic insect herbivores are not accounted for in the literature (reviewed by Potts et al. 2010; Gonzalez-Varo 2013). Although insect invasions may impact entire populations of host plants, the connection between exotic herbivore invasions and the disruption of plant-pollinator systems has apparently gone undocumented.

Frugivorous Birds

Mutualisms between birds and fruit-producing plants have been well studied since Snow's (1971) seminal paper that highlighted the ecological consequences of these symbiotic relationships. We now understand how the distributions of plant species can be regulated by bird frugivory and the subsequent dispersal of seeds (*e.g.*, Sekercioglu 2006; Wenny et al. 2011). Fruit selection in birds is governed by various fruit characteristics including nutritional content (Schaefer et al. 2003), dietary antioxidants (Schaefer et al. 2008) and secondary compounds (Cipollini and Levey 1997). Physical characteristics of fruit are also important as birds select sizes that are compatible with bill size and gape, with smaller fruits/seeds being consumed by a

greater number of species (Jordano 1995). Finally, selection of fruits may also be correlated with the size of fruit crops and the identity and density of nearby fruit-bearing species (*e.g.*, Murray 1987; Sargent 1990; Carlo et al. 2007; Ortiz-Pulido 2007; Prasad and Sukumar 2010; Smith and McWilliams 2013).

Frugivorous birds are important for overcoming the limitations of propagule dispersal for woody species recruitment. Frugivorous birds that are attracted to disturbances (treefall gaps) can have significant effects on the colonization of these sites by fruit-producing plants (Schemske and Brokaw 1981). The abundance of these vectors may depend on the amount of woody cover at each site and the availability of fruits in surrounding patches (Garcia et al. 2010). If exotic species provide an abundance of high energy fruit, frugivorous birds may contribute to their invasiveness (Renne et al. 2002). In areas where both exotic and native fruit-producing plants are present, frugivorous bird species can have significant influence over the distribution and abundance of native vs. exotic species (Richardson et al. 2000; Drummond 2005; Greenberg and Walter 2010).

Processes that are maintained by mobile link organisms (*e.g.*, pollinators and seed dispersers) may determine landscape-scale patterns of community assembly (reviewed by Lundberg & Moberg 2003; Sargent & Ackerly 2008). Understanding how interactions between host species and mobile link organisms are disrupted by disease may be central to predicting ecosystem resilience and recovery. As such, it will be important to recognize co-existing species that provide functional redundancy with respect to interactions with mobile link organisms.

Questions

Chapter 2

How does the removal of *P. borbonia* impact the regeneration and persistence of species in the understory layer? How are sprouting responses limited by nutrients and light in the greenhouse? How does the persistence of *P. borbonia* via sprouting affect light availability and potentially understory community dynamics in the field?

Chapter 3

How is the larval performance of *P. palamedes* affected by host plant species, and what are the oviposition preferences of adults? Specifically, what is the relative suitability of the exotic *Cinnamomum camphora* compared to the closely related *P. borbonia* (primary host)?

Chapter 4

What are the primary floral visitors of the orange fringed orchid (*Platanthera ciliaris*)? How important is visitation for successful pollination? How important is visitation by *P. palamedes*? Would LWD-induced declines of *P. palamedes* indirectly threaten *P. ciliaris*?

Chapter 5

Do the fruits of *P. borbonia* and *C. camphora* represent substitutable resources to frugivorous birds? Will LWD-induced declines in the availability of *P. borbonia* fruit increase the removal and subsequent dispersal of exotic *C. camphora* fruit?

CHAPTER 2

ANOTHER NATIVE TREE IN PERIL: PERSISTENCE OF *PERSEA BORBONIA* AND RESPONSES OF AN ASSOCIATED PLANT COMMUNITY

Abstract

There are numerous examples of how exotic insect pests and pathogens have altered the dominance of native tree species and the ecological processes and function related to those species. Less attention has been paid to the persistence of impacted species. In many cases, targeted species may persist in a functionally altered state via vegetative sprouting. However, the dynamics and ecological consequences of these sprouting responses are seldom documented. In the southeastern US, *Persea borbonia*, a common tree found in many Coastal Plain habitats, is the primary host of laurel wilt disease (LWD). While infection rates and crown dieback are catastrophically high (>90%), basal resprouting is a common response in this species. I simulated the effects of LWD prior to its arrival in coastal Mississippi by girdling and then removing the main stems of *P. borbonia* trees. I quantified the sprouting response of these trees and monitored the impact of removal on light availability and understory plant communities over a 2-year period. In the greenhouse, I quantified differences in sprout production due to nutrient and light availability. In the greenhouse, the stem and leaf biomass of vegetative sprouts was significantly greater in the high nutrient treatment. Light availability had no apparent effect on sprout biomass. In the field, removal of *P. borbonia* main stems resulted in a 50% increase in light transmission. All treated individuals produced sprouts and the size and number of sprouts were positively related to initial tree girth. Following the removal of *P. borbonia* from treatment plots in the field, *Ilex vomitoria* showed the greatest increase in basal area. However, both woody

seedlings and herbaceous plants showed no significant trends in composition and/or abundance over time. My results suggest that the loss of *P. borbonia* from the canopy layer may have little indirect effect on plant community dynamics. Sprout production is vigorous in *P. borbonia* and the capacity to persist and tolerate future disturbances may be enhanced on more nutrient rich sites. More work is required to understand the potential long-term persistence of *P. borbonia* via sprouting and the consequences this may have for associated plant and animal communities.

Introduction

In North America, several well documented cases of disease invasion have resulted in local and regional shifts in the structure and dominance of native trees, *i.e.*, Dutch elm disease (Dunn 1986), beech bark disease (Houston et al. 1979), and chestnut blight (Anagnostakis 1987). The chestnut tree historically was a foundation species in the forests of eastern North America but is now considered functionally extinct, having been reduced from a dominant canopy tree to a shrub that rarely flowers (Anagnostakis 1987, Ellison et al. 2005). However, we have only begun to understand the cascading effects that forest pests and pathogens can have on ecosystems at multiple trophic levels (Ellison et al. 2005; reviewed by Lovett et al. 2006).

In forested ecosystems, perturbation due to crown dieback and subsequent canopy gap formation alters light availability, temperature, and moisture, affecting seedling emergence, growth, and survival (*e.g.*, Bazzaz and Miao 1993; Pacala et al. 1994; Canham et al. 1996; Battaglia et al. 2000). While studies of recruitment and regeneration from seed and seedling have been central to traditional theories of gap dynamics (*e.g.*, Grubb 1977), the role of non-seed regeneration (*i.e.*, vegetative sprouting) had been largely overlooked until the last decade

(Bellingham and Sparrow 2000, Bond and Midgley 2001; Garcia and Zamora 2003; Knox and Clarke 2005; Keith et al. 2007; Clarke et al. 2010).

The ability of species to produce resprouts enables them to occupy a “persistence niche” (Bond and Midgely 2001). Unlike species characterized as obligate seeders, resprouting species have a high starch-storage capacity in root tissues. However, the rate of storage is regulated by nutrient availability (Knox and Clarke 2005). The theory of optimal allocation predicts that allocation to belowground storage occurs when photosynthetic production exceeds belowground demands (Bloom et al. 1985). Storage reserves then provide the raw materials for rapid resprouting following a disturbance that removes aboveground biomass.

In response to the aforementioned disturbances, the American chestnut (*Castanea dentata*), American elm (*Ulmus americana*), and American beech (*Fagus grandifolia*) are all known to persist via the vigorous production of vegetative sprouts. (Barnes 1976; Griffin 1989; Forrester et al. 2003). In northern New York, mortality of large *F. grandifolia* stems due to beech bark disease produced canopy gaps that were quickly filled by the resprouting of smaller stems. The persistence of these stems maintained contributions to the leaf litter, potentially limiting changes to nutrient cycling (Forrester et al. 2003). Forecasting the impacts of emerging forest pests and pathogens will require an integrated approach that examines both the capacity for targeted species to persist and how these responses may influence community dynamics and other ecological processes.

In the southeastern US, laurel wilt disease (LWD) is causing widespread mortality of several Lauraceae species since its introduction to Savannah, GA in 2002 (USDA Forest Service 2015a, b, Figure 2.1). The disease is caused by a fungal pathogen (*Raffaelea lauricola*) that is vectored by an exotic stem-boring ambrosia beetle (*Xyleborus glabratus*). The fungus spreads

into the xylem (apparently blocking water transport) and results in the wilting and mortality of main stems within a few months of infection (Fraedrich et al. 2008; Mayfield 2008). Among the species in which LWD has been found (including *Sassafras albidum* and *Cinnamomum camphora* (Smith et al. 2009a, 2009b)), infection rate is highest in *Persea borbonia*, a common sub-canopy species throughout the Atlantic and Gulf Coastal Plains (Brendemuehl 1990; Van Deelen 1991; Fraedrich et al. 2008). In populations of *P. borbonia* on the Atlantic Coastal Plain, LWD-induced mortality rates are as high as 97% (Speigel and Leege 2013). Basal resprouting has been observed in infected *P. borbonia* on the Atlantic and Gulf Coastal Plain (Fraedrich et al. 2008; Speigel and Leege 2013; Evans et al. 2013; A Chupp pers. obs.). In Georgia, 87% of infected trees produced stump sprouts but their long-term survival was not documented (Speigel and Leege 2013). On St. Catherine's Island, GA, a large percentage of trees produced sprouts but only 21% of basal resprouts survived after 5 years; deer browsing appeared to severely reduce sprout survival (Evans et al. 2013). Observations in Jackson County, MS, similarly suggest that the production and growth of resprouts in response to LWD is highly variable (A Chupp pers. obs.).

Although LWD is causing widespread mortality of most if not all native Lauraceae species, *Cinnamomum camphora* is an exotic member of Lauraceae that may be quite resistant. In the field and laboratory, systemic colonization of *C. camphora* by the fungal pathogen (*R. lauricola*) caused only localized branch dieback and in no case has complete canopy wilting been observed (Smith et al. 2009; Fraedrich et al. 2014). *Cinnamomum camphora* was introduced to Florida in 1875 (Langeland and Craddock Burks 1998), and recent checks of multiple plant databases indicate that its distribution continues to expand (USDA, NRCS 2014; Wunderlin and Hansen 2013). In the coastal southeastern US, *C. camphora* grows well in disturbed areas (e.g.,

along roadsides and power line right-of-ways) and is also present in forested habitats, where larger individuals reach the sub-canopy layer (A. Chupp pers. obs.). Recent empirical evidence suggests that given its chemical and physical similarities with *P. borbonia*, *C. camphora* may act as an alternative host plant for larvae of the native palamedes swallowtail (*Papilio palamedes*) and an alternative food source for overwintering frugivorous birds (Chupp and Battaglia 2014; Chupp and Battaglia In review). Given the apparent redundancy between *P. borbonia* and *C. camphora* and the resistance of *C. camphora* to LWD, *C. camphora* may be poised to co-opt the niche space of *P. borbonia*, however, further functional analyses of these species is required.

Recent studies have quantified LWD-induced mortality in *P. borbonia* populations and persistence via resprouting (Evans et al. 2013; Spiegel and Leege 2013); however, quantitative estimates of community-wide impacts are lacking. Such efforts will be vital to understanding the long term ecological effects of LWD. I hypothesized that field removal of *P. borbonia* (i.e., LWD simulation) will significantly increase light availability in the understory layer and lead to an increase in the abundance of shade intolerant plants including seedlings of non-native woody species (e.g., *C. camphora* and *Triadica sebifera*). I also hypothesized that results from growth and resprouting experiments in the greenhouse would suggest functional similarity between *P. borbonia* and *C. camphora* as indicated by their responses to different conditions of light and nutrient availability.

Methods

Study site

The study site (~ 5 hectares) was located in the Grand Bay National Estuarine Research Reserve (GBNERR) which encompasses 7,446 hectares of Jackson County in coastal

Mississippi. Within this reserve, *P. borbonia* is often a dominant sub-canopy component of bay forests (Adam Chupp pers. obs.). Laurel wilt disease was first reported in Jackson County, Mississippi in 2009 near Sandhill Crane National Wildlife Refuge (Riggins et al. 2010) and infected trees have recently been observed on the GBNERR (Adam Chupp pers. obs.). I have targeted an area within GBNERR where *P. borbonia* is abundant and the invasion of LWD is imminent. The habitat at this location is typified by Gulf Coastal upland pine forest with a slash pine (*Pinus elliottii*) overstory, a subcanopy dominated by *P. borbonia*, an open understory with several woody shrubs (e.g., *Myrica cerifera*, *Ilex vomitoria*, and *Ilex glabra*), and a patchy herbaceous layer. This area is immediately adjacent to a brackish tidal-marsh community dominated by black needle rush (*Juncus roemerianus*). At the end of the study, no *P. borbonia* trees at the study site had shown symptoms of LWD.

Experimental transects

Three east-west transects (transect 1 = 210 m, transect 2 = 270 m, transect 3 = 190 m) were established at my field site in October and November 2010 (Figure 2.2). Transect points were marked at 10 m intervals. At each 10-meter point, a line perpendicular to the transect created four quadrants (NE, NW, SE, SW). In each quadrant, the nearest *P. borbonia* tree ≥ 2.5 cm diameter at breast height (DBH) was tagged and measured for DBH and distance to point-marker (point-centered quarter method). Along all three transects, a total of 280 trees was tagged and measured in October and November 2010. These data were used to determine the density and basal area of *P. borbonia* within the field site (point centered quarter after Mitchell 2001).

To estimate light transmission through forest canopy layers and to quantify the extent of *P. borbonia* foliage, canopy photos were taken from both tree-centered (*P. borbonia*) and random locations. All canopy photos were snapped from a point 1 m above the ground using a

Nikon Coolpix 4500 with Nikon FC-E8 fisheye converter lens. Tree-centered canopy photos were taken 1 m south of randomly selected *P. borbonia* trees (previously tagged). To select random photo locations, distance and direction from randomly selected transect points were determined using a random numbers table. Canopy photos were analyzed for percent light transmission using the Gap Light Analyzer (GLA) imaging processing software (Frazer et al. 1999).

Field experiments with LWD simulation

To simulate LWD at the study site, I girdled and ultimately removed a subset of *P. borbonia* trees along transect 1. This experiment provided me the opportunity to study the effects of crown dieback and subsequent resprouting on plant community composition prior to the arrival and progression of LWD. From the 88 *P. borbonia* trees tagged along transect 1, 23 were randomly selected as potential center points for removal treatment plots. Six of the 23 randomly selected trees were used as center points for the treatment plots, each with a 10 m radius (31.4 m²). These trees were selected to insure that there was no overlap among plots and that plots contained a density of *P. borbonia* that was comparable to the overall density of *P. borbonia* within the community. I used the same method to establish 6 identically sized control plots along transect 2. All *P. borbonia* ≥ 2.5 cm DBH within each plot were tagged; totaling 86 and 130 tagged *P. borbonia* trees in treatment and control plots, respectively.

In March 2011, all 86 tagged *P. borbonia* within treatment plots were girdled. For girdling, an axe was used to make a double cut around the circumference of the main trunk between 0.5 and 1.0 m above ground level. A 2-3 cm deep layer of tissue was removed from between the double cut (Kilroy and Keith 1999). The DBH of each girdled tree was recorded and all stems (seedlings or sprouts < 1 m above ground) within a 0.5 m radius of each tree's base

were counted and flagged. In July 2011, three 2 x 2 m survey plots were sampled in each treatment and control plot (36 survey plots total) using randomly selected *P. borbonia* trees as center points. Each survey plot contained two 1 m² composition plots located diagonally from one another (72 composition plots total), within which I recorded percent cover of all herbaceous species and the density of woody seedlings (height < 1.5 m). Using the whole 2 x 2 m survey plots, I also recorded the basal diameter of woody shrubs (multiple main stems \geq 1.5 m above ground level) and the DBH of all trees (single main stem \geq 1.5 m above ground level). Composition surveys were repeated in 2012 and 2013 during the peak of the growing season (July – September).

In January 2012, I enlarged all treatment and control plots to a radius of 17.5 m (109.9 m²) and removed the aboveground portions of all *P. borbonia* trees within treatment plots. Increasing the plot size created a buffer zone of canopy disturbance around survey plots and more accurately represented the spatial extent of LWD which can impact > 90% of all *P. borbonia* trees within a forest patch over a 2-year period (Fraedrich et al. 2008; Spiegel and Leege 2013; Evans et al. 2014). Girdling trees 9 months prior to their removal was intended to simulate the progression of LWD. Previously girdled trees (*i.e.*, tagged trees within the original 10 m radius plot) were cut with a chainsaw at the point of girdling, leaving behind a stump and all sprouts that had emerged in response to girdling. Additional trees that had not previously been girdled (*i.e.*, trees in the area encompassed by plot enlargement) were measured for DBH and cut between 0.5 and 1.0 m above ground level. All portions of above-ground material were removed > 20 m from the plot center. On control plots, the DBH of each *P. borbonia* (\geq 2.5 cm DBH) within the enlarged 109.9 m² plot was recorded.

At the time of removal, I recorded the number of sprouts that had emerged from the trunk of the tree (below point of girdling) and from the ground within 0.5 m of the base of the tree. I also measured the basal diameter and DBH (if applicable) of the tallest sprout. These measurements were repeated in January 2013 and 2014.

Immediately following the removal of *P. borbonia* and again in January 2014, I measured light transmission in all 2 m² survey plots. Canopy photos were captured and analyzed using the methods and materials described above.

Greenhouse experiments

To quantify the sprouting responses of *P. borbonia* and *C. camphora*, a greenhouse study was initiated in January 2012. Seeds of both *P. borbonia* and *C. camphora* were germinated in the lab and immediately potted in sand (Premium Play Sand from Lowe's). Additional *P. borbonia* seedlings were also purchased from Nearly Native Nursery in Fayetteville, GA. All seedlings were placed in pots 12 cm in diameter and 24 cm in height to allow for vertical root growth. I randomly assigned seedlings into a two-way factorial design: two factors (nutrient and light) with two levels each (high and low). Light treatment was 15% of full light (low light) or 75% of full light (high light). For the low light treatment, plants were randomly placed into one of four shade houses. High and low nutrient treatments consisted of 15 ppm (low) and 75 ppm (high) of Peter's 20:10:20 (NPK) fertilizer once per week during watering. The concentrations were determined from reported minimum and maximum values of soil nitrogen content from southeastern Coastal Plain habitats where *P. borbonia* and *C. camphora* are found (Jin et al. 2010). I allowed seedlings to grow under treatment conditions for 16 months (initial growth period) before all aboveground biomass was excised in May 2013. This initial aboveground biomass was dried to a constant weight at 50 °C and then weighed; leaf and stem biomass were

recorded separately. Subsequent resprouts were allowed to grow for 9 months before being destructively sampled in February 2014. At this time, above- and belowground biomass were collected, dried, and weighed separately.

Statistical analysis

Average percent light transmission was compared between random and tree-centered (*P. borbonia*) points with a t-test. I used the same analysis to test for differences in the mean basal area of *P. borbonia* between control and treatment plots; separate tests were conducted prior to and after the expansion of plot size (*i.e.*, includes buffer). A repeated measures analysis of variance (ANOVA) was used to test for differences in percent light transmission due to plot type (control vs treatment), time (2012 vs 2014), and interactions between the two factors. For *P. borbonia* trees in treatment plots, I used linear regressions to examine the relationships between sprouting responses (number of sprouts, basal diameter of tallest sprout, and area of tallest sprout at breast height) and initial tree basal area. For each measure of sprouting response, I compared survey years using repeated measures ANOVA. Sprouting data were graphically examined for normality and homoscedasticity.

We used a permutational multivariate analysis of variance (PERMANOVA) to examine differences in herbaceous species composition and abundance due to plot type, year, and interactions between these two factors. Bray Curtis values of similarity/dissimilarity were used for this analysis and for constructing an ordination of the sample units (Bray and Curtis 1957). I used the percent cover of herbaceous species in each year of the surveys (2011, 2012, and 2013) to create an ordination of control and treatment plots (sample units); percent cover for each species was an average of both composition plots (1 m²) that occurred within the same survey plot (2 m²). The ordination was created using non-metric multidimensional scaling with the

DECODA software package (Minchin 1989). The PERMANOVA was conducted using the PRIMER software package (Clarke 1993). I also conducted an indicator species analysis across plot types and survey years (Dufrene and Legendre 1997). Indicator values were calculated from the relative abundance and frequency of occurrence for individual herbaceous species. Faithful occurrence and/or concentrated abundance within a single group of sample units (*i.e.*, plot type and year) generate a greater indicator value for a given species (McCune and Grace 2002). Indicator species analyses were conducted with the PC-ORD software package (McCune and Mefford 1999). I compared seedling density and shrub basal area in control vs treatment plots over time using repeated measures ANOVA. Pairwise comparisons were conducted using both the Tukey's *post hoc* least square means and the slice approach for simple effects. As with herbaceous species, seedling estimates were averaged between composition plots that occurred within the same survey plot (*i.e.*, density = individuals/m²). Species were combined at first and then re-analyzed using individual target species.

The effects of light (high vs low), nutrient (high vs low), and species (*C. camphora* vs *P. borbonia*) on the growth of greenhouse plants were analyzed using a three-way ANOVA; the following response variables were tested: 1) initial leaf biomass, 2) initial stem biomass, 3) resprouted leaf biomass as a percentage of the initial leaf biomass, 4) resprouted stem biomass as a percentage of the initial stem biomass, and 5) final root biomass. Pairwise comparisons were conducted using Tukey's *post hoc* least square means. Data were tested for normality and homoscedasticity. Percentages were log-transformed to more approximate a normal distribution. I used the SAS software package (SAS Institute Inc. 2011) to conduct all univariate analyses and data transformations.

Results

Field experiments with LWD simulation

The density of *P. borbonia* determined from the point-centered quarter method was 328 trees ha⁻¹. Seventy-five percent of tagged *P. borbonia* trees fell into size class 1 (2.5 – 7.5 DBH) and size class 4 (17.5 – 22.5 DBH) includes the largest tree tagged at 19.8 DBH (Figure 2.3). On vegetation survey plots, there was no difference in total per plot basal area of *P. borbonia* between control and treatment plots; this was true before plot enlargement ($t = -1.02$, $P = 0.355$) and after ($t = -0.09$, $P = 0.934$). Prior to girdling and removal, there was no significant difference in percent light transmission between random and tree-centered points ($t = -1.56$, $P = 0.121$). Following the removal of *P. borbonia*, light transmission was significantly greater on removal plots compared to control plots, a trend that was consistent across years ($F_{1,34} = 94.73$, $P < 0.001$) (Figure 2.4).

All 86 trees that I girdled and then removed produced sprouts that were alive during the final survey in 2014. The average number of sprouts produced per tree significantly declined over the course of my surveys from 13.6 ± 1.1 in 2012 to 9.0 ± 0.6 in 2014 ($F_{2,251} = 9.48$, $P < 0.001$). There was a significant positive effect of initial tree basal area (*i.e.*, stump basal area) on the number of sprouts produced (2012, $F_{1,84} = 10.52$, $P = 0.002$; 2013, $F_{1,84} = 7.11$, $P = 0.009$; 2014, $F_{1,84} = 5.06$, $P = 0.027$) (Figure 2.5). The number of sprouts was log transformed to correct for heteroscedasticity.

The average basal diameter of the tallest sprout increased significantly during each year of the survey ($F_{2,254} = 112.08$, $P < 0.001$) from 0.74 ± 0.03 cm in 2012 to 1.35 ± 0.06 cm in 2013 and 1.95 ± 0.08 cm in 2014. There was a positive effect of initial tree basal area on the basal diameter of the tallest sprout during each year of my survey; this effect was significant in 2012

($F_{1,84} = 18.61$, $r^2 = 0.18$, $P < 0.001$), 2013 ($F_{1,84} = 44.07$, $r^2 = 0.35$, $P < 0.001$) and 2014 ($F_{1,84} = 42.10$, $r^2 = 0.34$, $P < 0.001$) (Figure 2.6).

In 2012, 9 months after girdling, only 42% of the tallest sprouts had reached breast height (1.5 m) compared to 80% in 2013 and 92% in 2014. Because only half of the tallest sprouts on each tree had reached breast height by 2012, I discarded this year of data from the analyses. The average area of tallest sprouts at breast height was significantly greater in 2014 (1.62 ± 0.18) compared to 2013 (0.67 ± 0.09) ($t = 4.66$, $P < 0.0001$). I used the Satterthwaite approximation because of unequal variances between survey years. Initial tree basal area had a significant positive effect on the basal area of sprouts at breast height during both years (2013, $F_{1,67} = 26.57$, $r^2 = 0.28$, $P < 0.0001$; 2014, $F_{1,76} = 55.46$, $r^2 = 0.42$, $P < 0.0001$) (Figure 2.7).

A two-dimensional ordination of survey plots based on the percent cover of herbaceous species had a stress value of 0.21 (Figure 2.8). There was a significant interaction between plot type (treatment vs control) and survey year (2012, 2013, and 2014) (Pseudo- $F_{2,64} = 2.03$, $P = 0.046$). Differences between treatment and control plots were only significant in 2012 ($t = 1.60$, $P = 0.017$). Within control plots, there were differences in herbaceous species composition and percent cover in 2014 when compared to both 2012 ($t = 2.18$, $P = 0.011$) and 2013 ($t = 3.77$, $P = 0.001$). Across treatment plots, there were no significant differences among survey years. Species that were common to both control and treatment plots included *Andropogon virginicus*, *Juncus roemarianus*, *Panicum virgatum*, *Rubus argutus*, and *Spartina patens*. All these species had relatively high indicator values for both plot types and no significant differences in percent cover occurred between plot types for any of these species ($P > 0.05$). Although *Toxicodendron radicans* was a significant indicator of treatment plots (IV = 55.3, $P = 0.001$), its indicator value was highest in 2011 and declined in 2012 and 2013 following *P. borbonia* removal. *Imperata*

cylindrica, *Ipomea sagittata*, and *Dichanthelium* sp. were also significant indicators of treatment plots but showed no differences among survey years. See Appendix A for a full list of the species observed in both plot types.

Seedling density exhibited interacting effects between plot type (control vs treatment) and survey year (2011, 2012, and 2013) (ANOVA: $F_{2,67} = 5.24$, $P = 0.008$) (Figure 2.9). Both Tukey's and the slice approach produced similar results. Within control plots, the only significant difference in total seedling density occurred between 2012 (5.2 ± 1.2 seedlings/m²) and 2013 (6.5 ± 1.5 seedlings/m²) ($t = -3.08$, $P = 0.003$). Within treatment plots, there were no significant differences among years. Control plots consistently contained more seedlings than treatment plots but these differences were not significant during any year of study. Across both control and treatment plots four species (*I. glabra*, *I. vomitoria*, *M. cerifera*, and *P. borbonia*) represented approximately 90% of all seedlings during each year of the survey (Table 2.1). Several species including the exotics, *C. camphora* and *Triadica sebifera*, were rarely present in both control and treatment plots. For each seedling species I was unable to identify significant differences in density due to plot type, year, or interactions between the two. Among shrub species, *Ilex vomitoria* was the only species to show a significant increase in basal area across survey years (ANOVA: $F_{2,18} = 11.80$, $P < 0.001$), a pattern that was found only in treatment plots. A summary of the shrub and tree species found within survey plots is presented in Table 2.2.

Greenhouse experiments

Following an initial 16-month growth period, I found a significant interacting effect of species and nutrient level on initial leaf biomass (ANOVA: $F_{1,146} = 9.35$, $P = 0.003$). All pairwise comparisons of the species x nutrient interaction means of leaf biomass were significant

except for the comparison between low nutrient treatments for each species. Results were similar for initial stem biomass except high nutrient treatments did not differ between species (Figure 2.10). Results from total resprouted leaf and stem biomass mirror that of leaf and stem initial biomass, respectively (Figure 2.11). Resprouted leaf biomass (% of initial leaf biomass) was affected by an interaction between species and nutrient level (ANOVA: $F_{1,146} = 7.27$, $P = 0.008$). Pairwise comparisons showed that *P. borbonia* seedlings in high nutrient conditions produced a significantly higher percent increase in leaf biomass compared to all other treatment combinations; highly significant when compared to low nutrient *P. borbonia* ($P < 0.001$) and less significant when compared to *C. camphora* high and low nutrient treatments ($P = 0.047$ and $P = 0.023$, respectively) (Figure 2.11). Results were similar for final resprouted stem biomass (% of initial stem biomass), which again showed significant interacting effects of species and nutrient level (ANOVA: $F_{1,146} = 14.03$, $P < 0.001$). *Persea borbonia* seedlings in the high nutrient treatment were significantly higher when compared to all other species x nutrient treatment combinations (Figure 2.11). Finally, root biomass did not differ between species but instead showed significant differences due to the interacting effects of light and nutrient levels (ANOVA: $F_{1,146} = 13.51$, $P < 0.001$). High nutrient conditions produced greater root biomass under both high and low light conditions ($P < 0.001$ and $P < 0.001$, respectively). In addition, root biomass under the high light and high nutrient conditions was significantly greater than both conditions of low light/high nutrient ($P < 0.001$) and low light/low nutrient ($P < 0.001$) (Figure 2.12).

Discussion

In the southeastern US, dramatic losses of *P. borbonia* due to LWD have warranted investigations regarding the ecological role of this species. A small number of studies have examined *P. borbonia* populations and associated communities on the Atlantic Coast (Fraedrich et al 2008; Shield et al. 2011; Spiegel and Leege 2013; Evans et al. 2013). Here, I provide empirical data concerning the functional role of *P. borbonia* in a typical maritime forest along the northern Gulf Coast prior to the arrival of LWD. Such information will be vital to our understanding of the impacts of LWD on associated communities and the maintenance of functional services provided by *P. borbonia*.

The density of *P. borbonia* trees ($\text{DBH} \geq 2.5 \text{ cm}$) reported here ($328 \text{ trees ha}^{-1}$) is comparable to densely populated stands on the Atlantic Coast. At the Timucuan Ecological and Historic Preserve on Fort George Island, FL, observations of *P. borbonia* trees ($\text{DBH} \geq 2.5 \text{ cm}$) suggested a density of 290 ha^{-1} in habitat dominated by *P. borbonia*, live oak (*Quercus virginiana*), red cedar (*Juniperus virginiana*), and southern magnolia (*Magnolia grandiflora*) (Fraedrich et al 2008). Unfortunately, there are few studies that have documented the absolute density of *P. borbonia* and as LWD continues to decimate populations it will be impossible for us to determine the extent to which this has altered the structure and composition of communities. However, I have provided baseline data for investigating the stand-level impacts of LWD at my site and similar sites across the northern Gulf Coast.

The foliage produced by *Persea borbonia* was a substantial component of stand structure at my site. I documented the contribution of *P. borbonia* to the sub-canopy layer by showing a roughly 50% increase in light transmission following experimental removal of *P. borbonia*. In the Coastal Plain of South Carolina, infestations of LWD and subsequent high levels of *P.*

borbonia mortality have led to as much as 5-fold increases in photosynthetically active radiation (PAR) in these stands (Spiegel and Leege 2013). Based on prior observations of LWD-induced sprouting on the Atlantic Coastal Plain (A Chupp pers. obs.), I suspected that subsequent sprouting by infested *P. borbonia* would fill canopy gaps and decrease light transmission. However, analysis of canopy photos taken in 2014 at GBNERR failed to show such changes. Although sprouting was vigorous from around the base of tree trunks, few sprouts had reached the subcanopy layer three years after main stems were girdled. In addition, I found no evidence of root sprouting which contributes to sapling thicket formation in other cases of tree disease. In the northern hardwood forests of New York, dense thickets of sapling *Fagus grandifolia* are formed following the attack of adult trees by beech bark disease (Forrester et al. 2003). These thickets are highly competitive for above- and below-ground resources and prevent the recruitment of co-occurring species (e.g., *Acer saccharum*) (Hane et al. 2003; Giencke et al. 2014). While girdling failed to stimulate thicket formation of *P. borbonia* at my field site, such a response to LWD has been observed at sites on the Atlantic Coastal Plain (A Chupp pers. obs.; S Fraedrich pers. comm.). The extent and magnitude of this sprouting response and its effect on resource availability requires greater attention.

According to recent studies, basal resprouting by LWD-infected *P. borbonia* is a typical response and may occur in > 80% of infected individuals (Evans et al. 2013; Spiegel and Leege 2013). While this suggests that the vigorous sprouting observed on all girdled *P. borbonia* trees during my study is consistent with the effects of LWD, it should be noted that many LWD-infected individuals in Jackson County, Mississippi had not produced sprouts at least 2 years after infection (A Chupp pers. obs.). It is unclear what factors may be prohibiting some trees from producing sprouts. Although all individuals produced at least one sprout during my

greenhouse experiments, the results of these trials suggest that growth of *P. borbonia* resprouts is limited by nutrient availability. It should be noted that the closely related exotic species, *C. camphora*, did not exhibit the same response. While both species had greater initial biomass production in high nutrient treatments, only *P. borbonia* showed the same response during resprouting. I observed that even the smallest *P. borbonia* seedlings produced relatively large resprouts in the high nutrient treatment. Although I did not attempt to correlate sprouting responses with nutrient availability in the field, the greenhouse experiment suggested that sprout productivity and ultimately the persistence of *P. borbonia* are regulated by local nutrient conditions. Faster growing sprouts will have a better chance of surviving subsequent disturbances (*e.g.*, herbivory) and reaching the sub-canopy layer. For example, on St. Catherine's Island, GA, browsing of *P. borbonia* resprouts by deer may be promoting mortality and limiting persistence of LWD-infected individuals (Evans et al. 2013). In general, deer browsing can severely limit the regeneration of forested systems (Cote et al. 2004). Although I found no evidence of deer browsing at my site, I did observe substantial damage to resprouted foliage due to insect herbivory.

Areas of higher nutrient availability may offer the best opportunities for *P. borbonia* to regenerate and persist. In fire-prone systems, post-disturbance sprout production is regulated by the capacity for species to form underground storage reserves (*e.g.*, lignotubers) and accumulate starch when nutrient availability permits (Knox and Clarke 2005). Whereas the root structure of non-sprouting species is optimized for the efficient exploration of the upper soil layers, sprouting species are adapted for carbon storage and the penetration of deeper soil horizons (Paula and Pausas 2011). Under more fertile conditions (higher nutrient availability), sprouting species may have a competitive advantage due to these morphological/physiological features that permit

greater carbohydrate storage and utilization following disturbances (Knox and Clarke 2005). Upon harvesting the belowground biomass during greenhouse experiments, I noticed that > 90% of *P. borbonia* plants developed lignotubers. Superficial estimates of lignotuber size suggested that plants in the high nutrient treatments developed larger lignotubers. These observations combined with the aforementioned results of the greenhouse experiments suggest that the life history characteristics of *P. borbonia* are consistent with those of other resprouting species which exhibit a vigorous response to disturbances (*e.g.*, fire, disease, and deer browse). More research is needed to quantify the post-LWD sprouting capacity of *P. borbonia*, variability in this response, and the affects *P. borbonia* sprouting has on resource (light and nutrients) availability and the recruitment of co-occurring species.

As LWD removes *P. borbonia* from the canopy layer, changing abiotic conditions may drive shifts in plant composition and abundance. Comparisons between infested and uninfested sites have suggested an increasing dominance of other subcanopy species (*Magnolia virginiana* and *Gordonia lasianthus*) in areas that experienced LWD-induced mortality of *P. borbonia* (Spiegel and Legee 2013). However, it is unclear if these differences existed prior to LWD infestation; infested communities were not sampled pre-LWD arrival. In addition, control and treatment sites were not located within close proximity and encompassed different habitat types. Here, control (*P. borbonia* present) and treatment (*P. borbonia* removed) plots were compared within the same community following an initial sampling in 2011 (prior to removal). Subsequent changes in shrub layer species from 2011 to 2013 were relatively consistent between control and treatment plots, however, it is interesting to note that increases in *I. vomitoria* basal area were only significant on treatment plots. Whereas Spiegel and Legee (2013) reported increases in co-dominant species, *M. virginiana* and *G. lasianthus*, I suggest that co-occurring shrubs of

relatively high abundance, *I. vomitoria* and *Myrica cerifera*, will also increase in dominance following the invasion of LWD. Relative to other disturbances by forest insect pests (e.g., gypsy moth, hemlock woolly adelgid, and beech bark disease) which may take five to ten years to kill individual trees (reviewed by Lovett et al. 2006), LWD causes rapid mortality within months. As such, community turnover may occur rapidly and mature individuals of co-dominant species should be highly competitive for the resources left behind by *P. borbonia*. As mature trees and shrubs fill these gaps, the dynamics of the understory plant community may remain consistent with pre-LWD conditions.

Toxicodendron radicans, *Imperata cylindrica*, *Ipomea sagittata*, and *Dichanthelium* sp. were all indicators of treatment plots. However, there were no apparent trends in the abundances of these species over time that would indicate a response due to the removal of *P. borbonia*. Similarly, analyses of seedling densities failed to detect effects of the experimental removal. While an increase in seedling density was observed on control plots between 2012 and 2013, the biological significance of these results is questionable and additional robust analyses may be needed to tease apart these patterns. Overall, comparisons between control and treatment plots suggested that observed increases in light availability due to the removal of *P. borbonia* had minimal effect on the regeneration and/or recruitment of understory plants after 2 years. I should note that the experimental removal of *P. borbonia* and associated changes in light availability was greatly expedited compared to the natural progression of main stem decomposition and subsequent canopy collapse. If the abrupt changes to light conditions during my LWD simulation failed to produce detectable changes in understory plant composition/abundance, I submit that such shifts are unlikely under natural conditions.

We know very little about the long-term effects of LWD. Although changes to *P. borbonia* populations over time have been quantified (Evans et al. 2014), it is unclear what regulates both the initial production and long-term persistence of sprouts and how the effects of LWD on *P. borbonia* populations are re-shaping associated communities. I encourage the initiation of long-term surveys that encompass periods of pre- and post-LWD invasion in habitats across the distributional range of *P. borbonia*. These investigations will be crucial towards understanding how outbreaks of plant diseases and exotic invasions have shaped and will continue to shape terrestrial ecosystems.

Table 2.1. Average density of seedlings per m² for each species that was observed on control and treatment (*P. borbonia* removal) plots during each year of my composition survey.

	2011	2012	2013
Control plots (n = 16)			
<i>Acer rubrum</i>	0.13	0.06	0.34
<i>Bacharris halimifolia</i>	0.03	0.00	0.00
<i>Cinnamomum camphora</i>	0.00	0.00	0.03
<i>Ilex glabra</i>	3.50	2.97	3.47
<i>Ilex vomitoria</i>	1.31	1.13	1.41
<i>Myrica cerifera</i>	0.97	0.72	1.13
<i>Persea borbonia</i>	1.13	1.22	1.38
<i>Pinus elliottii</i>	0.22	0.19	0.19
<i>Quercus virginiana</i>	0.03	0.09	0.09
Total	7.31	6.38	8.03
Treatment plots (n = 16)			
<i>Acer rubrum</i>	0.00	0.00	0.09
<i>Bacharris halimifolia</i>	0.13	0.06	0.03
<i>Cinnamomum camphora</i>	0.00	0.06	0.06
<i>Ilex glabra</i>	1.03	1.13	1.13
<i>Ilex vomitoria</i>	0.56	0.59	0.91
<i>Myrica cerifera</i>	0.50	0.50	0.50
<i>Persea borbonia</i>	0.88	1.72	1.28
<i>Photinia pyrifolia</i>	0.03	0.00	0.03
<i>Pinus elliottii</i>	0.09	0.28	0.22
<i>Quercus virginiana</i>	0.06	0.00	0.03
<i>Triadica sebifera</i>	0.06	0.03	0.03
Total	3.34	4.38	4.31
Grand Total	10.66	10.75	12.34

Table 2.2. Total basal area (cm²) for shrub and tree species observed on control and treatment plots during each year of study. *Ilex vomitoria* was the only species to show a significant increase across years and these differences are indicated with different letters.

	2011	2012	2013
Control plots (n = 16)			
Shrubs			
<i>Ilex glabra</i>	16.9	25.0	25.1
<i>Ilex vomitoria</i>	23.8	35.7	45.4
<i>Myrica cerifera</i>	84.9	88.8	116.8
Total	125.6	149.5	187.3
Trees			
<i>Persea borbonia</i>	534.2	542.7	551.9
<i>Pinus elliottii</i>	6876.6	7153.5	7241.3
Total	7410.8	7696.2	7793.2
Treatment plots (n = 16)			
Shrubs			
<i>Baccharis halimifolia</i>	3.5	0.0	0.0
<i>Ilex glabra</i>	11.8	7.7	9.8
<i>Ilex vomitoria</i>	21.4 ^a	42.0 ^b	62.5 ^c
<i>Myrica cerifera</i>	30.0	35.7	41.8
Total	66.7	85.4	114.1
Grand Total	192.4	234.9	301.4
Trees			
<i>Persea borbonia</i>	617.5	33.2	57.3
<i>Pinus elliottii</i>	1378.7	1419.4	1496.8
Total	1996.2	1452.6	1554.1
Grand Total	9407.0	9148.7	9347.4

Distribution of Counties with Laurel Wilt Disease* by year of Initial Detection

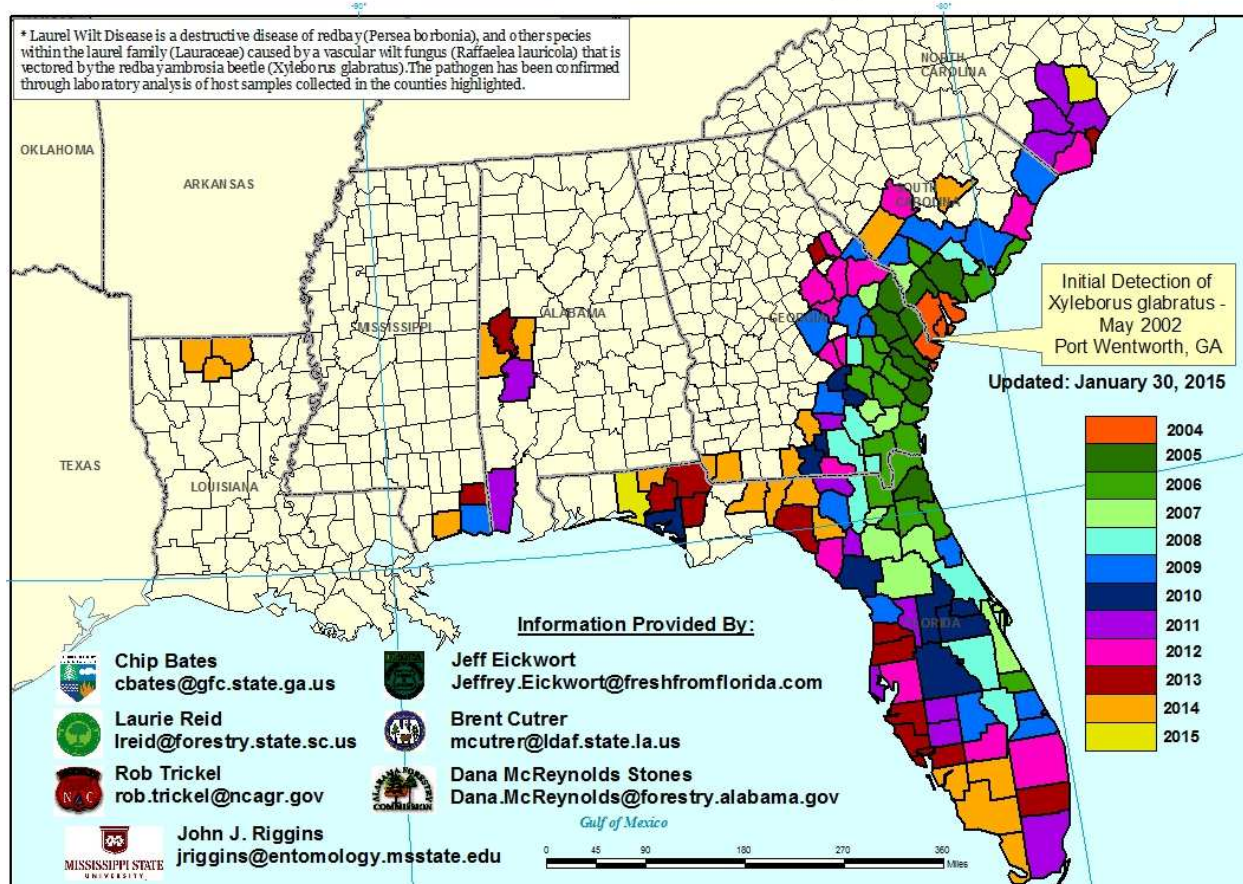


Figure 2.1. Distribution of laurel wilt disease by county and year of initial detection (USDA Forest Service 2015a)



Figure 2.2. Google Earth image showing field site and experimental transects at Grand Bay National Estuarine Research Reserve in Jackson County, Mississippi.

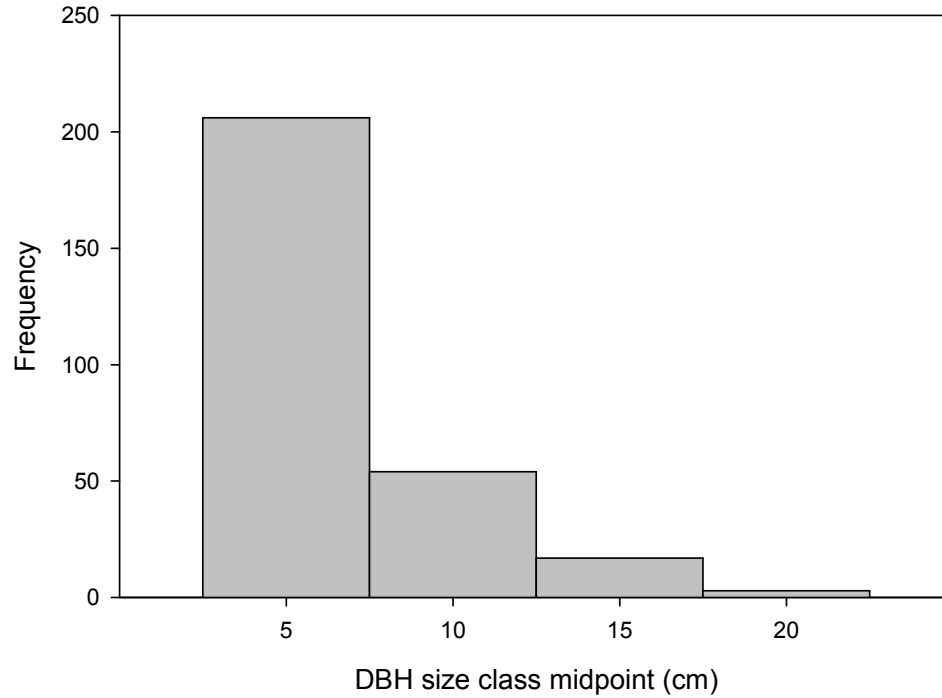


Figure 2.3. Frequency histogram representing tagged *P. borbonia* trees ($n = 280$) along three transects in a 5 hectare patch of maritime forest at GBNERR. Each size class encompasses 5 cm beginning with 2.5 cm DBH. Trees were selected using the point-centered quarter method.

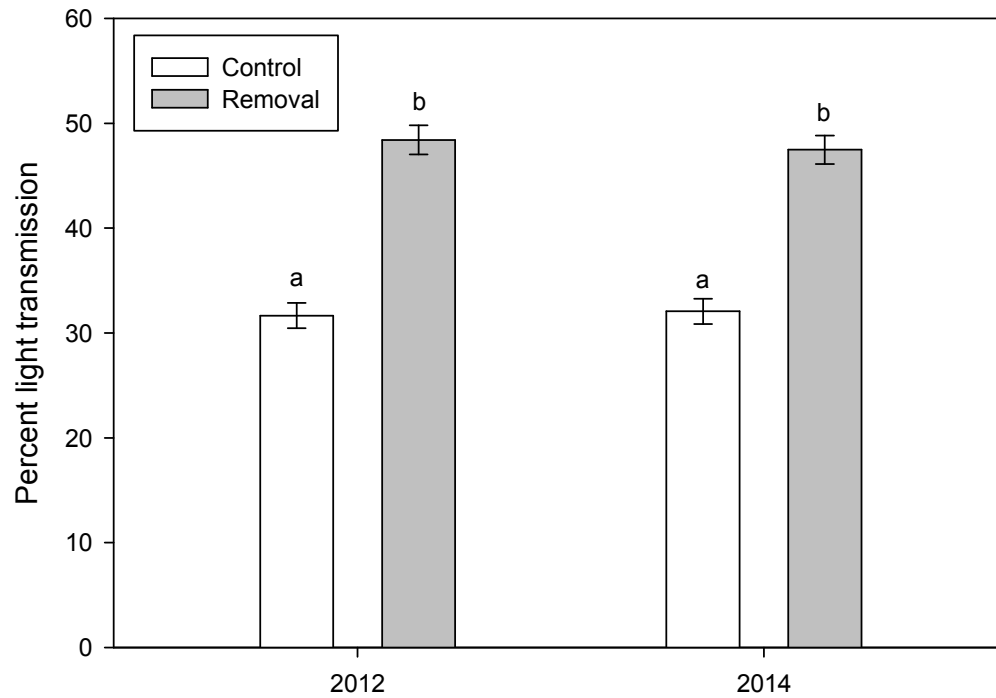


Figure 2.4. Percent light transmission on vegetation survey plots in 2012 and 2014. Values are based on analyses of canopy photos using GLA. Bars that do not share the same letter are significantly different from one another ($P < 0.05$). Error bars represent one standard error.

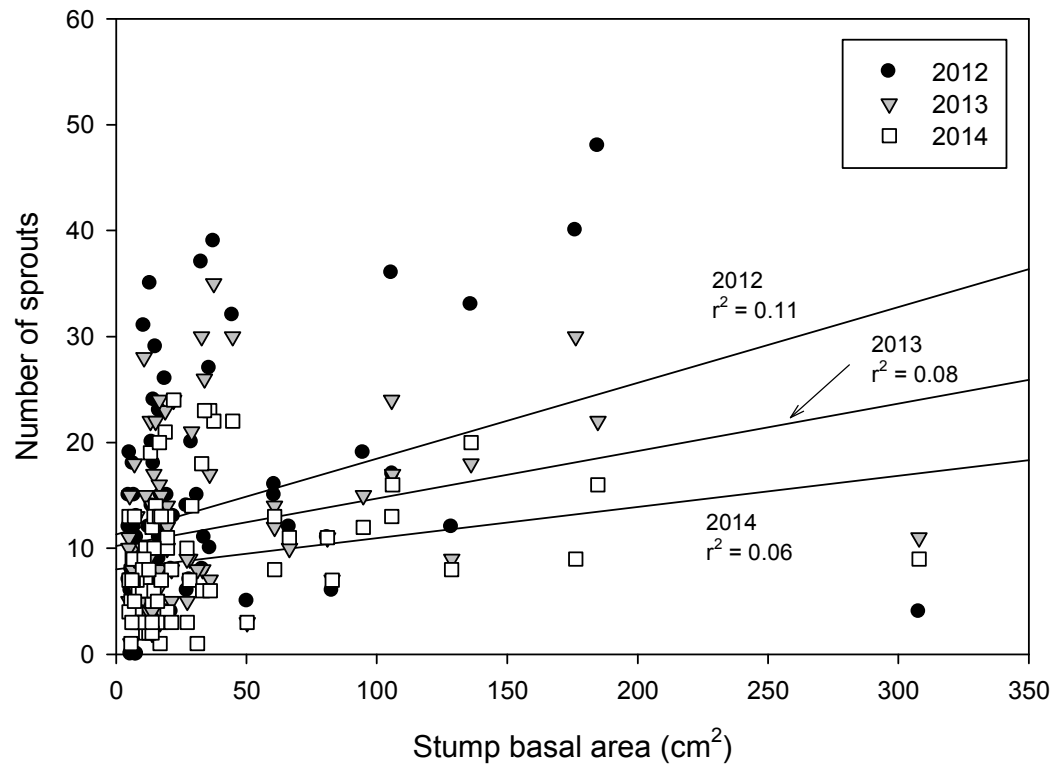


Figure 2.5. Relationship between stump basal area and the number of basal resprouts per tree present during each year of the survey. The 2012 survey was conducted 9 months after trees were girdled and just prior to complete stem removal. The same 86 trees were surveyed each year. All R^2 values are significant ($P < 0.05$).

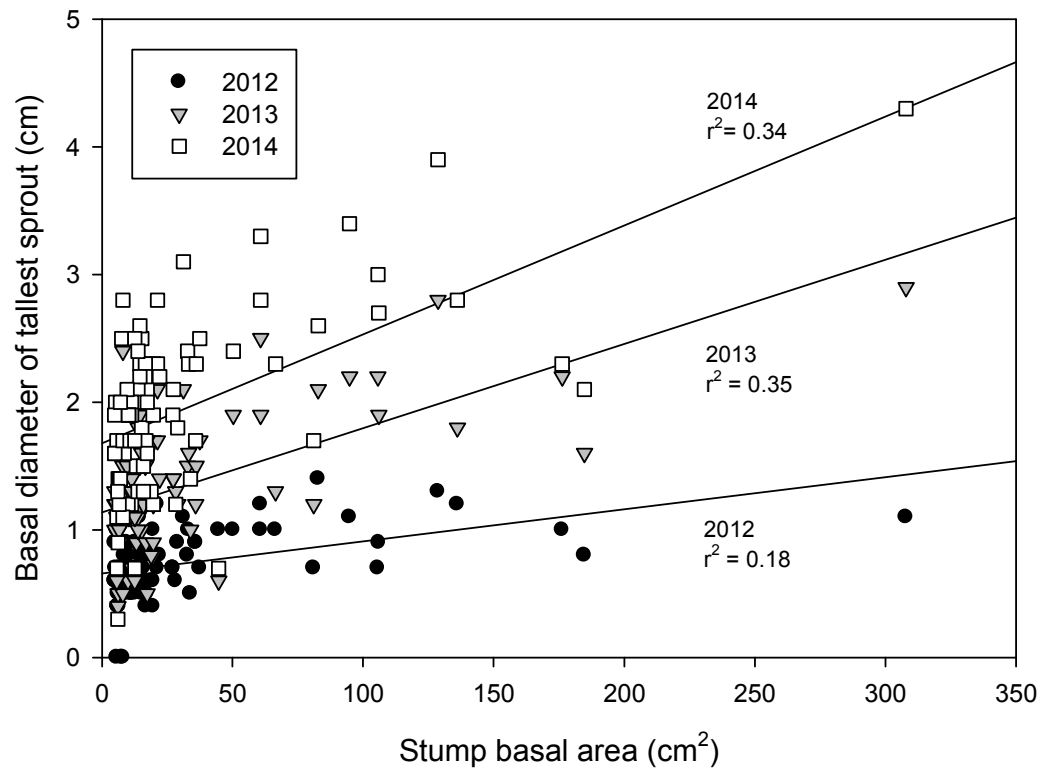


Figure 2.6. Relationship between stump basal area and the basal diameter of the tallest sprout during each year of the survey. The 2012 survey was conducted nine months after trees were girdled and just prior to complete stem removal. The same 86 trees were surveyed each year. All R^2 values are significant ($P < 0.05$).

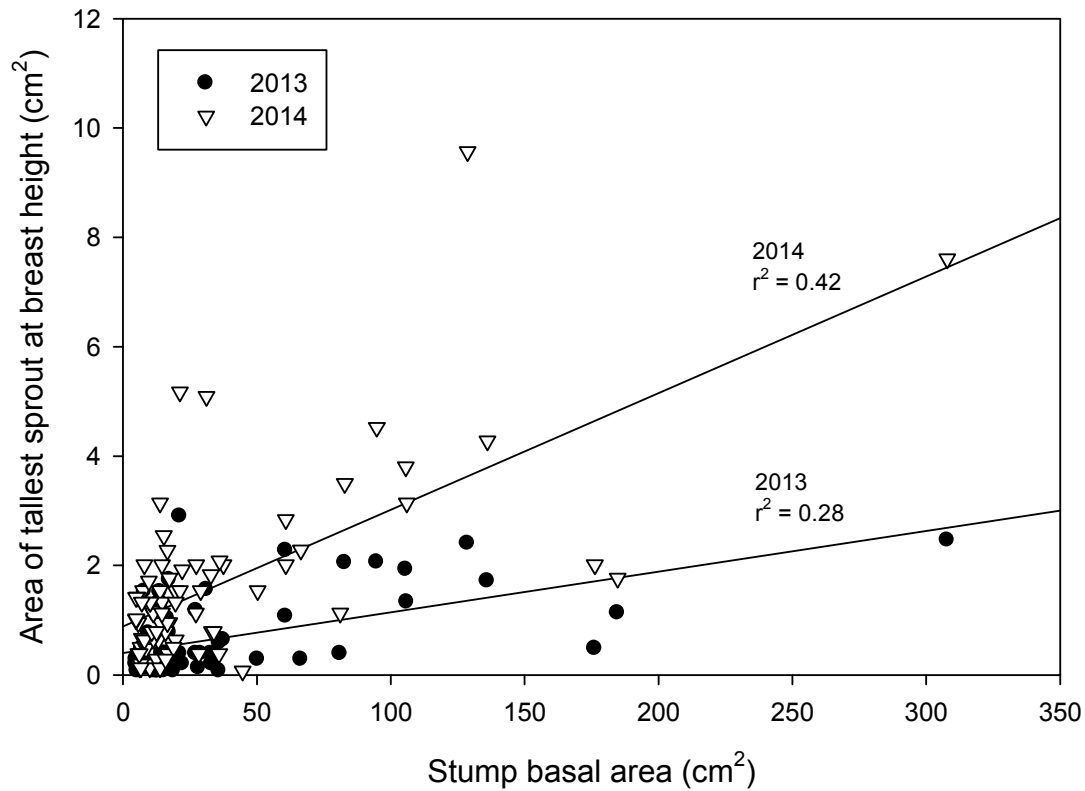


Figure 2.7. Relationship between stump basal area and the area of the tallest sprout at breast height during each year of the survey. Results from the 2012 survey were omitted due to a small sample size (*i.e.*, very few trees had sprouts that were at least breast height). From a total of 86 trees, sample sizes were 69 and 78 in 2013 and 2014, respectively. Both R^2 values are significant ($P < 0.05$).

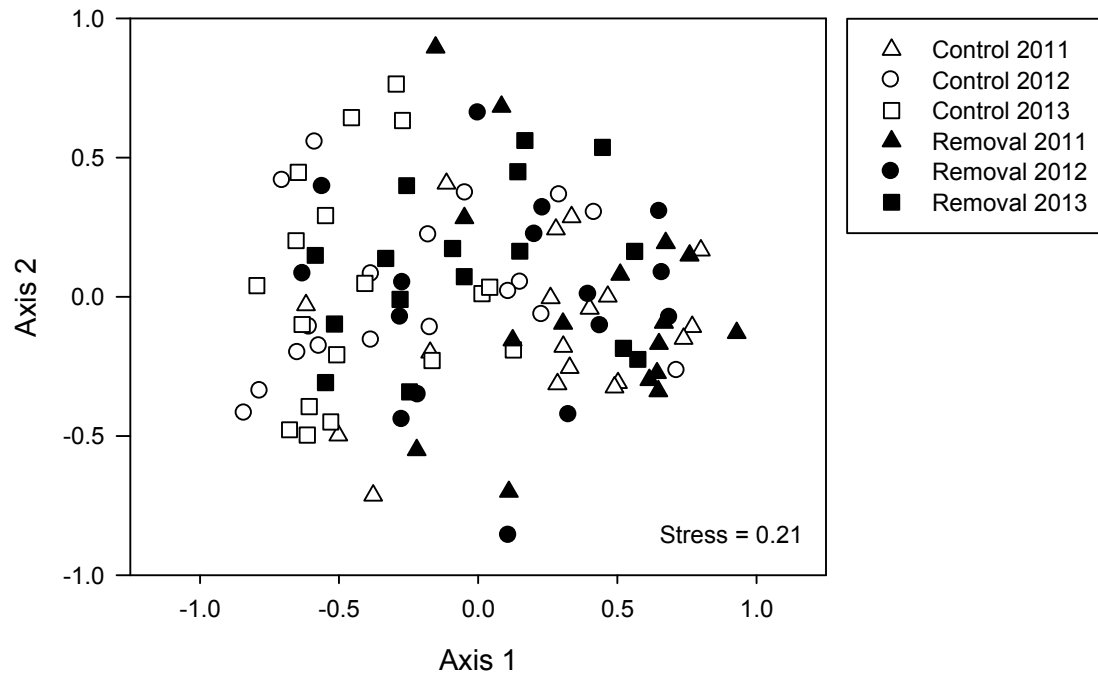


Figure 2.8. Non-metric multidimensional scaling ordination of herbaceous communities in control and removal plots (n=36) across three years. The ordination was constructed using the percent cover of each plant species in each year of the survey.

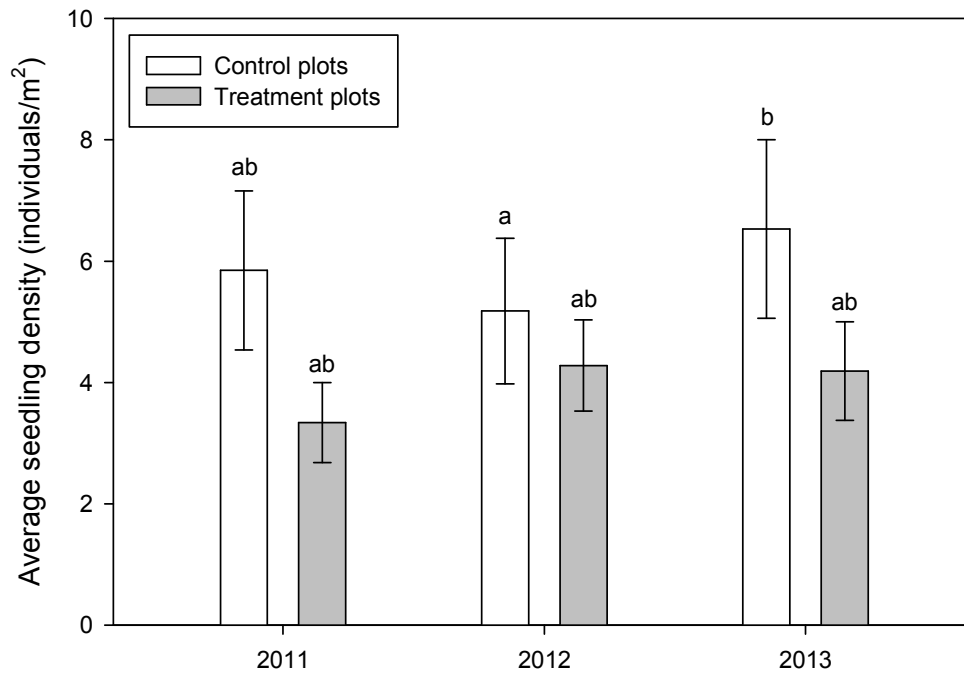


Figure 2.9. Average seedling density in control and removal plots ($n = 36$) during each year of my composition survey. There was a significant plot type by time interaction (ANOVA: $F_{2,67} = 5.24$, $P = 0.008$); pairwise comparisons were conducted using the slice approach. Bars that do not share the same letter are significantly different from one another ($P < 0.05$).

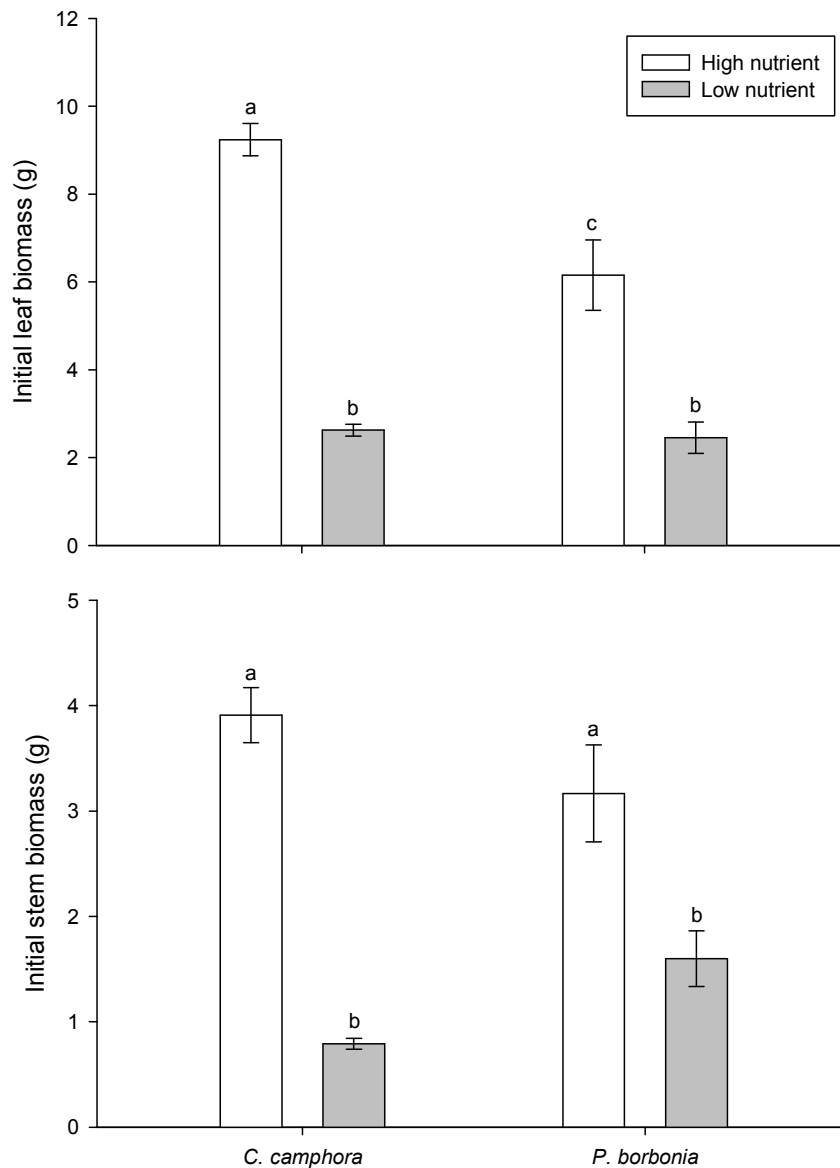


Figure 2.10. Initial leaf (above) and stem (below) biomass of *C. camphora* and *P. borbonia* seedlings grown under different light and nutrient conditions in the greenhouse. Light levels had no effect on initial leaf or stem biomass. There was a significant species by nutrient level interaction (ANOVA: leaf, $F_{1,146} = 9.35$, $P = 0.003$; stem, $F_{1,146} = 7.32$, $P = 0.008$); pairwise comparisons were conducted using Tukey's *post-hoc* least squares means. Bars that do not share the same letter are significantly different from one another ($P < 0.05$).

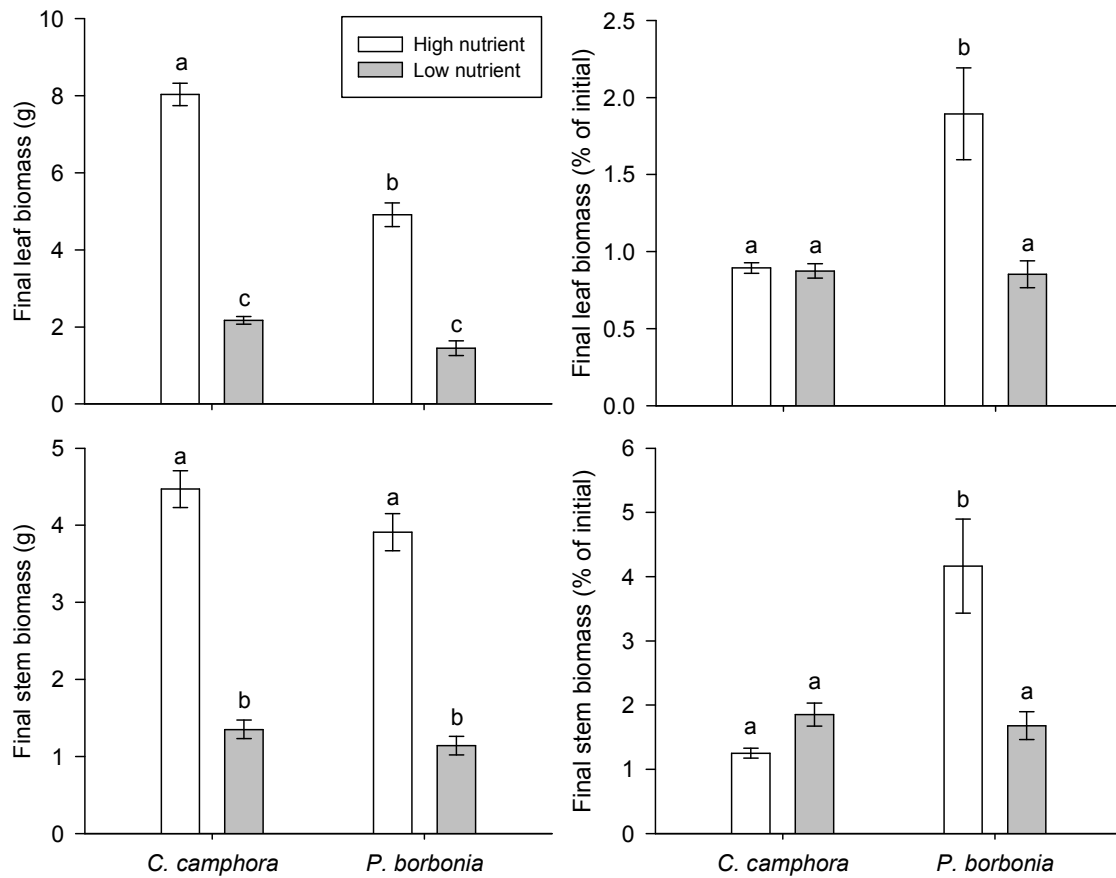


Figure 2.11. Final respouted leaf (above) and stem (below) biomass of *C. camphora* and *P. borbonia* seedlings grown in the greenhouse. Panels on the left show total biomass (g), whereas panels on the right show total biomass as a percentage of the initial biomass. Pairwise comparisons were conducted using Tukey's *post-hoc* least squares means. Bars that do not share the same letter are significantly different from one another ($P < 0.05$).

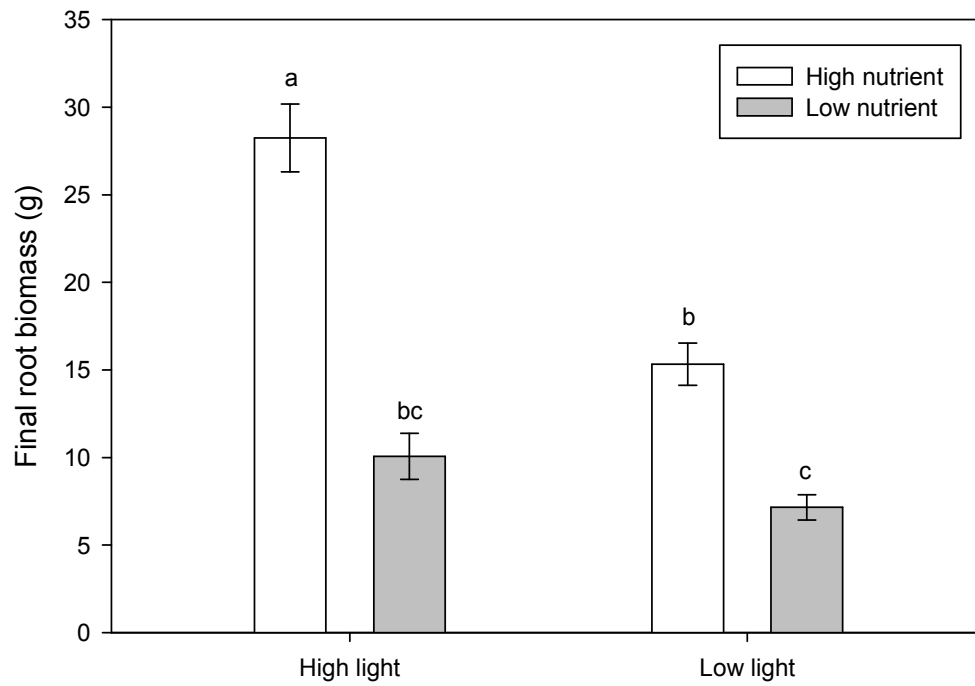


Figure 2.12. Final root biomass of *C. camphora* and *P. borbonia* seedlings grown under different light and nutrient conditions in the greenhouse. There was a significant light by nutrient level interaction (ANOVA: $F_{1,146} = 13.51$, $P = 0.0003$); pairwise comparisons were conducted using Tukey's *post-hoc* least squares means. Bars that do not share the same letter are significantly different from one another ($P < 0.05$).

CHAPTER 3

POTENTIAL FOR HOST SHIFTING IN *PAPILIO PALAMEDES* FOLLOWING INVASION OF LAUREL WILT DISEASE

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Abstract

In the southeastern US, laurel wilt disease (LWD) is causing widespread mortality of species in the Lauraceae. The principal target, *Persea borbonia*, is the primary larval host of *Papilio palamedes*, which is known to feed on other Lauraceae species. Among these potential hosts, the exotic *Cinnamomum camphora* is the only species that has shown resistance to LWD. I hypothesized that oviposition preference for *C. camphora* and *P. borbonia* would correspond to larval performances on these species and that the relative host suitability of *C. camphora* would indicate an opportunity for host-switching. I used laboratory experiments and field observations to compare performance and preference of *P. palamedes* between *C. camphora* and *P. borbonia* foliage. My results indicate moderate survivorship on *C. camphora* compared to *P. borbonia* and no differences in first and fourth instar growth rates between treatments. Fourth instars consumed relatively less of *C. camphora* foliage compared to that of *P. borbonia*, but metabolic efficiency did not differ between treatments. Rearing on the foliage of *P. borbonia* stump sprouts from LWD-infected trees resulted in significantly higher growth rates and metabolic efficiency as first and fourth instars, respectively. In the field and laboratory, I found no oviposition preference for *C. camphora*. While females laid eggs on *C. camphora* during laboratory trials, the same number of eggs was also laid on inanimate objects. I conclude that *C. camphora* is suitable for larval development but host-switching to this species by *P.*

palamedes will be primarily constrained by the ecological factors that govern oviposition behaviors.

Introduction

Species invasions and disease outbreaks can dramatically alter the relative abundances of native and exotic species and facilitate the formation of novel species associations (Agosta et al. 2010). Under these circumstances, new relationships between exotic and native species may form on the basis of compatibility and thus do not represent the outcome of a long history of coevolution; the term “ecological fitting” has been used to explain such novel associations (Janzen 1980, 1985; Agosta 2006; Agosta and Clemens 2008). By forming relationships with native species in the wake of disturbance, exotic species can maintain an interactive system (*i.e.*, herbivory, pollination, and dispersal) when they have functions that are similar to that of a native species (Zamora 2000). Such functional equivalence may provide resiliency to disturbance. On the other hand, associations with exotic species may alter ecological processes and degrade the function of native systems (Simberloff and Von Holle 1999). In either scenario, the results will have important implications for conservation programs. The initial steps of forecasting novel species associations and disseminating these predictions should be a major goal for theoretical conservation biologists.

For insect herbivores, which provide an important link between primary producers and higher trophic levels, predicting shifts in host plant associations may have broad implications for community dynamics and ecosystem processes (Sih et al. 1985). Such forecasts are complicated by the complex set of biological and ecological factors that can shape host selection at multiple insect life stages (see Pearse and Altermatt 2013; Pearse et al. 2013). Larvae of many insect

herbivores, such as those of the Lepidopterans, are relatively sedentary. Therefore, host plant selection is made by ovipositing adult females who should optimize fitness by selecting host plants that maximize the performance of their larval offspring (Jaenike 1978). However, interactions with exotic host plants may often result in suboptimal relationships between oviposition preference and larval performance (Karowe 1990, Larsson and Ekbom 1995; Schlaepfer et al. 2005; Gillespie and Wratten 2011). For example, female common coppers (*Lycaena salustius*) will recognize and oviposit on exotic buckwheat (*Fagopyrum esculentum*) despite poor larval performance on this species. The morphological and chemical similarities between *F. esculentum* and the ancestral (native) hosts of *L. salustius* are apparently driving the behavior of ovipositing females (Gillespie and Wratten 2011). Although analyses of oviposition behaviors suggest ecological fitting between *L. salustius* and *F. esculentum*, the novel host plant may be an evolutionary trap if the physiological performance of larvae remains low (Schlaepfer et al. 2005). Predicting novel host colonization requires an understanding of both the preference and performance of an insect herbivore on a potential host. By considering herbivore and host species traits and their evolutionary histories we can identify where good ecological fits may occur (Pearse et al. 2013). The availability and occupancy of potential hosts may be of utmost importance (Forister and Wilson 2013), especially in situations where exotic species invasions and disease outbreaks are permanently altering the relative abundances of host species.

In North America, several well-documented cases of forest disease and insect outbreaks, *e.g.*, chestnut blight (Anagnostakis 1987), hemlock woolly adelgid (Orwig and Foster 1998), and emerald ash borer (Haack et al. 2002), have resulted in dramatic declines in the dominance of native species. However, the greatest reductions in species richness are expected to occur among groups of insect herbivores that specialize on the impacted native species (Gandhi and Herms

2010). Despite this expectation, estimates of these effects on insect herbivores are rare (but see Work and McCullough 2000; Scriber 2004; Wagner 2007). To more completely understand the impacts of widespread forest disturbances, we need thorough documentation of herbivores and their associations before they become permanently altered (Gandhi and Herms 2010).

Throughout the Coastal Plain of the southeastern US, laurel wilt disease (LWD) has decimated populations of species in the Lauraceae family (USDA Forest Service 2015b). Although this newly discovered exotic fungal pathogen, *Raffaelea lauricola*, and its beetle vector, *Xyleborus glabratus* (Coleoptera: Curculionidae), have caused mortality in several Lauraceae species, most incidences of LWD are observed on redbay, *Persea borbonia* L. (Laurales: Lauraceae) (Fraedrich et al. 2008). In *P. borbonia* populations, mortality is > 95% for trees above 2.5 cm diameter at breast height (DBH). The symptoms progress rapidly as the fungal pathogen apparently blocks water transport in the xylem, resulting in canopy wilting and death within weeks to a few months (Fraedrich et al. 2008; Mayfield 2008; pers. obs. A Chupp). Although stump sprouting appears to be a common response in some populations of *P. borbonia*, re-infection of sprouts via *X. glabratus* and/or spreading of *R. lauricola* through the root system is evident (Spiegel and Leege 2013). As such, sprouting responses may do little to sustain populations of *P. borbonia*.

With the persistence of *P. borbonia* in question, there is concern for the herbivores which obtain resources from this species. Across the Gulf and Atlantic Coastal Plain, *P. borbonia* is a common sub-canopy species in many forested habitats and appears to play an important role as a food source for many native species (Brooks 1962; Goodrum 1977; Landers et al. 1979; Brendemuehl 1990; Van Deelan 1991, Leege 2006). In the literature, *P. borbonia* is perhaps best known as the primary larval host of the palamedes swallowtail butterfly, *Papilio palamedes*

Drury (Lepidoptera: Papilionidae). This long-tongued pollinator is abundant on the southeastern Coastal Plain and has a distribution which roughly mirrors that of *P. borbonia*. Laboratory observations suggest that female oviposition preferences and larval performance are highest on *P. borbonia* when compared to other species of Lauraceae (Brooks 1962; Scriber et al. 1991; Lederhouse et al. 1992). However, there are also accounts of *P. palamedes* using other species within the Lauraceae, including the exotic camphor tree, *Cinnamomum camphora* L. (Laurales: Lauraceae). In laboratory experiments, 15% of *P. palamedes* larvae survived when reared on *C. camphora* (Lederhouse et al. 1992). However, with such a small number surviving to adulthood ($n = 3$), conclusions drawn from other measures of larval performance (*i.e.*, lifetime larval growth rate, larval duration, and pupal mass) were insignificant. A year earlier, the same authors reported survivorship on *C. camphora* to be 50% (Scriber et al. 1991), however, larvae were reared for only 12 days, which is 1/3 of the total larval development time on *C. camphora* (Lederhouse et al. 1992). The studies by Scriber et al. (1991) and Lederhouse et al. (1992) provide minimal data regarding the performance of *P. palamedes* on *C. camphora*. In addition, I found no studies of adult female oviposition preferences for *C. camphora*. Altogether, it is unclear to what degree *P. palamedes* may use *C. camphora*.

Following the widespread mortality of *P. borbonia*, I submit several reasons for why *C. camphora* may be the best alternative host for *P. palamedes*. First, *C. camphora* has a close phylogenetic relationship with *P. borbonia* and shares morphological and chemical characteristics (Chanderbali et al. 2001, A. Chupp pers. obs). Such similarities have been useful for predicting trait matching (*i.e.*, ecological fitting) between plants and herbivores and subsequent colonization of novel plant species (as reviewed by Pearse et al. 2013). Second, *C. camphora* has a distribution which overlaps that of *P. borbonia* and is expanding throughout the

Atlantic and Gulf Coastal Plains; this sub-canopy tree is listed as a naturalized invasive species in eight states of the southeastern US, as well as California, Hawaii and the territory of Puerto Rico (USDA, NRCS 2014). Third, observations of LWD in *C. camphora* suggest a resistance to the disease and/or its beetle vector. In Florida and Georgia, infected individuals showed minimal stem die-off and in no case did complete canopy wilting occur (Smith et al. 2009). Results from single point inoculation trials in the field and laboratory failed to produce LWD symptoms in *C. camphora* despite systemic colonization by *R. lauricola*; multiple point inoculations caused only localized branch dieback (Fraedrich et al. In press). These laboratory and field trials provide the most recent evidence that *C. camphora* is more resistant to LWD than native Lauraceae species. Finally, successful development on *C. camphora* has been reported for several species of Papilionidae from North America [*Papilio glaucus* L. (Lepidoptera: Papilionidae) and *Papilio troilus* L. (Lepidoptera: Papilionidae)], Tasmania [*Graphium macleayanus moggana* Leach (Lepidoptera: Papilionidae)] and mainland Australia [*Papilio aegeus* Donovan (Lepidoptera: Papilionidae)] (Morris 1989; Scriber et al. 2006, 2007, 2008a, b). These observations suggest a pattern of compatibility between *C. camphora* and closely related *Papilio* spp.

The objective of this study was to test the suitability of *C. camphora* as a host for *P. palamedes*. However, like all Lepidopterans, *P. palamedes* has a complex life history and both larvae and adults have distinct interactions with host plants. I measured adult oviposition preference and larval performance on both *C. camphora* and *P. borbonia*. I hypothesized that adult females would display some preference for ovipositing on *C. camphora* and that larval performance would correspond with this preference. I provide empirical data on the nature of these interactions prior to widespread disturbance by LWD. Finally, I discuss the ecological factors that may also govern the potential colonization of *C. camphora*.

Methods

Larval survival, growth, and metabolic efficiency

Papilio palamedes eggs were obtained from adult females collected in Jackson County, Mississippi on the Grand Bay National Estuarine Research Reserve (GBNERR). Captured females were kept in clear plastic containers (35 x 20 x 13 cm) and placed in a VWR® signature diurnal growth chamber (Sheldon Manufacturing Inc.). Twigs of *P. borbonia*, which were collected from GBNERR, were also placed in the containers. Aquapics were used to maintain turgor pressure within stems and leaves. The growth chamber was maintained at 30 and 22°C during 16-hour day and 8-hour night cycles, respectively. Humidity was kept between 60 and 80% using a Hunter® 3.4 L humidifier (Model # 33119).

Eggs from 11 different females were kept in separate petri dishes in the growth chamber until hatching. Randomly selected larvae were assigned to one of three host-plant treatments: 1) foliage of *C. camphora* 2) foliage of healthy *P. borbonia* or 3) foliage of *P. borbonia* stump sprouts produced after LWD-induced canopy death (hereafter *P. borbonia* LWD). Although larvae were randomly selected, I systematically placed larvae from each family (*i.e.*, egg-laying female) into all three treatments. Healthy foliage of *C. camphora* and *P. borbonia* were collected from trees on GBNERR. Foliage of *P. borbonia* LWD was collected two kilometers north of GBNERR where impacts from LWD have been recently observed (A. Chupp pers. obs.). In the laboratory, larvae were reared individually in clear plastic containers (35 x 20 x 13 cm). Containers were lined with moist paper towels to maintain saturated humidity and fluorescent grow lights (L:D 16:8) maintained temperatures between 27 °C (lights on) and 23°C (lights off). Larvae were presented with foliage that was refreshed daily. The duration of each developmental stage was closely monitored and I recorded the date and time of larval mortality, molting, pre-

pupation, pupation, and adult emergence. I measured the initial mass of larvae in the following stages: neonate (*i.e.*, first instar), second instar, fourth instar, and pupa. Mass was measured to the nearest 0.1 mg and the time of each weighing to the nearest minute. The sex of each individual was determined only for emerged adults; the sex of larvae that died prior to this stage is unknown.

Growth rates (RGR) of each first, second, and fourth instar larva were calculated as follows:

$$\text{RGR} = [\ln (M_f) - \ln (M_i)] / T_{f-I},$$

where M_i is initial mass, M_f is final mass, and T_{f-I} is time elapsed in days. For calculations of first instar RGR, final weight (M_f) was multiplied by 0.9 to correct for overestimation of RGR due to initial gut filling (Lederhouse 1992). Larvae were weighed immediately after molting. Lifetime larval growth rates were calculated using the following equation:

$$\text{Lifetime RGR} = [\ln (DM_p) - \ln (DM_i)] / T_{ld},$$

where DM_p is pupal dry mass, DM_i is the dry neonate mass, and T_{ld} is larval duration in days (does not include the prepupal stage). Dry pupal mass (DM_p) was calculated as $0.219 \cdot M_p$ for males and $0.250 \cdot M_p$ for females, where M_p is pupal fresh mass. Dry neonate mass (DM_i) was calculated as $0.125 \cdot M_i$, where M_i is the fresh neonate mass. Conversions to dry mass avoided underestimation of lifetime RGR due to lower water content in pupae relative to larvae (Lederhouse 1992). I considered estimates of dry female pupal mass (*i.e.*, body size) as a surrogate for fecundity. Across a range of insect orders, female body size is commonly the primary constraint on insect fecundity (as reviewed by Honek 1993).

Indices of metabolic efficiency were calculated for each fourth instar larva. Larvae were weighed immediately after molting into the fourth instar and then closely monitored for the next 7 days. During this time I weighed the fresh mass of all leaves that were presented to larvae. At

the end of this period, I collected and dried (50°C) all uneaten leaf material and frass. The fresh weight of larvae was also recorded at this time. Larval fresh weight was multiplied by a constant (0.125) to approximate dry weight (Lederhouse et al. 1992, Ayers and Scriber 1994). To determine the initial dry weight of fresh leaves presented to larvae, I used a regression equation developed from the fresh and dry weights of leaves collected separately throughout the experimental period (n = 40 per treatment) (Levesque et al. 2002). I then calculated total food ingested (dry weight), total frass (dry weight), consumption rate (CR), approximate digestibility (AD), efficiency of conversion of digested food (ECD), and efficiency of conversion of ingested food (ECI). Calculation of these indices followed that of Scriber and Lederhouse (1983):

$$\text{CR} = \text{mg food ingested d}^{-1}$$

$$\text{AD} = [(\text{mg food ingested} - \text{mg frass}) / \text{mg food ingested}] \cdot 100$$

$$\text{ECD} = [\text{mg larval biomass gained} / (\text{mg food ingested} - \text{mg frass})] \cdot 100$$

$$\text{ECI} = (\text{mg biomass gained} / \text{mg food ingested}) \cdot 100$$

Adult oviposition preferences

Papilio palamedes females were captured in Jackson County, Mississippi on the GBNERR. To understand the relative preferences of adult females, I conducted both choice and no-choice experiments. In no-choice experiments, females were allowed to oviposit in clear plastic containers (35 x 20 x 13 cm) lined with paper towels. Females were presented with either foliage of healthy *P. borbonica* or *C. camphora*. Aquapics helped to maintain turgor pressure in stems and leaves. I also tested oviposition preferences using synthetic foliage. In preliminary observations, females often laid eggs on inanimate objects (*e.g.*, container surface) and trials with synthetic foliage were conducted to see if these behaviors could be stimulated by non-living plant material. This foliage was presented to a smaller subset of females and was similar in appearance to the living foliage of *P. borbonica* and *C. camphora*. In choice experiments, females were placed in wooden framed rearing cages (40 x 32 x 55 cm) lined with no-see-

um/mosquito netting. The larger space provided by rearing cages allowed for the physical separation of *P. borbonia* and *C. camphora* foliage in opposite corners of the enclosure. Synthetic foliage was not presented during these trials. Live stems were placed in water-filled Erlenmeyer flasks (125 mL) to maintain turgor pressure. The height and girth of presented foliage was consistent between host-plant types.

In both choice and no-choice experiments, enclosures were placed in a VWR® signature diurnal growth chamber (Sheldon Manufacturing Inc.). The growth chamber was maintained at 30 and 22°C during 16-hour day and 8-hour night cycles, respectively. Humidity was kept between 60 and 80% using a Hunter® 3.4 L humidifier (Model # 33119). In both experiment types, each female was observed for 72 hours. After this period, the foliage was removed and the total number of eggs laid on each host plant was recorded. I also recorded the number of eggs laid on inanimate objects (*i.e.*, the enclosure, flasks, or aquapics). To corroborate results from laboratory experiments, I recorded observations of oviposition and larval development in the field during extensive periods of live female capture. These observations were also documented during collection of host plant material in the field. I documented the size class of each tree upon which eggs were laid. All individuals < 1.5 m in height were included in size class 1. Individuals \geq 1.5 m in height were then classed by DBH as follows: size class 2 contained individuals < 7 cm DBH and size class 3 contained individuals \geq 7 cm DBH.

Statistical analyses

At each stage of larval development (1st – 4th instar, pre-pupa, and pupa), I analyzed differences in mortality among treatments (*i.e.*, host plant type) using contingency table analysis with Pearson's chi-squared test. For all measures of larval performance and metabolic efficiency, I used one-way ANOVA and Tukey's *post hoc* test to test for significant differences among

treatments; separate analyses of female pupal weight were also conducted. I used a randomized block model (one-way ANOVA) to test for a family effect on the growth rate of larvae during the first instar. Square-root transformations were applied to any data that were not normally distributed and/or violated the assumption of variance homogeneity.

To analyze female oviposition preferences during choice experiments, I used a one-sample t-test to determine if the proportion of eggs laid on *P. borbonia* or *C. camphora* significantly departed from 50%. In no-choice trials, I used a one-way ANOVA to test for significant differences in the number of eggs laid by females on the different host plants. In the statistical analyses for both choice and no-choice experiments, the number of eggs laid on inanimate objects was discarded. Square-root transformations were applied to all data that were not normally distributed. All statistical procedures were conducted using the SAS 9.2 software package (SAS Institute 2007).

Results

Larval survival, growth, and metabolic efficiency

We reared a total of 72 *P. palamedes* larvae (n = 23-25 per treatment). There were no significant differences in survivorship between larvae reared on the foliage of healthy *P. borbonia* and those reared on *P. borbonia* LWD (Figure 3.1). Survivorship was reduced for individuals reared on the foliage of *C. camphora*; significant declines occurred prior to the fourth instar ($\chi^2 = 7.38$, $P < 0.010$). On both *P. borbonia* treatments, no individuals died after the second instar whereas one individual died on *C. camphora* after the third instar (Figure 3.1).

Growth rates of larvae in the first instar were significantly higher for those reared on *P. borbonia* LWD ($F_{2,61} = 8.50$, $P = 0.0006$). First instar growth rates of larvae reared on healthy *P.*

borbonia and *C. camphora* did not differ (Figure 3.2). The randomized block model indicated no effect of family on growth rates. During the second-third instar period, growth rates were significantly lower for larvae reared on *C. camphora* when compared to both *P. borbonia* treatments ($F_{2,50} = 27.16$, $P < 0.0001$), which did not differ from each other (Figure 3.2). This same pattern was observed for lifetime larval growth rates where the *C. camphora* treatment produced significantly lower growth rates than both *P. borbonia* treatments ($F_{2,49} = 24.97$, $P < 0.0001$) which again did not significantly differ from one another. No significant differences among treatments were observed for larval growth rates during the fourth instar (Figure 3.2). Total larval duration (excludes pre-pupal and pupal stages) was significantly longer for larvae reared on *C. camphora* ($F_{2,29} = 22.77$, $P < 0.0001$) and there was no significant difference between *P. borbonia* treatments. There was also a significant effect of treatment on pupal mass ($F_{2,49} = 3.59$, $P = 0.0350$); *C. camphora* produced lighter pupae when compared to both *P. borbonia* treatments which again did not differ from each other (Figure 3.2). The same pattern was observed for female pupal mass (surrogate for fecundity) but there were greater differences between *C. camphora* and both *P. borbonia* treatments ($F_{2,22} = 8.53$, $P = 0.002$). Analysis of emerged adults revealed that females represented 55%, 50%, and 52% of individuals in *C. camphora*, *P. borbonia*, and *P. borbonia* LWD treatments, respectively.

During the fourth instar, more detailed measures of metabolic efficiency were made on a total of 48 larvae. Consumption rate and the mass of plant material ingested and excreted (frass) showed the same trend across treatments. All three measures were significantly lower for those larvae reared on *C. camphora* ($P < 0.0001$) while differences between larvae reared on *P. borbonia* and *P. borbonia* LWD were non-significant (Figures 3.3 and 3.4). Among all three host-plant treatments, there were significant differences in approximate digestibility (AD). The

AD of *C. camphora* was significantly higher than that of *P. borbonia* which was greater than that of *P. borbonia* LWD ($F_{2,45} = 15.91$, $P < 0.0001$, Figure 3.5). The efficiency of conversion of digested plant material (ECD) was significantly higher for larvae reared on *P. borbonia* LWD and there was no difference between *P. borbonia* and *C. camphora* ($F_{2,45} = 11.12$, $P = 0.0001$). Finally, the efficiency of conversion of ingested material to biomass (ECI) was significantly higher for larvae reared on *C. camphora* when compared to larvae reared on healthy *P. borbonia*. All other differences were non-significant (Figure 3.5).

Adult oviposition preferences

To collect adult females, I spent approximately 350 hours in the field. Additional hours of observation time were accumulated while collecting fresh foliage of *P. borbonia* and *C. camphora*. Although these collections were made daily, the total observation time was not quantified. During these collection periods, I witnessed egg laying by eight females. While I observed five *P. palamedes* females ovipositing on *P. borbonia* (two on size class 1, two on size class 2, and one on size class 3), no females of this species were seen laying eggs on *C. camphora*. However, three *P. troilus* females were observed ovipositing on *C. camphora* (one on size class 1 and two on size class 3). Oviposition events were verified by checking foliage for eggs.

In no-choice experiments, I used a total of 46 live-captured female *P. palamedes*; sample sizes for *P. borbonia*, *C. camphora*, and synthetic plant foliage were 20, 18, and 8, respectively. Eleven females oviposited a total of 451 eggs on *P. borbonia*; this includes one female who laid 222 eggs and was discarded from the statistical analyses. Twenty-four eggs were oviposited on inanimate objects during no-choice trials with *P. borbonia*. In no-choice experiments with *C. camphora*, two females laid a total of 22 eggs on host plant material and another 55 eggs on

inanimate objects. In trials with synthetic foliage, there were no eggs laid on the foliage or on inanimate objects. The total number of eggs laid by each female was square-root transformed to better approximate a normal distribution and all eggs laid on inanimate objects were omitted from statistical analyses. Significantly more eggs per female were laid on *P. borbonia* when compared to both *C. camphora* and synthetic foliage and there was no difference between *C. camphora* and synthetic foliage ($F_{2,43} = 7.99$, $P = 0.0011$).

In choice experiments, I used a total of 19 live-captured females. Six females laid a total of 154 eggs on *P. borbonia*. Two of those 6 females also laid 1 egg each on *C. camphora*. One of those two females also laid 3 eggs on inanimate objects that were later omitted during statistical analyses. There were no females that only oviposited on *C. camphora* or inanimate objects. The proportions of eggs laid on *P. borbonia* and *C. camphora* were square-root transformed to more approximate assumptions of normality and homogeneity of variance. A significantly greater proportion of eggs was laid on *P. borbonia* than would be expected due to chance (*i.e.*, 50%) ($t = 13.38$, $P < 0.0001$).

Discussion

While several factors may govern the colonization of novel host plants by herbivorous insects, understanding the relationship between adult oviposition preferences and larval performance is an essential part of forecasting novel host colonizations and the consequences of these host shifts (Keeler and Chew 2008; Forister and Wilson 2013). Here, using a native insect herbivore, *P. palamedes*, and an exotic host plant, *C. camphora*, I documented moderate levels of larval performance despite no oviposition preferences for this species in both choice and no-choice trials. Reports of this type (*i.e.*, no preference and moderate/high performance) have

rarely been documented in Lepidopteran species (but see Karowe 1990). On the contrary, observations of high preference and low performance on novel host plants are quite common, a trend that is more frequently observed in generalist species that are relatively less discriminating (e.g., Gripenberg et al. 2010; Harvey et al. 2010; Nakajima et al. 2013). In those circumstances, the host plant may function as an evolutionary trap when low performance leads to a reduction in the realized fitness of the native insect (Keeler and Chew 2008). However, selective processes can increase larval performance over time and lead to the successful colonization of a novel host (e.g. Thompson 1988). Because my results indicate that *P. palamedes* has no preference for ovipositing on *C. camphora*, I argue that the evolution of larval performance on this species has been minimal. Instead, I suggest that the physiology of *P. palamedes* larvae is largely pre-adapted to *C. camphora* foliage whereby the physical and chemical properties of leaf tissues are suitable for complete development. That is to say, based on larval performance, these two species make a relatively good fit despite no history of association and evolution of host-specific physiological adaptations.

Of the total number of eggs laid on *P. borbonia* and *C. camphora* (n = 629) during choice and no-choice trials, only 3.8% were placed on the foliage of *C. camphora*. While 18 females laid eggs on *P. borbonia*, only 4 females oviposited on *C. camphora*. However, in situations where egg laying on *C. camphora* was observed, I conclude that no preference was actually given to this species because an equal or greater number of eggs was laid on inanimate objects. This conclusion is also supported by field observations where I found no evidence of female oviposition or larvae on *C. camphora*. My laboratory results agree with studies that have shown that perfect discrimination of optimal hosts by egg laying herbivores is improbable (Rausher 1985). While captive butterflies may develop behaviors that are not consistent with wild

individuals (Lewis and Thomas 2001), the females used in my study were caught locally and kept in oviposition cages for no more than 72 hours. It is also interesting to note that in the eight females I tested on synthetic foliage, no eggs were laid on the foliage or on inanimate objects. I suggest that while *C. camphora* foliage is sub-optimal for oviposition, it may stimulate a less discriminating egg laying behavior in some cases (*i.e.*, no-choice trials where a small number of eggs were laid on both *C. camphora* and inanimate objects). In choice trials, I agree that ovipositing females may have difficulty discriminating between preferred and sub-optimal surfaces, thereby leading to “mistakes” when similar cues are being produced by different species (Fox and Lalonde 1993). In a natural setting, such behaviors can promote the colonization of novel host plants, especially when larvae perform well on these species (*e.g.*, Thompson 1988). While the results of my choice trials suggest that these mistakes occur roughly 3% of the time, it is unclear how often they would occur in nature where numerous biological and ecological factors may alter the perceived suitability of egg-laying substrates (Forister and Wilson 2013).

For larvae, the suitability of host plants is largely determined by the chemical constituents of plant tissues. Specifically, larvae are sensitive to the types and quantities of secondary compounds and the availability of nutrients (Slansky 1992). Adult insect herbivores may use these chemical signatures as “fingerprints” by which the most suitable larval host plants are recognized. For *Papilio palamedes* and other specialists, their senses are finely tuned as they target one species within a community of closely related species that may have very similar fingerprints (Feeny 1976). My results suggest an optimal relationship between oviposition preferences and larval performance whereby *P. palamedes* prefers to oviposit on the species that yields the highest larval performance. This relationship is well documented, especially in

specialist insect herbivores (as reviewed by Gripenberg et al. 2010). While the ability to discriminate only the most suitable host may be an advantage, it is commonly reported that specialization in general is disadvantageous to coping with disturbance (*e.g.*, McKinney 1997; Hobbs 2000; Colles et al. 2009; Clavel et al. 2011). Disturbances that cause widespread decline and possible extinction of a primary host species may be extremely threatening. Although adult phytophagous insects exhibit behavioral flexibility during host selection that can facilitate the selection of the most abundant host (Cunningham et al. 2001; West and Cunningham 2002), specialist insect herbivores may be less capable of such adaptations. Plasticity of oviposition behavior and subsequent novel host colonization will be required for a specialist herbivore like *P. palamedes* to persist in the wake of LWD.

During the course of this study, I recorded the first observations of LWD at the GBNERR in coastal Mississippi; mortality of *P. borbonia* was patchy ($n = 40-50$) and the presence of LWD was not yet pervasive. If the effects of LWD are similar to those on the Atlantic Coastal Plain, then 75-97% of *P. borbonia* trees will be dead within 2-4 years (Speigel and Legee 2013). Here, I conclude that subsequent stump sprout production and persistence will dictate the consequences of LWD for *P. palamedes*. My field observations indicated that female *P. palamedes* will readily oviposit on redbay of the smallest size class (height < 1.5 m), including sprouts. Laboratory results revealed that larval performance on the foliage of stump sprouts from infected *P. borbonia* was comparable to those reared on the foliage of healthy *P. borbonia*. In addition, fourth instar larvae feeding on sprout foliage converted digested leaf material into biomass more efficiently than in other treatments. These results suggest that the physical and/or chemical properties of foliage from *P. borbonia* sprouts could lead to enhanced performance on this species. I also observed that sprouts from experimentally cut trees in the field were heavily

colonized by herbivores compared to mature canopy foliage. While it has been frequently documented that seedlings and sprouts are better defended than mature plants, a recent meta-analysis indicated that ontogenetic patterns of secondary defense compounds are inconsistent and vary with a range of biotic factors including types of herbivores, defense traits, and plant life forms (Barton and Koricheva 2010 and citations therein). I suspect that *P. borbonia* sprouts are less defended and are therefore a more efficient nutrient source for developing larvae. Regardless, the relative availability of *P. borbonia* and *C. camphora* will be regulated by the persistence of these vegetative sprouts and will therefore be an important component of predicting novel host plant colonization in *P. palamedes* (Forister and Wilson 2013; Pearse et al. 2013).

While foreign host plants can provide new opportunities for native insect herbivores (*e.g.*, Siemann et al. 2006; Harvey et al. 2010), the colonization of these exotic species is more likely to occur in areas where the invader has been present for a longer period of time (Siemann et al. 2006). Following their initial establishment, novel host plants go through a period of “naturalization” where they accumulate herbivores; the equilibration of these herbivore communities may take centuries (Strong 1974). For *C. camphora*, which was introduced to Florida circa 1875 (Langeland and Craddock Burks 1998), it is unclear if populations throughout the southeastern US have completed this process of naturalization.

In the eight southeastern states where it occurs, *Cinnamomum camphora* is considered an exotic invasive species (USDA, NRCS 2014). In the coastal counties of Mississippi, Alabama, and Florida, it grows well in disturbed areas (*e.g.*, along roadsides and power line right-of-ways) and is also present in forested habitats where larger individuals reach the sub-canopy layer (pers. obs. A. Chupp). Comparisons of multiple plant databases indicate that its distribution is still

expanding. For example, in Florida, *C. camphora* is naturalized in 27 counties (USDA, NRCS 2014) but has been vouchered in 36 counties (Wunderlin and Hansen 2013). For these reasons, I argue that availability of *C. camphora* is sufficient to support herbivore populations across much of the southeastern Coastal Plain. While quite common in this region, this invader has not garnered the same level of attention as several other exotic tree species (*e.g.*, Chinese tallow) (Renne et al. 2002; Rogers and Siemann 2004; Battaglia et al. 2009). For such a widespread species that is continuing to invade new areas, there has been surprisingly little research focused on the ecology of *C. camphora* in its introduced range.

Here, I report field observations of *C. camphora* colonization by *P. troilus*. I witnessed oviposition by females and observed later instars on *C. camphora* foliage. Complete development of *P. troilus* on *C. camphora* was also reported in New Orleans, LA (Linda Auld pers. comm.). Interestingly, phylogenetic and biogeographic analyses of Lauraceae suggest that the primary host of *P. troilus* [spicebush, *Lindera benzoin* L. (Laurales: Lauraceae)] is more closely related to *C. camphora* than the primary host of *P. palamedes* (*P. borbonia*) (Chanderbali et al. 2002), corroborating the observed pattern that *P. troilus* appears to have greater compatibility with *C. camphora* than *P. palamedes*.

During field observations of *C. camphora*, I also confirmed the leaf rolling behavior of *P. troilus* larvae, a characteristic not exhibited by *P. palamedes*. In Lepidopterans, this behavior has been shown to reduce the risk of predation from carnivorous insects (Damman 1987). However, it has also been suggested that birds can cue in on leaf rolls, actually increasing predation rates in species that make larger and more conspicuous leaf rolls (Murakami 1999). The leaf rolling behavior has also been shown to increase the quality of leaf tissue. For example, the rolling of Japanese lilac [*Syringa reticulata* Blume (Lamiales: Oleaceae)] leaves by the larvae of the Holly

tortrix moth [*Rhopobota naevana* Hubner (Lepidoptera: Tortricidae)] increased leaf nitrogen content by 20% and reduced leaf toughness and total phenolic content by 21% and 55%, respectively. The mechanisms that underlie these changes are not understood, although other symbiotic organisms are apparently benefitting from them (Fukui et al. 2002). While the occupancy of *C. camphora* by *P. troilus* may preclude oviposition by female *P. palamedes* and/or provide competition for larvae, leaf rolls could also provide opportunities for improving larval performance. In any case, this leaf rolling behavior may explain much about the current and potential future interactions between *C. camphora*, *P. troilus*, and *P. palamedes*. Ultimately, the suitability of *C. camphora* for colonization by *P. palamedes* may be largely influenced by the occupancy of this novel host by *P. troilus*.

Although *C. camphora* was relatively unsuitable for oviposition by female *P. palamedes*, I also showed that larvae are physiologically capable of using this exotic host and in many cases individuals were very well adapted. While it is unclear how predation and other interspecific interactions would affect larval performance in a natural setting, my results suggest that *C. camphora* will not function as an evolutionary trap for *P. palamedes*. Instead, the future colonization of *C. camphora* by *P. palamedes* will depend largely on the factors influencing adult female oviposition preferences. Among these factors, I argue that host availability and occupancy will be most important following the impacts of LWD. The colonization of *C. camphora* could save *P. palamedes* from the heightened risk of extinction following the decline of its native primary and alternative hosts.

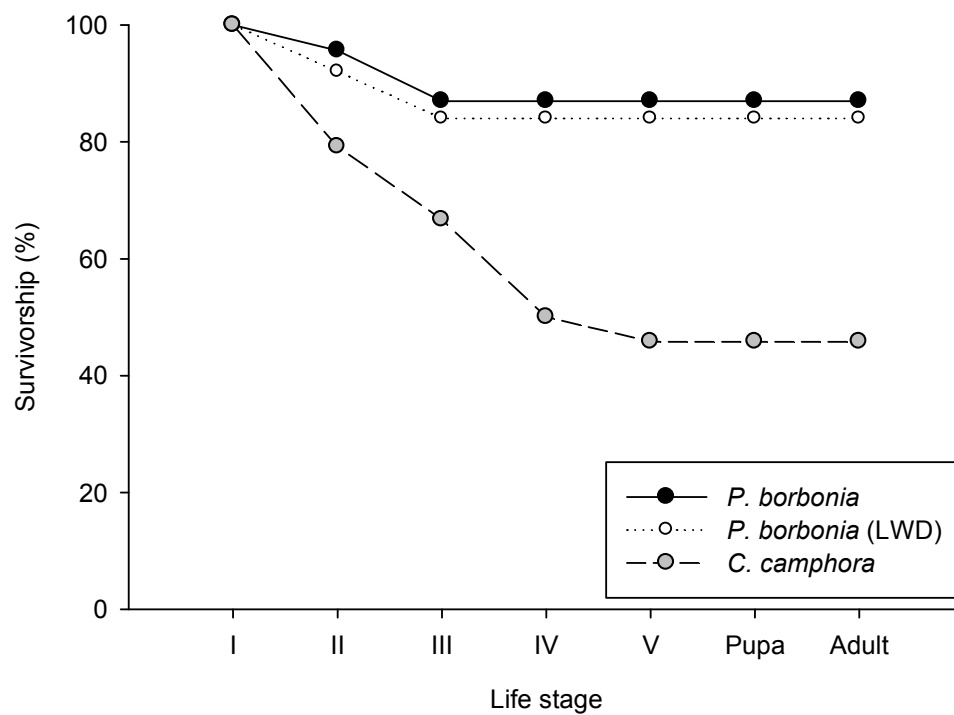


Figure 3.1. Survivorship of *P. palamedes* on three host plant treatments. Points represent the percentage of individuals that were alive at the beginning of each life stage.

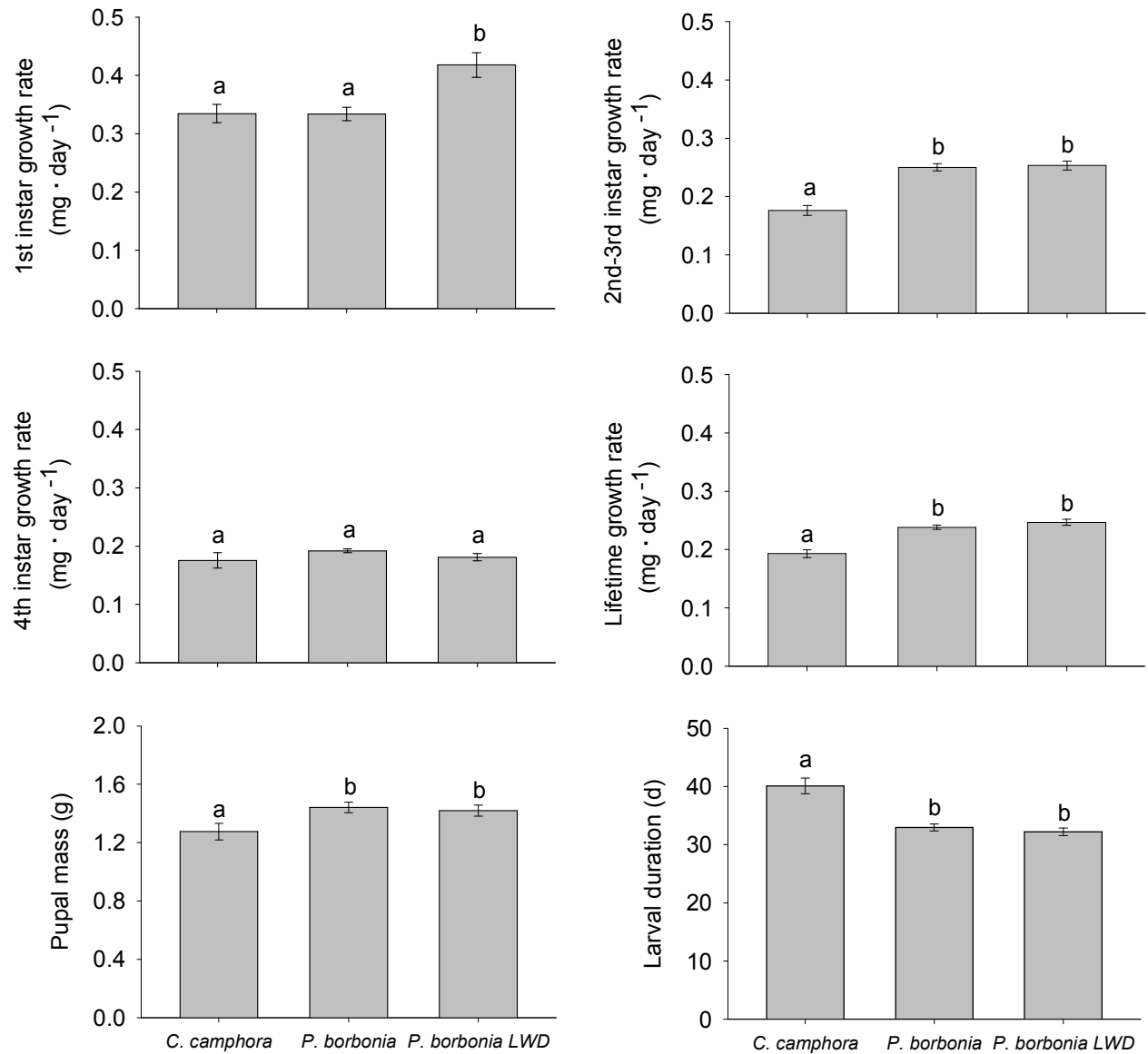


Figure 3.2. Measures of *P. palamedes* larval performance on three host plant treatments.

Samples sizes for first instar growth rate were from left to right: 19, 22, 23. Sample sizes for second-third instar growth rate were: 12, 20, 21. Sample sizes for all other measures were: 11, 20, 21. Bars represent the mean \pm standard error.

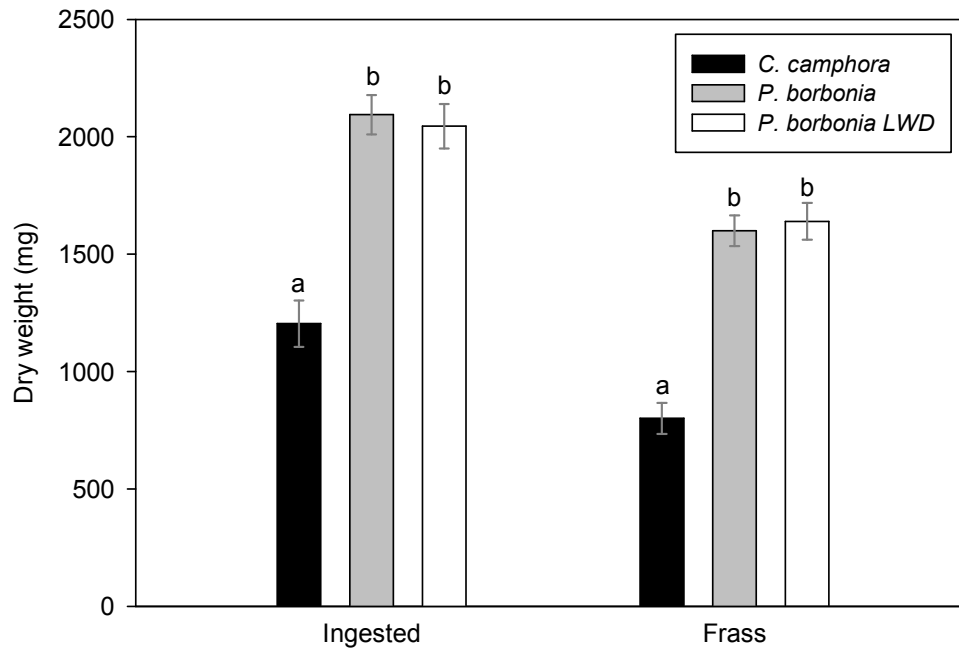


Figure 3.3. Amount of plant material ingested and excreted (frass) from larvae during a 7-day period of the fourth instar when reared on three host plant treatments. Bars represent the mean \pm standard error.

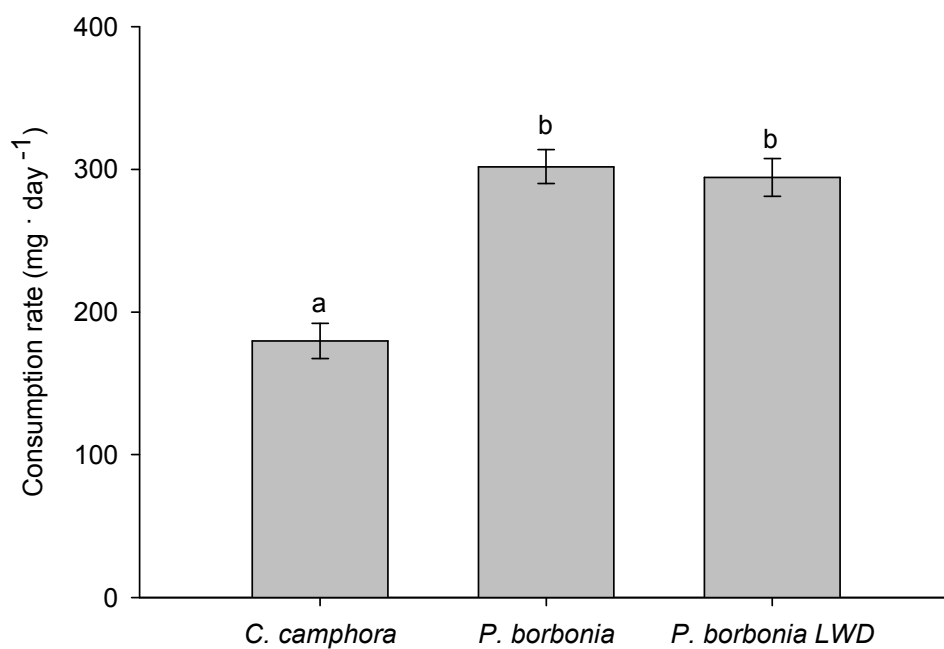


Figure 3.4. Consumption rate of larvae during a 7-day period of the fourth instar when reared on three host plant treatments. Bars represent the mean \pm standard error.

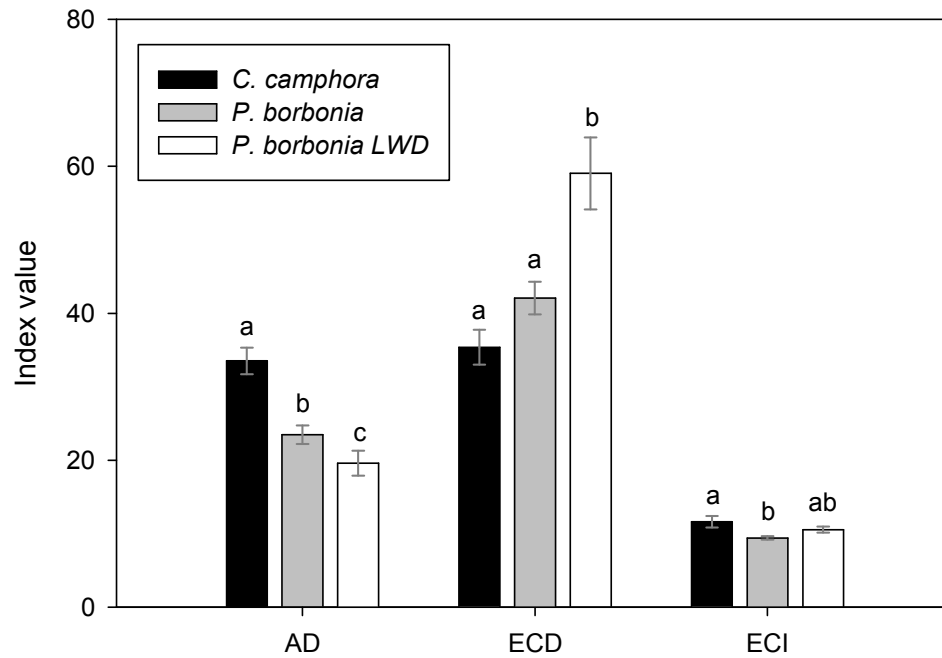


Figure 3.5. Metabolic indices of larvae during a 7-day period of the fourth instar when reared on three host plant treatments. AD = Approximate Digestibility, ECD = Efficiency of Conversion of Digested food, ECI = Efficiency of Conversion of Ingested food. Bars represent the mean \pm standard error.

CHAPTER 4

POTENTIAL DISRUPTION OF ORCHID-POLLINATOR INTERACTIONS DUE TO INDIRECT EFFECTS OF ALIEN INSECT INVASION

Abstract

Persea borbonia is the primary host of laurel wilt disease, a novel disease that is vectored by an exotic beetle and has caused widespread *P. borbonia* mortality in the southeastern US. Decline of *P. borbonia* jeopardizes *Papilio palamedes*, whose larvae feed primarily on its foliage, and consequently jeopardizes plants that depend on pollination by this butterfly. The objective was to determine the reliance of the orchid *Platanthera ciliaris* on *P. palamedes* for pollination and the relative availability of alternative pollinators. I monitored pollinator visitation and fruit set and measured nectar spur lengths of *P. ciliaris* flowers and proboscis lengths of its floral visitors over several days of peak flowering in Jackson County, MS, 2012. *Papilio palamedes* was the primary visitor with minimal visitation by *Phoebis sennae*. Lengths of *P. ciliaris* nectar spurs were similar to proboscis lengths of both pollinator species. Fruit set was moderate with access to pollinators ($55 \pm 10.8\%$), yet failed (0%) when pollinators were excluded. Visitation increased with inflorescence size but there was no such pattern in fruit set, indicating that fruit set was not limited by pollinator visitation within the range of visitation rates I observed. *Phoebis sennae* may provide supplemental pollination service but is likely constrained by habitat preferences that do not always overlap with those of *P. ciliaris*. Although preliminary, my results suggest that decline of *P. palamedes* due to laurel wilt disease could threaten the reproductive success and persistence of *P. ciliaris* populations.

Introduction

Disturbances by alien insect herbivores pose the greatest threat to native insect larvae that specialize on the impacted host species (Gandhi and Herms 2010). Accordingly, the pollination services provided by the adult stages of some native insects may also be threatened. For example, a number of native Lepidopteran species are imperiled by the loss of their larval hosts due to emerald ash borer (*Agrilus planipennis*), gypsy moth (*Lymantria dispar*), balsam wooly adelgid (*Adelges piceae*), and cottony cushion scale (*Icerya purchase*) (Work and McCullough 2000; Roque-Albelo 2003; Wagner 2007; Scholtens and Wagner 2007), but there have been no studies of how these losses may affect the plants they pollinate. Two recent reviews of world-wide pollinator declines corroborate this gap in our understanding of these disturbances; whereas numerous exotic plant invasions have been linked to reductions in pollinators, pollinator declines due to exotic insect herbivores are not accounted for in the literature (as reviewed by Potts et al. 2010; Gonzalez-Varo 2013). Given the indirect nature of these effects, they may be difficult to predict or document in complex systems. Moreover, basic information on the reproductive biology and ecology of native plants is often missing. I argue that the effects of insect invasions on plant-pollinator systems may be quite dramatic where entire populations of host plants are impacted but is largely undocumented because of the lack of pre-disturbance data.

In the southeastern US, the exotic redbay ambrosia beetle (*Xyleborus glabratus*) is vectoring a fungal pathogen (*Raffaelea lauricola*) that causes laurel wilt disease (LWD), resulting in widespread mortality of host species (Fraedrich et al. 2008). Introduced to the US near Savannah, GA in 2002, the disease and its vector are now dispersed across the Coastal Plain of South Carolina, Georgia, and Florida. Recent introductions of *X. glabratus* have resulted in LWD outbreaks in Alabama and Mississippi (USDA Forest Service 2015a). Infection occurs

when fungal spores are released from the mycangia of the beetle upon boring into a host tree. The fungus spreads into the xylem (apparently blocking water transport) and causes wilting and mortality of main stems within a few months of infection (Mayfield 2008). Although this exotic pathogen and its beetle vector have been identified in several Lauraceae species, most incidences of LWD are observed in native redbay trees (*Persea borbonia*) (Fraedrich et al. 2008), a common sub-canopy species in many forested habitats across the Atlantic and Gulf Coastal Plains (Van Deelan 1991). In populations of *P. borbonia* on the Atlantic Coastal Plain, LWD-induced mortality rates are $\geq 90\%$ (Fraedrich et al. 2008; Evans et al. 2013; Spiegel and Legee 2013), reaching as high as 98% in areas where LWD has been present for at least five years (Evans et al. 2013). *Persea borbonia* trees will resprout following main stem mortality, but long term survival is unlikely (Evans et al. 2013; Spiegel and Legee 2013). Such dramatic losses of this common species may have broader impacts on associated communities throughout the southeastern Coastal Plain.

Persea borbonia provides resources to a number of animal species (Brooks 1962; Goodrum 1977; Landers et al. 1979; Brendemuehl 1990; Van Deelan 1991, Legee 2006), but it is perhaps best known as the primary larval host of the Palamedes swallowtail butterfly (*Papilio palamedes*). *Papilio palamedes* is an abundant herbivore on the southeastern Coastal Plain and has a distribution that mirrors that of *P. borbonia*. While laboratory observations suggest that female oviposition preference and larval performance are highest on *P. borbonia*, successful larval development has also been observed *Sassafras albidum* (Brooks 1962; Scriber et al. 1991; Lederhouse et al. 1992). However, *S. albidum* is also highly susceptible to LWD (Smith et al. 2009a). The exotic camphor tree (*Cinnamomum camphora*) is the only co-occurring species of Lauraceae that shows resistance to LWD (Smith et al. 2009b). Laboratory and field observations

suggest *P. palamedes* larvae perform moderately well on *C. camphora* (46% survival and 4th instar growth rates similar to those reared on *P. borbonia*) but in choice and no-choice trials in the laboratory, adult females do not readily oviposit on this species (Chupp and Battaglia 2014). I hypothesize that invasion of LWD will result in dramatic declines of suitable hosts for *P. palamedes*. This prediction is supported by field counts of *P. palamedes* along transects in LWD-impacted and non-impacted areas; total counts of *P. palamedes* are four to seven times less at impacted sites (Formby et al. unpublished data). This trend will likely continue unless this specialist herbivore is capable of changing its host selection behaviors.

There may be negative consequences for those plant species whose successful pollination is dependent on visitation by *P. palamedes*. Adult *P. palamedes* retrieve nectar from a wide range of herbaceous plants (A. Chupp pers obs). However, it is unclear if *P. palamedes* provides important pollinator service to these plants. Throughout the southeastern US, populations of the orange-fringed orchid (*Platanthera ciliaris*) may rely heavily on *Papilio* spp., including *P. palamedes*, for reproductive success (Robertson and Wyatt 1990a). This large, terrestrial orchid is found in the acidic, nutrient poor soils of pine flatwoods, savannas, and bogs. The orange flowers of *P. ciliaris* are pollinated by large butterflies that make contact with pollinaria while retrieving nectar from long nectar tubes (Smith and Snow 1976; Folsom 1984; Robertson and Wyatt 1990a, b). The pollinaria stick to eyes of butterflies and are then brushed over stigmas on subsequent floral visits (Robertson and Wyatt 1990b). In mountain and coastal habitats, *P. ciliaris* populations may produce ecotypes based on co-evolutionary relationships with local pollinators (Robertson and Wyatt 1990a).

Co-evolution between plants and pollinators has often been inferred from the corresponding lengths of flower nectar spurs and proboscises of visiting pollinator species (see

Nilsson 1988 and citations therein). Long spurs limit access to nectar, thereby ensuring that long-tongued pollinators make contact with pollen while extracting nectar from the bottom of the spur. If there is sufficient overlap between the proboscis lengths and visitation rates of several pollinator species, then the loss of one species may have minimal effects on pollination services and plant fitness. Spatial variability in the identity, abundance, and morphology of *P. ciliaris* pollinators may exert different pressures on the morphology and ultimately fitness of *P. ciliaris*. Thus, estimates of the indirect effects of LWD on *P. ciliaris* may vary across its range.

The primary goal of this study was to characterize the *P. ciliaris* pollinator network in coastal Mississippi and provide baseline data prior to the arrival of LWD. While the geographic scope of this study was limited due to the already widespread impacts of LWD, I provide timely empirical data on species threatened by LWD. The objectives of this study were 1) to document the abundance of local pollinators and determine which species are the most frequent visitors of *P. ciliaris*; 2) to determine if visitation is necessary for successful pollination and fruit maturation; 3) to compare orchid spur length to the proboscis lengths of the most frequent floral visitors; and 4) to forecast the potential for LWD to disrupt pollination services for *P. ciliaris*.

Methods

Study site

The study site was located on the Grand Bay National Estuarine Research Reserve (GBNERR) in Jackson County, Mississippi, USA. In August 2012, I identified a population of *P. ciliaris* in an area of wet pine flatwoods that was surrounded on all sides by bald cypress-dominated (*Taxodium distichum*) wetlands. The pine flatwood vegetation consisted of a sparse canopy of slash and long-leaf pine (*Pinus elliottii* and *Pinus palustris*) and a diverse herbaceous

understory dominated by wiregrass (*Aristida stricta*). In addition to *P. ciliaris*, the site also contained a large population of the orange fringeless orchid (*Platanthera integra*), which is considerably smaller in stature compared to *P. ciliaris*. Due to fire suppression, several woody species (e.g., *Smilax laurifolia*, *Ilex glabra*, and *Hypericum* spp.) were also encroaching into this area.

Flower visitation

On 24-26 August 2012 (near peak flowering for the population), I recorded insect visitation to a total of 24 *P. ciliaris* plants. I recorded the number of open flowers on each plant (proxy for inflorescence size), tagged each plant with PVC pipe within 20 cm of plant, and recorded their GPS coordinates. Plants were at least 0.5 m apart. All observation sessions were conducted between 08:00 and 16:00 hrs, the period of visitor activity, as indicated by preliminary observations. During the survey period, the weather remained consistent with daily high temperatures of 28-31°C and partly cloudy skies with no rain (NOAA 2013).

We divided the observation plants into four groups in which individuals occurred in sufficiently close proximity to be observed simultaneously by one observer. Plants within a group were observed for a session lasting 30 or 60 minutes, after which the observer rotated to a different group. Because visits were very infrequent within some groups, and because I was interested in the relative, rather than absolute, frequency of the pollinator species, I focused my survey on two of the four groups ($n = 7$ and $n = 8$ plants) with higher visitation.

The observer sat within 6 m of the grouping of plants being monitored. A visit was recorded when an insect arrived at a plant and inserted its proboscis in the nectar tube of at least one flower. Each time a visitor arrived at a plant, I recorded the identity of the visitor and the total number of flowers probed. Each arrival to a plant was treated as a visit (therefore it is

unknown how frequently the same individual insect flew out of sight and later revisited the same plant). I calculated the visits per plant per hour, as well as the mean number and proportion of open flowers probed per visit for each species of visitor. I was not able to record the total number of visits to individual flowers.

Breeding system

To verify the importance of insect visitation for successful pollination and fruit set, I compared fruit set of inflorescences that were either bagged or open to pollinators. Potential pollinators were excluded from five plants not included in the visitation surveys by placing lightweight mesh bags (1 mm) over inflorescences of unopened flowers. The mesh bags were left on until all flowers had completely dried, at which point the inflorescences of all bagged specimens were collected. Dried inflorescences were collected from five of the plants used in the visitation observations (as open-pollinated controls). All specimens were placed in paper bags and kept in a drying oven at 50°C.

Successful pollination and fruit set were indicated by a widening of the ovary (Figure 4.1). To ensure that I was accurately recognizing ovaries with viable fruits, I dissected a small subset of ovaries ($n = 8$), and examined the seeds under a dissecting microscope (Olympus SZX12, 90x magnification) to verify viability (*i.e.*, embryonic enlargement, Figure 4.2). Unexpanded ovaries always contained seeds with undeveloped embryos, while expanded ovaries consistently harbored seeds with developing embryos. In cases cases when ovaries exhibited moderate widening, seed viability was assessed under the microscope by examining the relative size of the embryo. For each inflorescence, fruit set was quantified as the proportion of flowers that had expanded ovaries (containing at least some viable seeds).

Nectar spur and proboscis length

We collected two fully opened flowers from each of 22 randomly selected *P. ciliaris* plants. Flowers were placed in a 40% ethanol solution and returned to the laboratory for measurement. Each flower was removed from the ethanol solution and pinned to Styrofoam just prior to measuring. The pinning allowed me to effectively isolate the nectar spur and accurately measure its length from the apex to its junction with the expanded portion of the labellum (Robertson and Wyatt 1990a).

Upon completion of my visitation surveys, I also collected individuals of the pollinator species that visited *P. ciliaris* flowers. Individuals were captured in the field and immediately taken to the laboratory where they were frozen. For each species, an equal number of females and males was collected ($n = 10$ of each sex for two species, 40 total). The specimens were later removed from the freezer and allowed to thaw before heads were amputated. Removed heads were pinned to Styrofoam and each proboscis was unrolled and carefully held in place with pins and small strips of paper. Proboscis length was measured from the apex to its junction with the labrum (Robertson and Wyatt 1990a).

Statistical analyses

To analyze visitation by multiple visiting insect species, I considered the individual plants that were monitored to be the sample units. To test for differences in the number of visits per plant made by each pollinator species, I used a paired samples t-test. To calculate the mean number of pollinator visits per plant per hour, I pooled data for each plant across the total survey period. A linear regression analysis was used to determine if there was a relationship between the number of visits a plant received and a) the number of plants being observed in that group and b) the number of open flowers on that plant. To test whether the number of flowers probed per visit

differed between species, I used an independent samples t-test with individual visit as the sample unit. This same method of analysis was used to test for differences in the proportion of open flowers probed per visit between visiting species. For all t-tests, when the assumption of equality of variance was violated, results from the Satterthwaite approximation were used. Linear regression analysis was used to determine if there was a relationship between the total number of flowers per inflorescence and the proportion of flowers that were successfully pollinated and set fruit; only results from unbagged plants were included in this analysis. One-way ANOVA and Tukey's post hoc test (where warranted) were used to test for differences among the lengths of pollinator proboscises and nectar spurs. Variances of nectar spur and proboscises lengths were compared using homogeneity of variance tests (Levene's). For each pollinator species, I also tested for differences in proboscis lengths between males and females using independent samples t-tests. Square-root transformations were applied to any data that did not meet normality and equality of variance assumptions. All statistical procedures were conducted using the SAS 9.2 software package (SAS Institute 2007).

Results

Flower visitation

During my three-day survey period, 11 total hours of observation time were recorded. Visitors were observed on 15 of the 24 plants that were monitored (48 visits total). *P. palamedes* (n = 44 visits) and cloudless sulfur (*Phoebis sennae*; n = 4 visits) were the only two species of visitor observed during this period (Table 4.1). The average number of visits plant⁻¹ hour⁻¹ (\pm standard error) was higher for *P. palamedes* (0.53 ± 0.12) than *P. sennae* (0.03 ± 0.02) ($t = 4.53$, $df = 23$, $P < 0.001$). The mean number of flowers visited per visit was similar between *P.*

palamedes (3.61 ± 0.42) and *P. sennae* (2.25 ± 0.95) ($t = 1.32$, $df = 4$, $P = 0.26$). The mean proportion of open flowers visited per visit was significantly higher for *P. palamedes* visits (0.28 ± 0.04) compared to *P. sennae* (0.11 ± 0.05) (Satterthwaite $t = 2.65$, $P = 0.032$, $df = 7.3$) (Figure 4.3). There was no apparent relationship between plant visitation (total number of visits to a given plant) and the number of plants in its patch ($r^2 = 0.02$, $F_{1,22} = 0.48$, $P = 0.49$). However, there was a marginally significant relationship (positive) between plant visitation and the number of open flowers on individual plants ($r^2 = 0.16$, $F_{1,22} = 4.21$, $P = 0.05$).

Breeding system

The average number of flowers on each inflorescence was 15.6 ± 3.6 on bagged specimens and 29.0 ± 4.4 on unbagged specimens. On bagged specimens, successful fruit set did not occur on any of the 78 flowers. However, on unbagged specimens, an average of 55% (± 10.8) of flowers had successfully set fruit. Results from a regression analysis indicated that there was no relationship between the total number of flowers on an unbagged inflorescence and the proportion that set fruit ($r^2 = 0.01$, $F_{1,3} = 0.03$, $P = 0.87$).

Nectar spur and proboscis length

Average spur length estimated from 44 flowers (22 plants) was 29.10 ± 0.33 (SE) mm. *Papilio palamedes* and *P. sennae* were the only two species of visitor observed during the survey period and thus proboscis length was measured on these two species only. Average proboscis lengths of *P. palamedes* and *P. sennae* were 29.06 ± 0.30 mm and 29.12 ± 0.22 mm, respectively. Results of analysis of variance suggested no significant differences in lengths among proboscises of *P. palamedes* and *P. sennae* and spurs of *P. ciliaris* ($F_{2,59} = 0.01$, $P = 0.99$) (Figure 4.4). Mean proboscis lengths were similar ($t = 1.85$, $P = 0.08$, $df = 18$) in male (29.58 ± 0.32 mm) and female (28.55 ± 0.47 mm) *P. palamedes* ($t = 1.85$, $P = 0.08$, $df = 18$), and also did

not differ between sexes of *P. sennae* (male: 28.97 ± 0.27 mm, female: 29.27 ± 0.36 mm) ($t = 0.69$, $P = 0.50$, $df = 18$). The variance of nectar spur lengths did not differ from that of *P. palamedes* proboscis lengths ($F_{20,19} = 1.37$, $P > 0.05$). However, variance of *P. sennae* proboscis lengths was lower than for nectar spur lengths ($F_{20,19} = 2.54$, $P < 0.05$).

Discussion

These observations of *P. ciliaris* and its pollinators precede the arrival of LWD within the study area. This disease indirectly threatens *P. palamedes* (Chupp and Battaglia 2014, Formby et al. unpublished data), the primary floral visitor of *P. ciliaris* at my field site. Two species, *P. palamedes* and *P. sennae*, were observed visiting the flowers of *P. ciliaris*. The identity of these primary visitors is consistent with observations from the Atlantic Coast (Robertson and Wyatt 1990a), but the proportion of visits by each species differed substantially. *Papilio palamedes* represented 92% of my observations while it accounted for only 63% of visits (2-year average) in the surveys conducted by Robertson and Wyatt (1990a); despite inter-annual variation in the total number of individuals they observed, the proportion of visits made by *P. palamedes* and *P. sennae* was consistent between years (Robertson and Wyatt 1990a). Overall, I found that *P. sennae* was much less abundant than implied by the observations of Robertson and Wyatt (1990a). *Phoebis sennae* prefers edges and open areas while *P. palamedes* is more closely associated with forested habitats (e.g., Devries 1987; Haddad 1999; Haddad and Baum 1999). At the site of my surveys, the sparse pine canopy and often thick understory layer may be less suitable for *P. sennae* than other more open and/or disturbed areas (like those. The median of a nearby highway (I-10) contained very high densities of *P. sennae*, presumably attracting individuals away from less favorable neighboring habitats (A Chupp pers obs). In addition, the

availability of larval host plants (*Cassia* spp.) influences habitat suitability and temporal fluctuations in the local abundance of *P. sennae* may have also been a factor during my short survey period.

While visitation by *P. sennae* was minimal, *P. palamedes* visited 62% of the plants that were monitored. As pollinator exclusion bags resulted in 0% fruit set on bagged inflorescences, I conclude that visitation by *P. palamedes* was primarily responsible for pollination and fruit set. This result is consistent with previous findings which confirmed that *P. palamedes* carried significantly more pollinaria than *P. sennae* (Robertson and Wyatt 1990b). However, among unbagged inflorescences, only 55.2% of flowers set fruit and variability among plants was high ($\pm 10.8\%$ std err). In South Carolina, variability in fruit set was explained by differences between the lengths of *P. ciliaris* nectar spurs and pollinator proboscises whereby greater similarity was correlated with higher rates of pollination success and fruit set (Robertson and Wyatt 1990a). Here, I report only moderate fruit set in *P. ciliaris* despite results which indicate the average lengths of individual nectar spurs and pollinator proboscises are well matched.

If nectar spur lengths are optimal for ensuring pollination, then it remains unclear why these results suggest a lower rate of fruit set than what has been observed in other populations (Robertson and Wyatt 1990a). I point out that proboscis length of *P. palamedes* ranged from 26.3 to 31.2 mm and males tended to have longer proboscises (29.6 ± 1.0 mm) than females (28.5 ± 1.5 mm). Such discrepancy could explain lower fruit set if males visited flowers more frequently than females and were able to rob nectar without making contact with pollinia. Although I was unable to document the sex of individual visitors, my sampling of *P. palamedes* and *P. sennae* populations indicated that males were indeed more abundant or at least more likely to be captured near my site. Documentation of pollinator sex ratios is not common, but it has been

shown that male *Papilio helenus* and *P. protenor* visit the flowers of *Clerodendron trichotomum* more frequently than females (Suzuki et al. 1987).

Alternatively, if the floral visitors of *P. ciliaris* are providing efficient pollen delivery, resource limitation could then explain variability in fruit set and why plants with larger inflorescences (*i.e.*, more open flowers) attracted more visitors but did not produce a greater number of fruits than plants with smaller inflorescences. I note that the average inflorescence size as dictated by the number of flowers per plant at my site (11.9 ± 1.2) is at the low end of what has been documented for this species (10-50 per plant) (Smith and Snow 1976; Folsom 1984). In *Platanthera bifolia*, fertilizer treatments increased capsule production in plants with smaller inflorescences, indicating poorer nutrient stores in these individuals (Mattila and Kuitunen 2000). As with differences in the abundance of *P. sennae* between this study and that of Robertson and Wyatt (1990b), I suggest that biotopic or microhabitat differences are responsible for the smaller inflorescences and reduced fruit set reported here. Resource availability (*i.e.*, light and nutrients) at my survey site may be increasingly threatened by competition with woody species that are invading the understory layer. Unfortunately, the fires that naturally maintained these habitats have been suppressed and prescribed burning at the GBNERR is limited by the complexity of land ownership and resultant need for increased personnel and funding for burns (Will Underwood pers comm). Successful conservation will require careful analyses of the local factors that pose immediate threats to these communities and timely intervention.

Although the availability of abiotic resources and pollinators (specifically *P. palamedes*) may interact to determine the fitness of *P. ciliaris* and the maintenance of populations, I predict a marked decline in the reproductive success of *P. ciliaris* plants following LWD. Expected LWD-

induced declines of *P. palamedes*, whose larvae primarily feed on *P. borbonia* (Brooks 1962; Scriber et al. 1991; Lederhouse et al. 1992), may dramatically reduce pollination service to *P. ciliaris* populations. As an abundant pollinator, *P. palamedes* may also serve as the primary pollinator of other native plants, including the white-fringed orchid (*Platanthera blephariglottis*) which also harbors nectar in exceptionally long nectar spurs (Smith and Snow 1976). This study provides empirical evidence for how the indirect effects of an alien insect may disrupt pollination service and reduce the reproductive success of a native plant. Such information can allow land managers to prepare contingency plans for the conservation of these endangered communities. I urge future research on the effects of exotic alien insects to consider the indirect effects on native insect herbivores and the plants they pollinate.

Table 4.1. Pollinator activity on *P. ciliaris*. Visits are the number of times an individual of that species was observed nectaring on the flowers of individual plants. *Papilio palamedes* and *P. sennae* accounted for 44 and 4 visits, respectively. Mean \pm SE values are given in the last row of the table.

Group	Plant ID	Number of flowers	Observation time (hrs)	Number of visits		Total visits	Visits plant ⁻¹ hour ⁻¹
				<i>P. palamedes</i>	<i>P. sennae</i>		
1	1	19	5	9	1	10	2
1	2	22	5	8	1	9	1.8
1	3	9	5	1	0	1	0.2
1	4	20	5	5	2	7	1.4
1	5	21	5	2	0	2	0.4
1	6	5	5	2	0	2	0.4
1	7	5	5	0	0	0	0
2	8	20	2	0	0	0	0
2	9	9	2	2	0	2	1
2	10	13	2	0	0	0	0
2	11	7	2	0	0	0	0
2	12	7	2	0	0	0	0
2	13	14	2	0	0	0	0
2	14	9	2	0	0	0	0
3	15	9	1.5	1	0	1	0.7
3	16	20	1.5	0	0	0	0
4	17	10	2.5	1	0	1	0.4
4	18	10	2.5	3	0	3	1.2
4	19	5	2.5	2	0	2	0.8
4	20	9	2.5	1	0	1	0.4
4	21	11	2.5	1	0	1	0.4
4	22	12	2.5	2	0	2	0.8
4	23	14	2.5	4	0	4	1.6
4	24	5	2.5	0	0	0	0
		11.9 \pm 1.2	3.0 \pm 0.3	1.8 \pm 0.5	0.17 \pm 0.10	2.0 \pm 0.6	0.6 \pm 0.13



Figure 4.1. Expanded and unexpanded ovaries on a dried *P. ciliaris* inflorescence. The swelling of ovaries indicated fruit maturation which was verified through examination of dissected seeds (Figure 4.2).

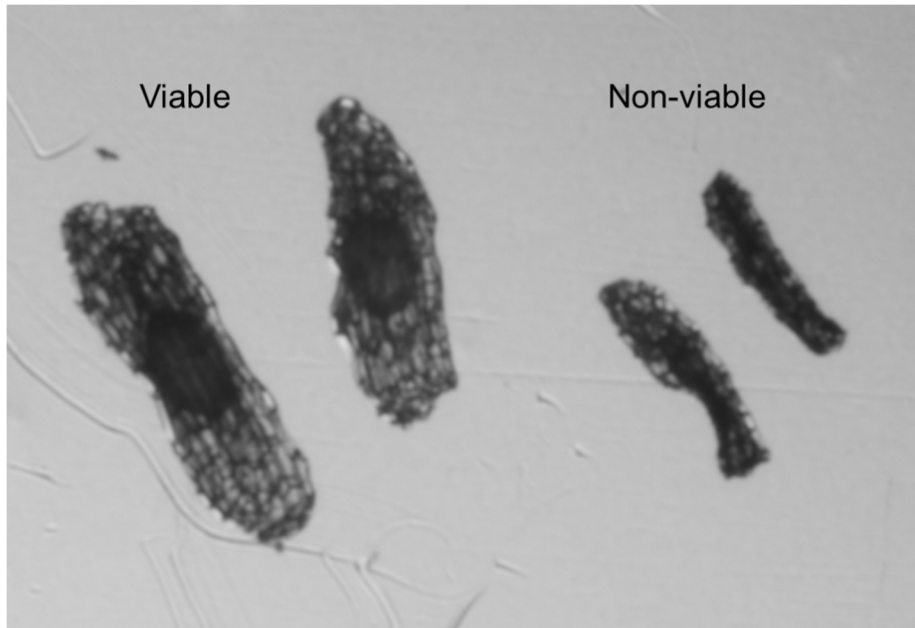


Figure 4.2. Viable and non-viable seeds that were dissected from expanded and unexpanded *P. ciliaris* ovaries, respectively. Viable seeds contain enlarged embryos in the center of the seed. Viewed at 90x magnification.

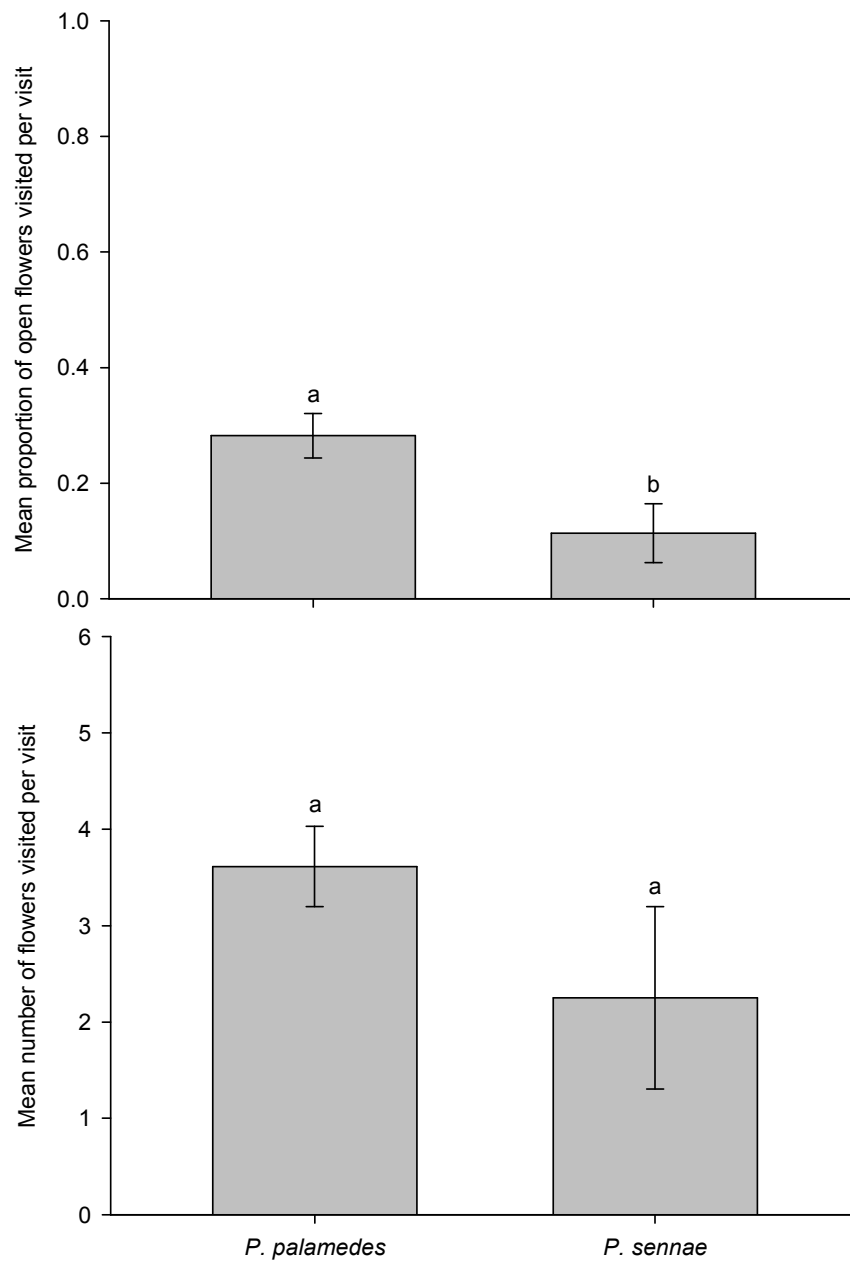


Figure 4.3. Mean proportion of open flowers visited per visit (top) and mean number of flowers visited per visit (bottom) by *P. palamedes* (44 visits) and *P. sennae* (4 visits). Different letters indicate significant differences between species ($P < 0.05$).

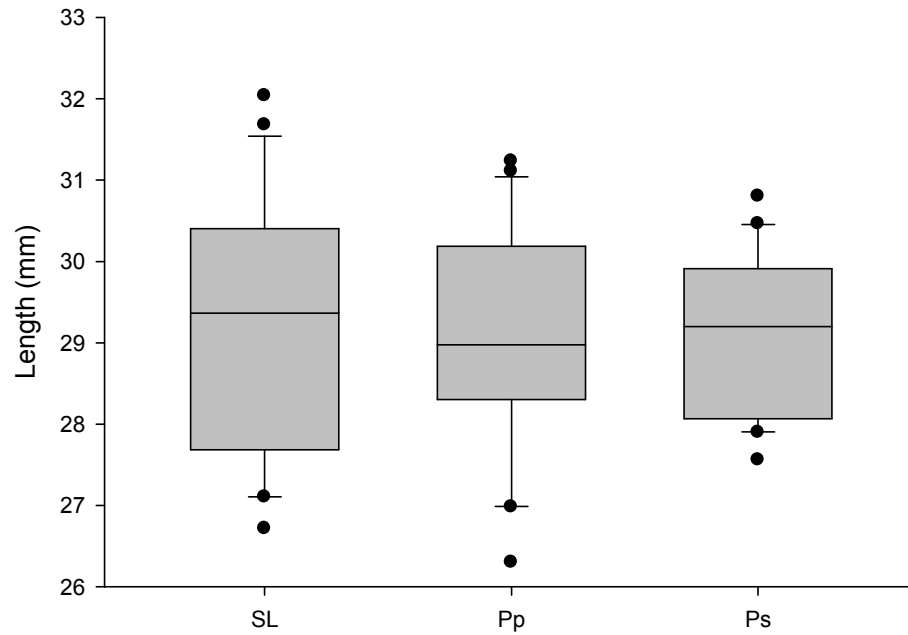


Figure 4.4. Relationship between nectar spur length of *P. ciliaris* (SL) and the proboscis lengths of *P. palamedes* (Pp) and *P. sennae* (Ps). The horizontal line is the median and the boxes and error bars represent the 10th, 25th, 75th, and 90th percentiles. Black dots are outliers. There were no significant differences ($P > 0.05$).

CHAPTER 5

BIRD FORAGING PREFERENCES FORECAST INCREASES IN EXOTIC SPECIES DISPERSAL DUE TO EXOTIC DISEASE

Abstract

Disturbances that alter relationships between plants and seed-dispersers can provide opportunities for exotic plant species to expand their population size and/or distribution. Specifically, disturbances such as exotic tree diseases that decrease the relative abundance of native fruit bearing trees may encourage the consumption and subsequent dispersal of exotic fruit by frugivorous birds. However, accounts of these impacts are scarce due to the lack of pre-disturbance data and consideration for these indirect effects of alien insect invasion. The primary objective of this study was to quantify free-ranging bird preferences for the fruits of native (*Persea borbonia*) and exotic (*Cinnamomum camphora*) trees (Lauraceae) and predict future patterns of fruit consumption and subsequent propagule dispersal of *C. camphora*. With the inevitable decline of *P. borbonia* due to laurel wilt disease, I investigated redundancy between *C. camphora* and *P. borbonia* with respect to fruit characteristics (physical and chemical) in the laboratory and bird preferences in the field at the Grand Bay National Estuarine Research Reserve in coastal Mississippi. Across two winter survey periods I observed fruit removal from artificial infructescences and documented bird species using motion-activated cameras. I also manipulated background species upon which displays were hung (*Myrica cerifera* and *Triadica sebifera*) and the accessibility of the displays. Foraging bouts on both *P. borbonia* and *C. camphora* fruits were documented for three bird species (*D. carolinensis*, *T. migratorius*, and *C. guttatus*). There was no difference in fruit selectivity between species during year one of my

survey, but there was a significant preference for *C. camphora* in year two, which coincided with statistically lower mean daily temperatures. Background tree species and accessibility had no apparent effect on fruit preference. Total polyphenols and pulp:seed ratio were significantly higher in *C. camphora* fruit. I conclude that the fruits of *C. camphora* and *P. borbonia* represent nearly substitutable resources for native birds. However, several native species may prefer *C. camphora* fruit in times of energetic stress. The decline of *P. borbonia* due to laurel wilt disease will likely increase the consumption of *C. camphora* fruits and dispersal of its seeds, which could ultimately increase the distribution and abundance of this exotic species.

Introduction

The disruption of mutualistic relationships can have cascading effects leading to co-extinctions and is a serious threat to global biodiversity (Aslan et al. 2013). These disruptions can create opportunities for exotic species to form beneficial relationships with indigenous species and subsequently displace other native species. For example, exotic plant species whose fruits are consumed by native and/or exotic birds can have greater invasion potential due to the subsequent dispersal of propagules (reviewed by Richardson et al. 2000); many of the most invasive weeds produce fleshy fruits and propagules that are primarily bird-dispersed (Cronk and Fuller 1995, Richardson et al. 2000). However, it has been shown that bird-dispersed exotic plants may have stiff competition for avian seed-dispersers in areas where bird-dispersed native plants are also abundant and have similar fruit characteristics and fruiting phenology as those exotic plants (Smith et al. 2013). In these situations, exotic species may fail to become invasive despite an abundance of fruit-consuming birds (Debussche and Isenmann 1990). In fact, there are

numerous ecological and biological factors that regulate the formation of mutualistic relationships between exotic plants and frugivorous birds.

Fruit foraging in birds is tied to preferred nutritional rewards (Schaefer et al. 2003), dietary antioxidants (Schaefer et al. 2008) and/or fewer secondary compounds (Cipollini and Levey 1997). Recent evidence suggests that birds prefer fruits rich in anthocyanins and polyphenols (antioxidants) during periods of oxidative stress (*e.g.*, migration) (Bolser et al. 2013). Birds also preferentially forage on fruits according to sizes that are compatible with bill size and gape, with smaller fruits/seeds being consumed by a greater number of species (Jordano 1995). In addition, there is an environmental context to fruit selection whereby the removal of fruits is correlated with the size of fruit crops and the identity and density of nearby fruit-bearing species (*e.g.*, Murray 1987, Sargent 1990, Carlo et al. 2007, Ortiz-Pulido 2007, Prasad and Sukumar 2010, Smith and McWilliams 2014). Observations of this “neighborhood effect” are among the most common and have been documented across many groups of fruit-eating species.

The neighborhood effect is compelling because it suggests that frugivory patterns are governed by more general rules concerning resource relations and that fruit consumption is determined by the chemical composition of all available fruits. Relationships may be complementary (consumption of one resource increases the value of another) or antagonistic (consumption of one resource decreases the value of another) (*i.e.*, Tilman 1980, 1982). Resources such as those provided by fruits may also be perfect substitutions for one another in which case they should be equally preferred by frugivorous birds (Whelan et al. 1998). Understanding the resources provided by fruits to frugivorous birds will be important for predicting how disturbances alter the distributions of exotic and native fruit-producing species. When native and exotic plant resources are substitutable, the invasion potential of exotic fruit-

bearing plants may be enhanced by disturbances (*e.g.*, invasions of species/diseases) that reduce the abundance of native fruit-producing species. In other words, frugivorous birds may subsidize more of their diet with exotic fruits (potentially dispersing more seeds) when the resources provided by those exotic fruits are similar to those of a displaced native species.

In the southeastern US, an exotic ambrosia beetle (*Xyleborus glabratus*) is vectoring a pathogenic fungus (*Raffalea lauricola*), causing laurel wilt disease (LWD) in many native Lauraceae species (Fraedrich et al. 2008). Introduced to the US in 2002 near Savannah, GA, LWD and its beetle vector are now widespread in South Carolina, Georgia, and Florida. The disease has more recently emerged in several counties in Alabama and Mississippi (USDA, Forest Service 2015a). The fungus, which is introduced to host trees by the stem boring beetle, *X. glabratus*, spreads quickly through the xylem tissue. Mortality of main stems can occur within only a few months of initial infection (Mayfield 2008).

Although LWD has been identified in several Lauraceae species, the majority of occurrences are in redbay (*Persea borbonia*), an abundant fruit-bearing tree found in the understory and sub-canopy of many Atlantic and Gulf Coastal Plain habitats (Van Deelen 1991, Fraedrich et al. 2008). *Persea borbonia* co-occurs with several woody species including *Myrica cerifera* (native), *Triadica sebifera* (exotic), and the closely related Lauraceous species, *Cinnamomum camphora* (exotic); all of these species produce winter-ripening fruit that may attract over-wintering birds. Unlike *M. cerifera* and *T. sebifera* which produce waxy fruits (Place and Stiles 1992, Baldwin et al. 2008), *P. borbonia* and *C. camphora* have fleshy fruits that likely contain higher sugar concentrations and are very similar in appearance (A Chupp pers obs). Based on these superficial characteristics, I hypothesized that the fruits of *P. borbonia* and *C. camphora* represent substitutable resources for overwintering birds. *Persea borbonia* and *C.*

camphora are closely related species in the Lauraceae (Chanderbali et al. 2001), however, due to LWD, projections for the long-term persistence of these species are very different.

On the Atlantic Coastal Plain, mortality rates of *P. borbonia* populations are as high as 97%, and the persistence of *P. borbonia* stump sprouts is doubtful as the fungal pathogen may be reintroduced by beetles and by dispersal through root systems (Evans et al. 2014, Spiegel and Leege 2013). Conversely, *Cinnamomum camphora* has shown resistance to LWD. The few individuals that are infected show only minimal stem die-off (Smith et al. 2009a) whereas in other Lauraceae species, *i.e.*, *Sassafras albidum*, the entire canopy succumbs to the disease (Smith et al. 2009b). Results from single point inoculation trials in the field and laboratory failed to produce LWD symptoms in *C. camphora* despite systemic colonization by *R. lauricola*; multiple point inoculations caused only localized branch dieback (Fraedrich et al. in press). Although *C. camphora* is identified as an exotic invasive species in eight states of the southeastern US, its range is still expanding across this region. In Florida, *C. camphora* is naturalized in 27 counties but has been documented in 9 other counties (USDA, NRCS 2014, Wunderlin and Hansen 2014). While it grows well in anthropogenically altered areas (*e.g.*, roadsides and residential/commercial developments), large fruiting individuals are also observed in relatively undisturbed forested habitats (A Chupp pers. obs.). Dispersal by birds may play a crucial role in the distribution of this species. Although preferences for *C. camphora* fruits have been observed in Asian and Australian bird species (Corlett 2005, Neilan 2006), I found no documentation of North American bird preferences for the fruits of *P. borbonia* or *C. camphora*; only general accounts suggesting the importance of *P. borbonia* fruits for wildlife (Goodrum 1977, Brendemuehl 1990).

If the fruits of *P. borbonia* and *C. camphora* represent substitutable resources to frugivorous birds, then I expect both positive and negative consequences. On one hand, *C. camphora* could provide birds with a supplemental resource in the wake of LWD and the decline of *P. borbonia* fruits. On the other hand, preference for *C. camphora* could lead to the increased dispersal of this exotic plant, potentially increasing its invasiveness, and subsequently threatening other native plant species. The primary objective of this study was to quantify the relative preferences of birds for the fruits of *P. borbonia* and *C. camphora* on the northern Gulf Coast. My goal was to document the nature of these relationships prior to disturbance by LWD. Although individual bird species will differ in their preferences, my overarching hypothesis was that fruits of *P. borbonia* and *C. camphora* represent nearly substitutable resources (based on morphology and chemistry) and that fruit removal rates of *C. camphora* and *P. borbonia* by frugivorous bird species will be equivalent. Here, I provide the first quantitative observations of bird frugivory on *P. borbonia* and *C. camphora* fruits in the southeastern US and provide a forecast for the indirect effects of LWD on the consumption of *C. camphora* fruit and the subsequent dispersal of propagules.

Methods

Study site

Bird frugivory was observed at Grand Bay National Estuarine Research Reserve (GBNERR) in Jackson County, Mississippi. The study site corresponded to an area that was within 100m of a 1.5 km stretch of Bayou Heron Road (Figure 5.1). The area included maritime forest, pine savanna, and highly disturbed habitats (*i.e.*, power line right-of-ways, parking lots, and fire lanes). Savannas consisted of a sparse slash pine overstory (*Pinus elliottii*) and several

native woody plants in the understory including *P. borbonia*, *Myrica cerifera*, *Ilex glabra*, and *Ilex vomitoria*; two exotic woody plants (*C. camphora* and *Triadica sebifera*) were also present in the understory layer. Observations were collected during winter months (December-January) and so I targeted bird species at GBNERR that are considered winter or permanent residents (Woodrey and Walker 2009). Due to this timing, I also expected low day-to-day variability in local bird abundances relative to studies of birds along their fall migration route (Willson and Whelan 1993, Whelan and Willson 1994, Whelan et al. 1998).

Artificial displays

During two winter seasons (December 2012–January 2013 and January 2014) fruits of *P. borbonia* and *C. camphora* were presented to free ranging birds on artificial infructescences. Similar displays have been successfully used to assess fruit choices of both captive and free-ranging migratory birds (Thompson and Wilson 1978, Whelan and Willson 1994, Whelan et al. 1998). Each artificial infructescence consisted of a 1 cm diameter wooden dowel rod (30 cm in length) with 10 pieces of 16-gauge black wire (~8 cm in length) inserted perpendicularly through holes in the dowel rod (~2 cm between each hole). Wire pieces were inserted such that an equal portion of wire extended from each side of the dowel rod (Figure 5.2). Fruits were impaled on both ends of all 10 wires (20 fruits per infructescence). Fruits were only partially impaled so that they could be easily removed but also not fall off inadvertently.

Fruit analyses

We also collected fruits of both species for chemical and morphological analyses. The pulp and seeds of these fruits were separated and dried to a constant weight at 55 degrees C. The seed and pulp of each fruit were then weighed separately and the pulp:seed ratio was calculated for each species. The pulp of some fruits was milled and shipped to Alkemist labs in Costa Mesa,

CA where it was analyzed for total polyphenols (as gallic acid uv-vis spectrophotometry) and nutritional content (calories, fat, carbohydrate, protein, and moisture). Each analysis was based on one sample per species of fruit, except for total polyphenols for which four samples were used.

Selectivity experiments

Artificial infructescences were displayed on two different “background” species (*M. cerifera* and *T. sebifera*) that are very common at GBNERR. Both of these species produce waxy, lipid-rich fruits and are unlike the fleshy fruits (*i.e.*, higher sugar content) of *P. borbonia* and *C. camphora* (Place and Stiles 1992; Baldwin et al. 2008). Birds may be more likely to select fruits when they are presented with a background of fruits that are nutritionally complementary and more abundant (Whelan et al. 1998). Therefore, by selecting *M. cerifera* and *T. sebifera* as background tree species I hoped to increase the visibility of the displays so that preferences could be evaluated more readily. Across both years of the survey 66 different background trees (*M. cerifera*, $n = 32$; *T. sebifera*, $n = 34$) were used. These trees were dispersed throughout the survey area and each tree contained an abundant fruit crop. All background trees were ≥ 20 m apart. Trees of each species were selected so that no fruit-bearing individuals of the other species were within 20 m.

The artificial infructescences were displayed for 3-5 days at a time, after which new background trees were selected. Displays placed on different individual trees were considered replicates (one display per tree). During survey periods, I always had an equal number of replicates on each background species. To begin, 10 replicate displays were deployed at a time but was later increased to 12. Each display contained an equal number of *P. borbonia* and *C. camphora* fruits, which were kept separate on opposite sides of the display. Artificial

infructescences were attached to background tree branches with rubber bands. Because accessibility can impact the removal of fruits by captive and free-ranging birds (*e.g.*, Whelan and Willson 1994), I was careful to place displays in positions where perches were available for birds to easily access both sides of the display. Displays were checked each day at sunset or just after (17:00-18:00 hr). At this time, I recorded the number of fruits taken of each species and replaced all removed fruits.

Fruit accessibility experiments

After determining the relative preferences of *P. borbonia* and *C. camphora* fruits when both are equally accessible, a behavioral titration approach was used to determine the strength of these preferences (after Moermond and Denslow 1983, Whelan and Willson 1994). In January 2014, I used a subset of background trees (*M. cerifera* and *T. sebifera*) that received high levels of bird activity during previous selectivity experiments. Fruit of the more preferred species was placed in less accessible positions. These less accessible displays were hung vertically from the bottom of a perpendicular branch such that no perches were nearby. At the same time, displays containing fruit of the less preferred species were hung in a highly accessible position as described above. Therefore, two displays, each containing 20 fruit of one species, were simultaneously placed on each background tree. Displays were left in this arrangement for 2-3 days. These trials were then repeated but with the accessibility of species switched. Displays were checked at sunset as described above.

Camera trapping

During 10 days of the survey in January 2014, I used a motion/heat activated camera to document fruit removal by bird species. The camera monitored displays during both selectivity and accessibility experiments. I chose to monitor displays on background trees that received the

highest rates of fruit removal. The camera (Bushnell NatureView HD Model #119438) was mounted on a tripod and placed 1-2 m from a display. The camera was set to take three pictures in rapid succession (3 seconds) followed by a 2 second delay before more pictures could be triggered. The camera was active from sunrise to sunset. Photos were used 1) to verify visitation by specific species, 2) to determine the relative frequency that each species visited displays, and 3) to document patterns of fruit removal and selectivity during individual foraging bouts. A foraging bout was considered to be any continuous series of photographs (not separated by more than 2 minutes) capturing the same species. Within a given foraging bout, the number of fruits removed was determined by examining the first and last images of the series. In cases where these details were indiscernible, fruit preferences could not be calculated for these foraging bouts and were therefore discarded. Because individuals could not be identified in photographs, it is possible that some individuals were represented in more than one foraging bout.

Statistical Analyses

Relative preferences were quantified with Manly's α (Manly et al. 1972) which can be adapted for situations where food is depleted over the course of daily foraging bouts (Chesson 1983). Manly's α ranges from 0 to 1; $\alpha = 0$ when the food type is not represented in the diet and $\alpha = 1$ when it is the only food type in the diet (Chesson 1983). Results from the same background tree during 3-5 day periods were pooled and α was calculated from these summed data. Because fruit removal rates may be affected by temperature (*e.g.*, Kwit et al. 2004), I examined winter temperatures across both years of my survey. Winter temperatures were calculated as mean daily temperature (average of daily high and low) for each day that displays were active (obtained from NOAA NERR CDMO 2014). Mean daily temperatures were compared between the two years of selectivity experiments using an independent samples t-test.

Because α is calculated as a proportion of fruits removed, these data were arcsine square root transformed to meet assumptions of homoscedasticity and normality. For the results of selectivity experiments, a two-way analysis of variance (ANOVA) was used to compare differences in α across years and types of background trees. One-sample t-tests were used to examine significant effects more closely; within each treatment I tested if α significantly differed from 0.5 ($\alpha = 0.5$ = no preference). The direction of significant differences indicated whether the fruits of *P. borbonia* or *C. camphora* were preferred ($\alpha < 0.5$ = preference for *C. camphora*, $\alpha > 0.5$ = preference for *P. borbonia*). Results from Wilcoxon Signed Rank tests were used if departures from normality were still detected after the data were transformed. A two-way ANOVA was also used to assess the effect of fruit accessibility and tree background on α . Again, any significant effects were further analyzed with one-sample t-tests.

Manly's α was also calculated for individual foraging bouts that were captured on camera. In many cases, birds removed only one species of fruit during an individual foraging bout. As such, α values were often either 0 or 1 depending on whether the bird selected *P. borbonia* or *C. camphora*. In some cases birds selected both types of fruit or did not remove any fruit at all. Contingency tables (2 x 3) and Pearson's chi-squared tests were used to determine if the number of foraging bouts observed differed among the following foraging bout types: 1) no removal of either fruit, 2) removal of both fruit types, and 3) removal of just one species of fruit. One contingency table was constructed for each of the three experimental treatment types (equal accessibility, *P. borbonia* less accessible and *C. camphora* less accessible). A Pearson's chi-squared test was also used to determine if the frequency of foraging bouts observed differed between cases when just *P. borbonia* was removed versus those in which only *C. camphora* was removed. Within each experimental treatment, Wilcoxon Signed Rank tests were used to

examine if α significantly deviated from 0.5 for each species in which 5 or more foraging bouts were observed.

Differences in pulp and seed weight, pulp:seed ratio, and total fruit polyphenols between species were examined using t-tests. All statistical tests and data transformations were completed using SAS 9.3 statistical software (SAS Institute Inc. 2011).

Results

Fruit analyses

Percent total polyphenol was higher for *C. camphora* than *P. borbonia* ($t = 3.21$, $P = 0.049$; Table 5.1). The pulp of individual *C. camphora* fruits was significantly heavier than that of *P. borbonia* ($t = 11.07$, $P < 0.001$) whereas *C. camphora* seeds were significantly lighter ($t = 13.03$, $P < 0.001$). The pulp:seed ratio was higher for *C. camphora* (0.995) compared to *P. borbonia* (0.337) ($t = 29.15$, $P < 0.001$).

Selectivity experiments

In December and January of 2012/2013 (year 1), 3480 *P. borbonia* and *C. camphora* fruits (1740 of each species) were presented on displays. Displays were hung in 50 different background trees (25 *M. cerifera* trees and 25 *T. sebifera* trees). Across 16 days, birds removed 249 *P. borbonia* fruits and 286 *C. camphora* fruits. In January of 2014 (year 2), 2280 total fruits (1140 of each species) were displayed on 22 different background trees (11 of each species). Birds removed 237 *P. borbonia* and 427 *C. camphora* fruits. Manly's α differed between years (ANOVA: $F_{1,43} = 5.95$, $P = 0.019$) but did not differ between background tree species (ANOVA: $F_{1,43} = 2.65$, $P = 0.112$). Manly's α did not significantly differ from 0.5 (*i.e.*, no preference) in year one of the survey ($t = 0.18$, $P = 0.86$) but it did differ from 0.5 in year two ($t = -4.42$, $P <$

0.001), when more *C. camphora* fruits were consumed. Manly's α calculated for *P. borbonia* was 0.31 ± 0.04 (mean \pm standard error) and therefore *C. camphora* fruits were more preferred ($\alpha = 0.69 \pm 0.04$) in year two. During the periods in which selectivity experiments were active, mean daily temperature was significantly higher in year one (13.1 ± 1.0 °C) compared to year two (6.7 ± 1.8 °C) ($t = 3.16$, $P = 0.006$) (Figure 5.3).

Fruit accessibility experiments

In January 2014, displays were placed in 10 different background trees (six *T. sebifera* and four *M. cerifera*). Twenty different trials were conducted over a 14-day period: 10 trials where *C. camphora* fruits were highly accessible and *P. borbonia* fruits were less accessible, and 10 trials where fruit accessibility was switched. I presented a total of 860 fruits of each species, and birds removed 545 fruits of *P. borbonia* and 671 fruits of *C. camphora* (Table 5.2).

Background tree type and fruit accessibility had no effect on α (respectively, ANOVA: $F_{1,16} = 2.87$, $P = 0.110$; $F_{1,16} = 0.02$, $P = 0.89$). However, a t-test revealed that α (0.40 ± 0.04) significantly deviated from 0.5 ($t = -2.32$, $P = 0.032$), indicating a preference for *C. camphora* fruits during these trials.

Camera trapping

During both selectivity and accessibility experiments, I recorded a total of 1139 photographs of the following bird species: gray catbird (*Dumetella carolinensis*), American robin (*Turdus migratorius*), hermit thrush (*Catharus guttatus*), brown thrasher (*Toxostoma rufum*), and eastern towhee (*Pipilo erythrophthalmus*). *Turdus migratorius* was represented in the greatest number of photos (44%), followed by *D. carolinensis* (36%) and *C. guttatus* (14%). From these photos, I identified a total of 59 individual foraging bouts that allowed for an accurate count of fruit removed. The number of foraging bouts was greatest for *D. carolinensis* (31) (shown in

Figure 5.4), followed by *T. migratorius* (18) and *C. guttatus* (9). No foraging bouts were recorded for *P. erythrophthalmus* (Table 5.3). During accessibility experiments, there were significantly more foraging bouts where only one fruit type was removed compared to those in which both types of fruit were removed and cases where no fruit was removed. However, there was no difference in the number of foraging bouts in which *P. borbonia* or *C. camphora* were preferred ($\chi^2 < 3.84$, $P > 0.05$).

Across the three experimental types, there were five cases where five or more foraging bouts by the same species were captured in photos. The most foraging bouts were recorded for *D. carolinensis*, which had five or more bouts in each of the three experimental types. In the experiments in which *P. borbonia* fruit was less accessible, photos also captured at least five bouts by *T. migratorius* and *C. guttatus* (Table 5.3). In each case where at least 5 bouts were recorded ($n = 5$), α values calculated from the individual foraging bouts did not significantly differ from 0.5 ($P > 0.05$), indicating no evidence of fruit type preference.

Discussion

Results from both field trials and laboratory analyses indicate that the fruits of *P. borbonia* (native) and *C. camphora* (exotic) represent nearly substitutable resources for overwintering birds. I show that fruit characteristics (physical and chemical) and bird preferences for the fruits of these species are similar across two winter foraging seasons. Relative to *P. borbonia*, *C. camphora* appears to offer similar resources, enabling this species to acquire native mutualistic partners. In addition, observations from camera trapping suggest that the same native bird species are consuming both *P. borbonia* and *C. camphora* fruits.

The results of my experiments represent the aggregated preferences of at least four overwintering bird species (*D. carolinensis*, *T. migratorius*, *C. guttatus*, and *T. rufum*). One or more foraging bouts were photographed for each of these species. Photographs of *D. carolinensis*, *T. migratorius*, and *C. guttatus* documented removal of both *P. borbonia* and *C. camphora* fruits by each species across multiple foraging bouts. These generalist frugivores are known to forage on the fruit of many shrub species including non-native species (e.g., Bartuszevige and Gorchov 2006, Gleditsch and Carlo 2011). In central Pennsylvania, the fruits of two exotic shrubs, *Lonicera maackii* and *Lonicera morrowii*, were large dietary components of *D. carolinensis* and *T. migratorius* (Gleditsch and Carlo 2011). Observations of mist-netted birds in Ohio showed that both *T. migratorius* and *C. guttatus* defecated viable seeds of *L. maackii* (Bartuszevige and Gorchov 2006). The mutualism between *Lonicera* spp. and native birds has not only increased dispersal rates for *Lonicera* spp. but it has also affected interactions between frugivores and native plants (McCay et al. 2009, Gleditsch and Carlo 2011). In coastal areas of South Carolina and Louisiana, consumption of *Triadica sebifera* fruits by *T. migratorius* and other native birds has contributed to the invasiveness of this exotic tree (Renne et al. 2002). In the case of *C. camphora*, I submit that it is unclear how gut passage of these seeds may impact germination and seedling growth rates; seed retention time will also affect dispersal distances. For *C. camphora* and other species, such factors may vary by species of bird (reviewed by Traveset 1998, Jordaan et al. 2011, Ward and Labisky 2004). While more work needs to be done, my results suggest that at least three native bird species eat *C. camphora* fruits, potentially facilitating the spread of this exotic species.

Despite the apparent redundancy in the characteristics of *P. borbonia* and *C. camphora* fruit, nutritional differences on a per fruit basis may affect preferences of energetically stressed

birds and the relative dispersal rates of these species. Exotic species that have relatively smaller seeds and offer more pulp sugar per fruit than indigenous species may have large invasion potential (Gosper and Vivian-Smith 2010). Although the removal rate of non-native *C. camphora* fruit was generally similar to that of indigenous *P. borbonia* fruit, removal rates of *C. camphora* fruits showed a significant increase during the second year of the selectivity experiments. This experimental period, where these fruits were clearly preferred over those of *P. borbonia*, coincided with significantly lower mean daily temperatures relative to the first year of my survey. Low temperatures increase the energy demands of birds (Calder and King 1974) and reduce the abundance of insects upon which they feed (Thompson and Willson 1979). Lower temperatures should therefore increase dependence on fruit as a resource subsidy. A nine year study of *M. cerifera* in South Carolina showed that mean time to fruit removal by birds was positively correlated with mean winter temperature (Kwit et al. 2004). Birds may choose those fruits with the highest nutritional rewards, especially in periods of extreme energetic demand (e.g., cold temperatures and/or during migration). I argue that the greater nutritional rewards offered by *C. camphora* fruits led to greater consumption during the coldest period of my survey. While fruits of each species contained similar nutritional contents per unit mass, individual *C. camphora* fruits had considerably larger pulp:seed ratios than *P. borbonia* fruits. On average, each *C. camphora* fruit contained 0.04 g more pulp than *P. borbonia* fruits (Table 5.1). I conclude that each *C. camphora* fruit contains a substantially larger nutritional reward that may be relatively more attractive during periods of energetic stress.

There are also other chemical constituents of fruit that may increase preferences depending on metabolic demands. *Cinnamomum camphora* fruit pulp contained a significantly higher percentage of total polyphenols compared to *P. borbonia* (Table 5.1). Studies have shown

that temperate frugivorous birds prefer diets that are supplemented with total polyphenols and other classes of antioxidant compounds such as anthocyanins, carotenoids, and flavonoids (Cantoni et al. 2008, Schaefer et al. 2008, Senar et al. 2010, Bolser et al. 2013). In addition to total polyphenols, it is likely that the fruits of *C. camphora* are enriched with these and other antioxidant compounds. The oils produced in the tissues of *C. camphora* have been used as healing agents in Asian cultures for centuries (Lawless 2013). Recent work has provided scientific evidence of the anti-inflammatory and antioxidant effects of *C. camphora* extracts (Lee et al. 2006, Hu et al. 2011). Interestingly, the seed oil of *C. camphora* contains extremely high levels of medium-chain triacylglycerol, which is very stable to oxidative reduction (Hu et al. 2011). Such chemical characteristics of *C. camphora* fruit may make it an attractive dietary supplement for frugivorous birds, especially during periods of elevated oxidative stress (e.g., during migration and extreme cold).

In some situations, frugivorous birds may become dependent on the fruits of *C. camphora* and other exotic plant species. In northern New South Wales, Australia, the fruits of *C. camphora* are the principal dietary component of several native bird species. In fact, Date et al. (1996) concluded that the presence of *C. camphora* was important for buffering these fauna against the effects of widespread habitat destruction. In Pennsylvania, greater local abundance of native bird species was due to the presence of exotic fruiting *Lonicera* spp. (Gleditsch and Carlo 2011). At this point, I'd like to acknowledge that there is growing interest and considerable debate over the value of non-native species and the novel interactions they form with native species (Hallett et al. 2013). In many cases, including those highlighted above, exotic plant species can provide beneficial ecological functions for native birds (Impey et al. 2002; Jones and Bock 2005). Despite concern over the proliferation of exotics and their effects on native species,

there has been a shift towards thinking about the services exotic species provide, especially where restoration is not economically feasible (Hobbs et al. 2009). In situations where a key or dominant native is inevitably in decline, understanding how exotic species may provide functional redundancy is especially important. While it is critical to discuss the beneficial resources that exotic species provide to native species, I also maintain that increased dispersal and subsequent invasion of these exotic species can be highly detrimental to the persistence of other native species.

We have provided the first quantitative observations of frugivorous birds consuming the fruits of *C. camphora* and *P. borbonia* in the southeastern US. In addition, I have quantified the relative preferences for these fruits and documented removal using motion activated photography prior to the arrival of LWD. The fruits of *C. camphora* are physically and chemically similar to those of *P. borbonia* but appear to offer greater rewards per fruit. I conclude that the relative preferences shown by overwintering native birds for the fruits of *C. camphora* indicate the potential for increased reliance on the resources provided by these fruits and a subsequent increase in the invasiveness of this species following LWD-induced declines of *P. borbonia*.

Table 5.1. Chemical properties of pulp and mass of *C. camphora* and *P. borbonia* fruits. Total polyphenols, dry weights, and pulp:seed ratio are shown as mean \pm standard error. Significant differences between fruits of each species ($P < 0.05$) are indicated with different letters.

	<i>C. camphora</i>	<i>P. borbonia</i>
Calories (Cal/100g)	476	566
Calories from fat (Cal/100g)	239	340
Fat (g/100g)	26.6	37.8
Carbohydrates (g/100g)	52.8	49.8
Protein (g/100g)	6.42	6.62
Moisture (g/100g)	5.02	1.77
Total polyphenols (%)	1.76 ± 0.37^a	0.54 ± 0.08^b
Pulp dry weight (g)	0.114 ± 0.002^a	0.074 ± 0.003^b
Seed dry weight (g)	0.115 ± 0.002^a	0.230 ± 0.009^b
Pulp:seed ratio	0.995 ± 0.018^a	0.337 ± 0.014^b

Table 5.2. Results of selectivity and accessibility experiments. Selectivity experiments were conducted in December 2012-January 2013 (Year 1) and January 2014 (Year 2). Accessibility experiments were completed in January 2014. No fruit preference occurred when $\alpha = 0.50$; $\alpha < 0.50$ indicated a preference for *C. camphora* fruit and $\alpha > 0.50$ suggested a preference for *P. borbonia* fruit. Significant preference indicated with * $P < 0.05$, ** $P < 0.001$.

	Selectivity Experiments		Accessibility Experiments	
	Year 1	Year 2	<i>P. borbonia</i> less accessible	<i>C. camphora</i> less accessible
Fruits presented				
<i>P. borbonia</i>	1740	1140	360	500
<i>C. camphora</i>	1740	1140	360	500
Fruits removed				
<i>P. borbonia</i>	249 (14%)	237 (21%)	300 (83%)	245 (49%)
<i>C. camphora</i>	286 (16%)	427 (37%)	348 (97%)	323 (65%)
Mean α	0.51 \pm 0.06	0.31 \pm 0.04**	0.41 \pm 0.05*	0.40 \pm 0.07*

Table 5.3. Observations collected from photos across three experimental types for each bird species. Manly's α was averaged across foraging bouts for each species within each experimental type; a grand average \pm standard error is also presented.

Species	Photos	Foraging bouts	Fruit removed		Manly's α
			<i>P. borbonia</i>	<i>C. camphora</i>	
<i>Selectivity Experiment</i>					
<i>T. migratorius</i>	23	2	2	1	0.50
<i>D. carolinensis</i>	107	12	8	17	0.36
<i>C. guttatus</i>	41	1	1	0	1
<i>Accessibility Experiment (P. borbonia less accessible)</i>					
<i>T. migratorius</i>	440	15	12	41	0.37
<i>D. carolinensis</i>	201	7	8	5	0.64
<i>C. guttatus</i>	105	5	7	3	0.69
<i>T. rufum</i>	53	1	0	1	0
<i>Accessibility Experiment (C. camphora less accessible)</i>					
<i>T. migratorius</i>	26	1	1	0	1
<i>D. carolinensis</i>	117	12	21	4	0.72
<i>C. guttatus</i>	19	3	1	6	0.03
<i>T. rufum</i>	4	0	0	0	NA
<i>P. erythrophthalmus</i>	3	0	0	0	NA
Total	1139	59	61	78	0.53 \pm 0.11



Figure 5.1. Google Earth image of the survey area at the Grand Bay National Estuarine Research Reserve in Jackson County, Mississippi USA. Displays were placed on trees located within 100m of Bayou Heron Road between the “survey area start” and “survey area end” points.

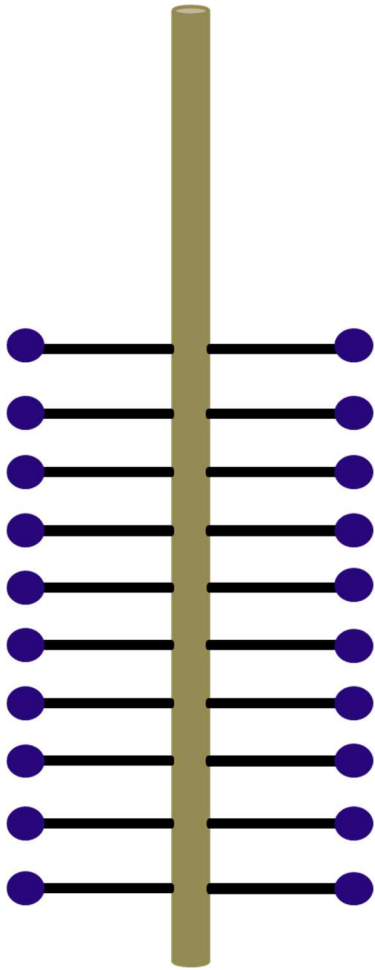


Figure 5.2. Diagram of artificial fruit displays. Each display consisted of a wooden dowel rod, approximately 30cm in length, and 10 metal wires inserted through the rod. Fruits were partially impaled on both ends of each metal wire.

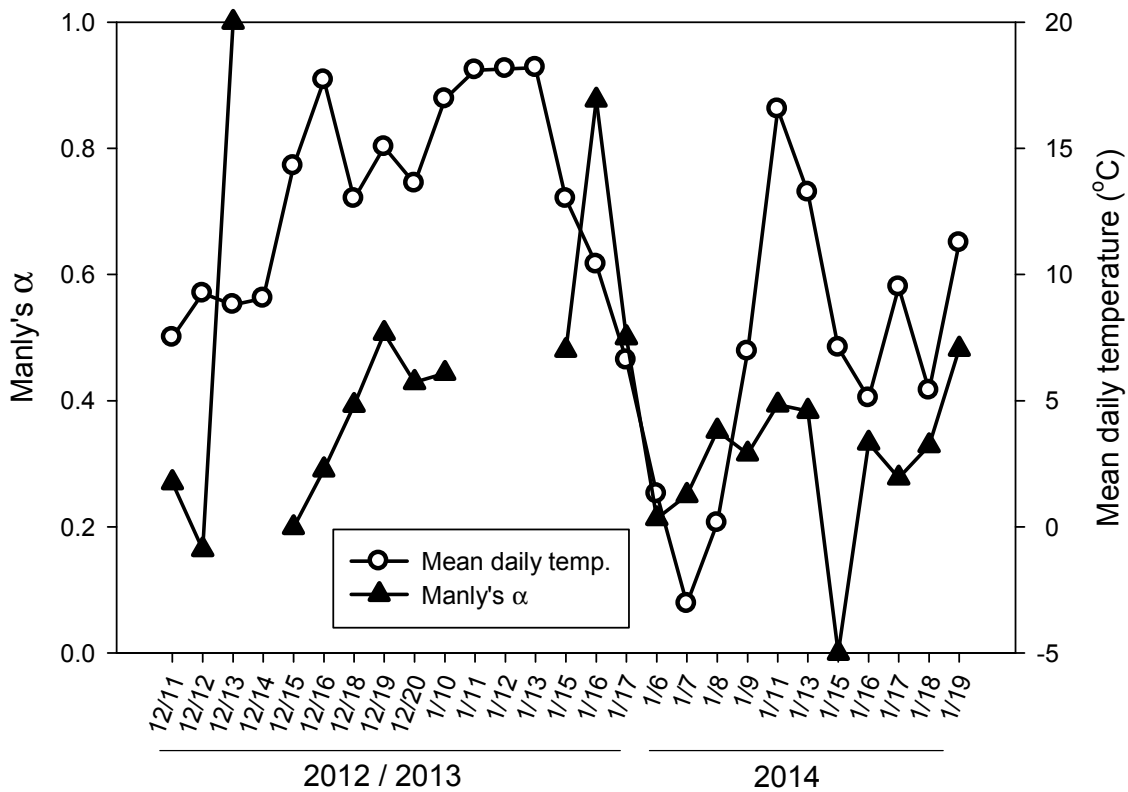


Figure 5.3. Mean daily temperatures (°C) and Manly's α as calculated from each day of the selectivity experiments. No fruit preference occurred when $\alpha = 0.50$; $\alpha < 0.50$ indicates a preference for *C. camphora* fruit and $\alpha > 0.50$ suggests a preference for *P. borbonia* fruit. The first survey year (2012/2013) is shown on the left and year two (2014) is on the right.



Figure 5.4. Motion-activated photo of *D. carolinensis* just prior to its removal of a *C. camphora* fruit from an artificial display during the selectivity experiment.

CHAPTER 6

CONCLUSION

Laurel wilt disease is a fungal pathogen (*Raffaelea lauricola*) that has spread rapidly across the southeastern US due to the invasion of its beetle vector (*Xyleborus glabratus*) in 2002. The impacts of this disease have been devastating for many native species in the Lauraceae family. Among populations of the primary host (*Persea borbonia*), infection rates and crown dieback are catastrophically high. However, this species has shown a large capacity for persistence via resprouting from the base of main stems. While other disease-inflicted species have persisted as vegetative resprouts (e.g., *Castanea dentata* and *Fagus grandifolia*), their ecological functions have been reduced along with their size. The overarching goal of this dissertation was to further define the ecological role of *P. borbonia* prior to invasion of LWD in coastal Mississippi. In chapters two through five, I provided empirically based conclusions that highlight the nature of interactions between *P. borbonia* and several species at multiple trophic levels. The conclusions of these chapters predict dramatic direct and indirect consequences of LWD.

In chapter two, I found that the foliage produced by *Persea borbonia* was a substantial component of stand structure at my site. I documented the contribution of *P. borbonia* to the canopy layer by showing a roughly 50% increase in light transmission following experimental removal of *P. borbonia*. In the field, basal sprouting of *P. borbonia* was vigorous in response to girdling and main stem removal (i.e., LWD simulation). Results of greenhouse trials suggested that growth of *P. borbonia* resprouts is limited by nutrient availability. It should be noted that the closely related exotic species, *C. camphora*, did not exhibit the same response. I concluded that,

areas of relatively higher nutrient availability may offer the best opportunities for *P. borbonia* to regenerate and persist via sprouting. While the removal of *P. borbonia* and subsequent sprouting had no detectable effects on understory plant recruitment and regeneration after two years, I predicted that impacts from LWD will benefit co-occurring dominant sub-canopy/understory species, *I. vomitoria* and *M. cerifera*.

In chapter three, I concluded that although *C. camphora* is relatively unsuitable for oviposition by female *P. palamedes*, larvae were physiologically capable of using this exotic host and in many cases individuals performed quite well. While it is unclear how predation and other interspecific interactions would affect larval performance in a natural setting, my results suggested that *C. camphora* will not function as an evolutionary trap for *P. palamedes*. Instead, the future colonization of *C. camphora* by *P. palamedes* will depend largely on the factors influencing adult female oviposition preferences. Among these factors, I argue that host availability and occupancy will be most important following the impacts of LWD.

In chapter four, I predicted a marked decline in the reproductive success of *P. ciliaris* plants following the impacts of LWD. During visitation surveys, *P. palamedes* was the primary floral visitor of this large terrestrial orchid. Expected LWD-induced declines of *P. palamedes*, whose larvae primarily feed on *P. borbonia* (Brooks 1962; Scriber et al. 1991; Lederhouse et al. 1992; Chupp and Battaglia 2014), may dramatically reduce pollination service to *P. ciliaris* populations. As an abundant pollinator, *P. palamedes* may also serve as the primary pollinator of other native plants, including the white-fringed orchid (*Platanthera blephariglottis*) which also harbors nectar in exceptionally long nectar spurs (Smith and Snow 1976). In chapter four, I provided some empirical evidence for how the indirect effects of an alien insect may disrupt pollination service and reduce the reproductive success of a native plant. Such information can

allow land managers to prepare contingency plans for the conservation of these endangered communities. I urge future research on the effects of exotic alien insects to consider the indirect effects on native insect herbivores and the plants they pollinate.

In chapter five, I provided the first quantitative observations of overwintering, frugivorous birds consuming the fruits of *C. camphora* and *P. borbonia* in the southeastern US. In addition, I quantified the relative preferences for these fruits and documented removal using motion activated photography. The following bird species were captured in photos: *Dumetella carolinensis*, *Turdus migratorius*, *Catharus guttatus*, and *Toxostoma rufus*. There was no significant difference in selectivity between fruit types during year one of the survey but there was a significant preference for *C. camphora* in year two, which coincided with significantly lower mean daily temperatures. I found that the fruits of *C. camphora* are physically and chemically similar to those of *P. borbonia* but appear to offer greater rewards per fruit. I concluded that the relative preferences shown by overwintering native birds for the fruits of *C. camphora* indicate the potential for increased invasiveness of this species following LWD-induced declines of *P. borbonia*.

Laurel wilt disease is spreading rapidly across the southeastern US, removing mature *P. borbonia* and leaving behind at most immature sprouts. My conclusions suggest that the greatest consequences of this changing function of *P. borbonia* will be mediated by *P. palamedes*, frugivorous birds and co-occurring sub-canopy species (e.g., *I. vomitoria*, *M. cerifera*, *C. camphora*). I have provided important baseline empirical data to which future studies may look for comparison with post LWD-impacted communities.

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Appendix B. Average percent cover of herbaceous species within control and removal sub-plots during each year of the survey.

	2011	2012	2013
Control (n = 18)			
<i>Ampelopsis arborea</i>	0.0	0.0	0.1
<i>Andropogon virginicus</i>	3.3	3.3	3.6
<i>Centella asiatica</i>	0.3	0.1	0.1
<i>Dichanthelium</i> sp.	2.5	1.1	1.5
<i>Euthamia</i> sp.	1.1	0.3	0.3
<i>Juncus roemerianus</i>	4.2	2.5	2.5
<i>Panicum virgatum</i>	6.1	2.5	2.9
<i>Rhynchospora</i> sp.	0.8	0.0	0.3
<i>Rubus argutus</i>	7.5	2.8	4.2
<i>Setaria geniculata</i>	0.3	0.3	0.3
<i>Smilax bona-nox</i>	1.4	0.8	1.4
<i>Smilax laurifolia</i>	0.6	0.0	0.0
<i>Solidago odora</i>	0.8	0.6	0.6
<i>Solidago stricta</i>	0.6	0.6	1.1
<i>Spartina patens</i>	32.5	18.5	10.3
<i>Toxicodendron radicans</i>	2.2	1.0	1.4
Removal (n = 18)	0.0	0.0	0.0
<i>Ampelopsis arborea</i>	0.0	0.0	0.1
<i>Andropogon glomeratus</i>	0.0	0.0	0.1
<i>Andropogon virginicus</i>	1.7	2.5	3.0
<i>Centella asiatica</i>	0.0	0.3	0.3
<i>Dichanthelium</i> sp.	3.9	4.2	4.0
<i>Eleocharis</i> sp.	0.0	0.0	0.1
<i>Eupatorium serotinum</i>	0.3	0.0	0.3
<i>Euthamia</i> sp.	0.3	0.7	0.0
<i>Imperata cylindrica</i>	4.2	10.4	9.6
<i>Ipomea sagitata</i>	1.4	0.6	0.8
<i>Juncus roemerianus</i>	2.8	3.2	2.5
<i>Panicum virgatum</i>	6.9	5.4	4.4
<i>Rubus argutus</i>	5.0	2.5	3.2

	2011	2012	2013
<i>Scleria</i> sp.	0.0	0.1	0.3
<i>Setaria geniculata</i>	0.0	0.0	0.4
<i>Smilax bona-nox</i>	0.6	0.3	0.3
<i>Solidago odora</i>	2.5	0.6	1.4
<i>Solidago stricta</i>	1.1	0.3	0.3
<i>Spartina patens</i>	39.2	22.2	18.1
<i>Toxicodendron radicans</i>	8.3	2.6	4.0

Appendix C. Point centered quarter data from experimental transects at GBNERR. Tag ID's are those of *P. borbonia* trees ≥ 2.5 cm dbh.

Transect	Tag ID	Distance	DBH 1	DBH 2	DBH 3	DBH 4	Size Class	Quadrant
1	1001	1.62	5.4				1.000	NE
1	1002	3.74	5.9				1.000	SE
1	1003	8.81	7.5				2.000	SW
1	1004	0.63	4.8	2.5			1.000	NW
1	1101	8.97	2.6	2.5			1.000	NE
1	1102	20.02	4.3				1.000	SE
1	1103	6.24	2.7				1.000	SW
1	1104	8.67	3.5				1.000	NW
1	1201	7.72	4.8				1.000	NE
1	1202	6.98	4.3				1.000	SE
1	1203	3.69	4.4				1.000	SW
1	1204	7.82	3.4	2.7			1.000	NW
1	1301	9.98	4.1				1.000	NE
1	1302	2.84	4.7				1.000	SE
1	1303	4.88	8.2	6.0			2.000	SW
1	1304	2.33	4.1				1.000	NW
1	1401	9.81	13.3				3.000	NE
1	1402	12.17	3.8				1.000	SE
1	1403	6.44	2.8				1.000	SW
1	1404	1.73	5.0				1.000	NW
1	1501	4.36	8.9	9.7			3.000	NE
1	1502	3.08	9.2				2.000	SE
1	1503	5.31	4.4				1.000	SW
1	1504	3.6	9.8	11.8			3.000	NW
1	1601	10.64	8.8				2.000	NE
1	1602	2.73	5.0				1.000	SE
1	1603	0.43	4.8	3.4			1.000	SW
1	1604	10.81	7.7				2.000	NW
1	1701	8.32	10.5				2.000	NE
1	1702	5.75	11.5	9.6			3.000	SE
1	1703	3.28	4.5				1.000	SW
1	1704	6.73	2.9				1.000	NW
1	1801	36.12	13.7				3.000	NE
1	1802	1.69	4.2				1.000	SE
1	1803	5.59	2.8				1.000	SW
1	1804	8.82	5.4				1.000	NW

Transect	Tag ID	Distance	DBH 1	DBH 2	DBH 3	DBH 4	Size Class	Quadrant
1	1901	7.91	4.5				1.000	NE
1	1902	4.4	3.7				1.000	SE
1	1903	4.02	5.7				1.000	SW
1	1904	1.94	5.3				1.000	NW
1	11001	3.1	6.3				1.000	NE
1	11002	9.29	3.0				1.000	SE
1	11003	8.1	3.2				1.000	SW
1	11003	2.58	4.7				1.000	NW
1	11101	2.15	2.9	10.2			2.000	NE
1	11102	5.58	4.3	4.3			1.000	SE
1	11103	4.45	4.3				1.000	SW
1	11103	1.41	3.5	4.6			1.000	NW
1	11201	7.88	4.7				1.000	NE
1	11202	8.01	3.7				1.000	SE
1	11203	6.48	2.7	4.3	3.374		1.000	SW
1	11204	1.27	2.9				1.000	NW
1	11301	3.31	3.1				1.000	NE
1	11302	3.52	4.5				1.000	SE
1	11303	9.51	3.1				1.000	SW
1	11304	5.19	3.5	3.0	9.549		2.000	NW
2	2001	2.76	8.2				2.000	NE
2	2002	1.54	5.6				1.000	SE
2	2003	14.9	4.0				1.000	SW
2	2004	3.86	4.4				1.000	NW
2	2101	4.89	7.2	3.7	3.0		2.000	NE
2	2102	34.27	2.9				1.000	SE
2	2103	6.9	2.7	2.3	3.0		1.000	SW
2	2104	1.5	2.8				1.000	NW
2	2201	3.23	2.9				1.000	NE
2	2202	3.56	4.2	2.8			1.000	SE
2	2203	5.28	8.5				2.000	SW
2	2204	3.95	3.0				1.000	NW
2	2301	4.34	5.8				1.000	NE
2	2302	3.23	3.8				1.000	SE
2	2303	2.29	15.0				3.000	SW
2	2304	3.42	13.2				3.000	NW
2	2401	3.17	9.5	3.0			2.000	NE
2	2402	6.57	4.0				1.000	SE
2	2403	3.24	7.9				2.000	SW
2	2404	3.41	4.5				1.000	NW

Transect	Tag ID	Distance	DBH 1	DBH 2	DBH 3	DBH 4	Size Class	Quadrant
2	2501	0.92	2.9	3.3			1.000	NE
2	2502	8.47	7.6				2.000	SE
2	2503	9.17	3.6				1.000	SW
2	2504	5.2	3.2				1.000	NW
2	2601	4.21	2.6	2.5			1.000	NE
2	2602	7.1	13.3				3.000	SE
2	2603	2.22	4.5				1.000	SW
2	2604	5.53	2.5				1.000	NW
2	2701	0.65	5.0				1.000	NE
2	2702	6.02	7.1				1.000	SE
2	2703	7.12	15.7				3.000	SW
2	2704	4.51	3.9				1.000	NW
2	2801	8.73	5.2				1.000	NE
2	2802	5.99	9.0				2.000	SE
2	2803	6.76	9.8				2.000	SW
2	2804	2.98	3.3				1.000	NW
2	2901	2.19	6.6				1.000	NE
2	2902	14.54	9.2				2.000	SE
2	2903	2.14	4.0				1.000	SW
2	2904	2.61	3.0				1.000	NW
2	21001	3.33	2.7				1.000	NE
2	21002	4.16	9.8	7.3	5.3		3.000	SE
2	21003	4.74	4.4				1.000	SW
2	21004	11.03	6.9	4.3			2.000	NW
2	21101	1.12	3.3				1.000	NE
2	21102	2.96	5.1				1.000	SE
2	21103	5.74	3.8				1.000	SW
2	21104	4.87	3.8	3.2	2.8		1.000	NW
2	21201	5.57	11.3				2.000	NE
2	21202	9.88	4.8				1.000	SE
2	21203	6.37	5.0				1.000	SW
2	21204	5.53	4.1	7.9	5.1	2.5	2.000	NW
2	21301	4.38	2.6				1.000	NE
2	21302	4.71	2.5				1.000	SE
2	21303	5.95	7.6				2.000	SW
2	21304	4.12	10.8	7.1			3.000	NW
3	3001	7.78	7.5				2.000	NE
3	3002	8.46	5.6				1.000	SE
3	3003	5.49	4.8				1.000	SW
3	3004	5.13	3.4				1.000	NW

Transect	Tag ID	Distance	DBH 1	DBH 2	DBH 3	DBH 4	Size Class	Quadrant
3	3101	2.39	2.5				1.000	SE
3	3102	2.18	3.1				1.000	SE
3	3103	6.82	4.0				1.000	SW
3	3104	4.5	7.7				2.000	NW
3	3201	2.07	2.8				1.000	NE
3	3202	5.21	2.7				1.000	SE
3	3203	4.63	2.8				1.000	SW
3	3204	1.86	8.8				2.000	NW
3	3301	3.31	2.8				1.000	NE
3	3302	4.56	4.5				1.000	SE
3	3303	2.87	4.4				1.000	SW
3	3304	2.93	2.8				1.000	NW
3	3401	2.43	7.8	8.2			2.000	NE
3	3402	3.41	3.6				1.000	SE
3	3403	7.47	3.9				1.000	SW
3	3404	4.39	4.2				1.000	NW
3	3501	4.02	4.2				1.000	NE
3	3502	4.08	2.9				1.000	SE
3	3503	4.51	3.2				1.000	SW
3	3504	6.03	4.8				1.000	NW
3	3601	7.2	9.6				2.000	NE
3	3602	6.08	5.8				1.000	SE
3	3603	1.52	6.9				1.000	SW
3	3604	4.82	7.4	4.1			2.000	NW
3	3701	1.5	6.1				1.000	NE
3	3702	2.45	6.2				1.000	SE
3	3703	1.98	8.1				2.000	SW
3	3704	6.75	5.5				1.000	NW
3	3801	6.23	3.7				1.000	NE
3	3802	4.47	3.5				1.000	SE
3	3803	12.05	2.5				1.000	SW
3	3804	2.68	2.5				1.000	NW
3	3901	13.91	2.7				1.000	NE
3	3902	19.74	4.1	6.5			2.000	SE
3	3903	6.71	2.9				1.000	SW
3	3904	12.28	5.9	3.4			1.000	NW
3	31001	5.8	9.0				2.000	NE
3	31002	7.65	8.1	2.9			2.000	SE
3	31003	2.38	3.2				1.000	SW
3	31004	13.74	11.6				2.000	NW

Transect	Tag ID	Distance	DBH 1	DBH 2	DBH 3	DBH 4	Size Class	Quadrant
3	31101	4.6	17.7				4.000	NE
3	31102	2.75	6.2	9.1			2.000	SE
3	31103	4.33	11.6				2.000	SW
3	31104	12.23	3.4				1.000	NW
3	31201	3.51	4.3				1.000	NE
3	31202	2.09	7.0				1.000	SE
3	31203	4.89	6.4				1.000	SW
3	31204	7.36	4.0	6.5			2.000	NW
3	31301	0.44	6.6				1.000	NE
3	31302	1.53	4.7				1.000	SE
3	31303	3.05	4.3	4.4			1.000	SW
3	31304	4.42	5.8				1.000	NW

Appendix D. Diameter at breast height of all *P. borbonia* trees ($\text{dbh} \geq 2.5$ cm) within treatment (removal) and control plots. Each row represents a different individual with one or more stems.

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
1303	Treatment	8.2	6		
1303	Treatment	4.7			
1303	Treatment	4.4			
1303	Treatment	5.9	3.3		
1303	Treatment	2.5	3.9		
1303	Treatment	2.8			
1303	Treatment	5			
1303	Treatment	6			
1303	Treatment	5			
1303	Treatment	3.8			
1303	Treatment	4.1			
1303	Treatment	13.3			
1303	Treatment	4.4			
1303	Treatment	3.5	3		
1303	Treatment	5.5			
1303	Treatment	2.6			
1303	Treatment	8.9			
1303	Treatment	5.4			
1303	Treatment	3.5			
1303	Treatment	4.8			
1303	Treatment	5.7			
1303	Treatment	5.7			
1303	Treatment	3.7			
1303	Treatment	2.5			
1303	Treatment	5			
1303	Treatment	5.3			
1303	Treatment	2.6			
1303	Treatment	4.3			
1303	Treatment	3.1			
1303	Treatment	6.7			
1303	Treatment	6.4			
1303	Treatment	4.6			
1303	Treatment	5.3			
1303	Treatment	3.6			
1303	Treatment	2.6			
1303	Treatment	9.2	9.9		

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
1504	Treatment	10.3	12		
1504	Treatment	9.3			
1504	Treatment	7.7			
1504	Treatment	10.5			
1504	Treatment	5.2			
1504	Treatment	6.2			
1504	Treatment	3			
1504	Treatment	3.4			
1504	Treatment	4.4			
1504	Treatment	2.6			
1504	Treatment	4.2	5.5		
1504	Treatment	2.5			
1504	Treatment	2.8			
1504	Treatment	9.8			
1504	Treatment	3.6			
1504	Treatment	10	9.2		
1504	Treatment	3			
1504	Treatment	2.6			
1504	Treatment	6.6	3		
1504	Treatment	2.5	2.6		
1504	Treatment	7.8			
1504	Treatment	4.9	2.6		
1504	Treatment	2.5			
1504	Treatment	2.6			
1504	Treatment	3	3.5	3.5	
1504	Treatment	3.3			
1504	Treatment	2.8	4.7		
1504	Treatment	3.6	4.2		
1504	Treatment	2.6			
1504	Treatment	4.5	5.2		
1504	Treatment	6			
1504	Treatment	5.8			
1504	Treatment	5.9			
1504	Treatment	5.2			
1504	Treatment	5			
1504	Treatment	3			
1504	Treatment	5.3			
1504	Treatment	5.5	2.7		
1703	Treatment	8			
1703	Treatment	8			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
1703	Treatment	11			
1703	Treatment	6.2			
1703	Treatment	4.8	2.6		
1703	Treatment	6.2			
1703	Treatment	9.5	11.5		
1703	Treatment	6.4			
1703	Treatment	3.1			
1703	Treatment	4.6			
1703	Treatment	3	3.4	3.4	
1703	Treatment	4.5	2.5		
1703	Treatment	3.2			
1703	Treatment	4.7			
1703	Treatment	4			
1703	Treatment	3.1			
1703	Treatment	4.7			
1703	Treatment	9.9			
1703	Treatment	3.6			
1703	Treatment	4.7			
1703	Treatment	3.2			
1703	Treatment	5.5			
1703	Treatment	3.4			
1703	Treatment	2.5			
1703	Treatment	2.5	3.7		
1703	Treatment	5.5			
1703	Treatment	2.5			
1703	Treatment	4.2			
1703	Treatment	2.6			
1703	Treatment	2.7	3.7		
1703	Treatment	2.8			
1703	Treatment	5.4			
1703	Treatment	4.8			
11103	Treatment	3.8	4.3		
11103	Treatment	5.4	4.1		
11103	Treatment	10.6	2.9		
11103	Treatment	2.8			
11103	Treatment	3.5			
11103	Treatment	2.9			
11103	Treatment	4.9	4.4		
11103	Treatment	3.8			
11103	Treatment	2.7			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
11103	Treatment	3.5	3.2	2.9	3.5
11103	Treatment	4.8			
11103	Treatment	3.4			
11103	Treatment	3.1			
11103	Treatment	4.4	5.3	2.5	
11103	Treatment	8.2			
11103	Treatment	5.7			
11103	Treatment	4.2			
11103	Treatment	3			
11103	Treatment	10.2			
11103	Treatment	6			
11103	Treatment	3.5			
11103	Treatment	3.7			
11103	Treatment	3.2	5	8.3	3.5
11103	Treatment	8			
11103	Treatment	4.7			
11103	Treatment	6.7			
11103	Treatment	5.1			
11103	Treatment	2.8			
11103	Treatment	3.3			
11103	Treatment	5.2			
11103	Treatment	4.3			
11103	Treatment	7.3			
11103	Treatment	2.8			
11103	Treatment	4			
11103	Treatment	4.4	4	3.9	
11103	Treatment	2.5			
11103	Treatment	3.8			
11103	Treatment	3.8			
11103	Treatment	4.7	4.5		
11103	Treatment	3.3			
11103	Treatment	4.7			
11103	Treatment	2.8			
11103	Treatment	4.4			
11103	Treatment	5.7	4.7	4.2	
11103	Treatment	2.6			
11103	Treatment	2.8			
11103	Treatment	4.2			
11103	Treatment	4.5			
11103	Treatment	2.8			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
11103	Treatment	4.1	3.8		
11103	Treatment	4.5			
11103	Treatment	4.5			
11103	Treatment	5.7			
11103	Treatment	10.3	9.6		
11103	Treatment	4			
11103	Treatment	4.9	2.5		
11103	Treatment	2.9			
4104	Treatment	5			
4104	Treatment	3.8			
4104	Treatment	2.9			
4104	Treatment	6.6			
4104	Treatment	5.4			
4104	Treatment	3.5	2.7		
4104	Treatment	5			
4104	Treatment	11.5	3		
4104	Treatment	4			
4104	Treatment	5.8			
4104	Treatment	5.7			
4104	Treatment	12.1			
4104	Treatment	18.6			
4104	Treatment	2.6	2.5		
4104	Treatment	16.2			
4104	Treatment	4.5			
4104	Treatment	4.3	4		
4104	Treatment	2.5			
4104	Treatment	5			
4104	Treatment	5.3			
4104	Treatment	2.8			
4104	Treatment	6			
4104	Treatment	11.6			
4104	Treatment	3.1	3.6	9.8	
4104	Treatment	16.8			
4104	Treatment	13.7			
4104	Treatment	6.8			
4104	Treatment	4.5			
4104	Treatment	3.3			
4104	Treatment	3.7			
4104	Treatment	3.7			
4104	Treatment	2.6			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
4104	Treatment	12			
4104	Treatment	10.6			
4104	Treatment	14.6			
4104	Treatment	3.8			
4104	Treatment	5.7			
4104	Treatment	3			
4104	Treatment	12.7	12		
4104	Treatment	13.3			
4104	Treatment	3.2			
4104	Treatment	3.7			
4104	Treatment	3.1			
4104	Treatment	3.5			
4104	Treatment	3.5			
4104	Treatment	5.2	3.1		
4104	Treatment	2.9	4.6		
4104	Treatment	3.4			
4104	Treatment	3.5			
4104	Treatment	4.1			
4502	Treatment	5.1			
4502	Treatment	5.1			
4502	Treatment	3.5			
4502	Treatment	5.5			
4502	Treatment	5.8			
4502	Treatment	6.2			
4502	Treatment	5.2			
4502	Treatment	4.4			
4502	Treatment	2.6			
4502	Treatment	13.1			
4502	Treatment	6.3	4.3		
4502	Treatment	9.1	4.2		
4502	Treatment	8.4			
4502	Treatment	6			
4502	Treatment	7.5	3.5		
4502	Treatment	5.7			
4502	Treatment	2.5			
4502	Treatment	2.5			
4502	Treatment	2.5			
4502	Treatment	3.2			
4502	Treatment	2.5			
4502	Treatment	5			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
4502	Treatment	2.7			
4502	Treatment	3			
4502	Treatment	6			
4502	Treatment	4.5			
4502	Treatment	7.4			
4502	Treatment	4.8			
4502	Treatment	5.3			
4502	Treatment	4.7			
4502	Treatment	4.5			
4502	Treatment	2.9			
4502	Treatment	3.5			
4502	Treatment	5.3			
4502	Treatment	9.5			
4502	Treatment	8.2			
4502	Treatment	7.3			
4502	Treatment	2.6			
4502	Treatment	3.9			
4502	Treatment	3.3			
4502	Treatment	4.8			
4502	Treatment	3.8			
2301	Control	5.9			
2301	Control	4.4			
2301	Control	2.6			
2301	Control	3			
2301	Control	5			
2301	Control	3.4			
2301	Control	5.4			
2301	Control	2.6			
2301	Control	5.1			
2301	Control	3.4			
2301	Control	12.7			
2301	Control	5.8			
2301	Control	3			
2301	Control	15.8			
2301	Control	3.2			
2301	Control	3.9			
2301	Control	2.8			
2301	Control	2.5			
2301	Control	4.5			
2301	Control	3.2			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
2301	Control	2.7			
2301	Control	6.4			
2301	Control	4.2			
2301	Control	2.6			
2301	Control	3.1			
2301	Control	8.9			
2301	Control	3.7	3.2		
2301	Control	3.3			
2301	Control	2.6			
2301	Control	3.7	5.2		
2301	Control	5			
2301	Control	2.7			
2301	Control	2.7	4.6		
2301	Control	2.8			
2301	Control	11.8			
2301	Control	6.1			
2301	Control	9.8			
2301	Control	4.1			
2301	Control	2.6			
2301	Control	4.5			
2301	Control	4			
2301	Control	3.6	2.9		
2301	Control	8.4			
2301	Control	4.7			
2301	Control	9.8	3.1		
2301	Control	5.3			
2301	Control	2.8			
2301	Control	3.7			
2301	Control	2.6			
2301	Control	4.2			
2301	Control	7.3			
2301	Control	3.9			
2301	Control	4.3			
2301	Control	4.7			
2301	Control	3.1			
2301	Control	3.8			
2301	Control	5.5	4.5		
2301	Control	4.4			
2301	Control	3.8			
2301	Control	2.6	3.6	3.8	

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
2301	Control	3.7	6		
2301	Control	4			
2301	Control	4.3	2.8		
21001	Control	10.2	7.4		
21001	Control	5.3	5.2		
21001	Control	2.8			
21001	Control	3.9			
21001	Control	3.9			
21001	Control	4.4			
21001	Control	2.7			
21001	Control	5			
21001	Control	6.4			
21001	Control	4.2			
21001	Control	3.2			
21001	Control	4.3			
21001	Control	6.5			
21001	Control	5.3			
21001	Control	3.2			
21001	Control	4.1	6		
21001	Control	2.6			
21001	Control	2.6			
21001	Control	3.5			
21001	Control	2.8	3.5	4.1	
21001	Control	3.7			
21001	Control	3.3			
21001	Control	10.2			
21001	Control	9.5			
21001	Control	5.2			
21001	Control	14.2			
21001	Control	3.5			
21001	Control	3.7			
21001	Control	4			
21001	Control	2.7			
21001	Control	5.5			
21001	Control	3.4			
21001	Control	3.9	2.8		
21001	Control	3.3			
21001	Control	5.6			
21001	Control	4.5			
21001	Control	3.7			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
21001	Control	3.7			
21001	Control	4.5			
21001	Control	3			
21001	Control	3.4			
21001	Control	5.7			
21001	Control	5.5			
21001	Control	7.1	4		
21001	Control	4.2			
21001	Control	5.3			
21001	Control	5.5	5.8		
21001	Control	4			
21001	Control	7.2			
21001	Control	4.4			
21001	Control	2.6			
21201	Control	11.2			
21201	Control	5.6			
21201	Control	4.5			
21201	Control	3.7			
21201	Control	3.7			
21201	Control	2.5			
21201	Control	2.5			
21201	Control	4.5			
21201	Control	3			
21201	Control	7	5.2		
21201	Control	3.4			
21201	Control	3.4			
21201	Control	3.9	2.8		
21201	Control	5.3			
21201	Control	3.3			
21201	Control	3.8			
21201	Control	2.5			
21201	Control	5.1			
21201	Control	8.6	11		
21201	Control	4.3			
21201	Control	3			
21201	Control	4.8	4.9		
21201	Control	6	4.3		
21201	Control	3.6			
21201	Control	3.7			
21201	Control	5.2			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
21201	Control	7.7			
21201	Control	2.8			
21201	Control	3.9	2.5		
21201	Control	5.1			
21201	Control	4.3	5.5	8.3	
21201	Control	2.8			
21201	Control	11.2	7.5		
21201	Control	6.1	3.2		
21201	Control	3.3			
21201	Control	2.6			
21201	Control	3.3			
21201	Control	3.5			
21201	Control	6			
21201	Control	4.2	3.5		
21201	Control	3.7	6.3	4	
21201	Control	7.1			
21201	Control	7.5	10.2		
21201	Control	3.7			
21201	Control	5.7			
21201	Control	5.2			
21201	Control	7.1	4		
21201	Control	2.9			
21201	Control	5.2	4.3		
5001	Control	11.2			
5001	Control	3			
5001	Control	2.5			
5001	Control	2.8			
5001	Control	10.2			
5001	Control	3.9			
5001	Control	2.8			
5001	Control	3.1			
5001	Control	3.4			
5001	Control	2.5			
5001	Control	3.7			
5001	Control	2.5			
5001	Control	5.8	2.8		
5001	Control	3.2			
5001	Control	3.3			
5001	Control	10.1	7.1	3	
5001	Control	3.1			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
5001	Control	2.8			
5001	Control	2.6			
5001	Control	3.3			
5001	Control	2.6			
5001	Control	3.6			
5001	Control	2.6			
5001	Control	2.6			
5001	Control	2.6			
5001	Control	4.3	5.5	8.3	
5001	Control	3.6	3.7	2.7	
5001	Control	4.2			
5001	Control	4.6			
5001	Control	3.5			
5001	Control	2.6			
5001	Control	2.8			
5001	Control	4.5			
5001	Control	7.9			
5001	Control	6.1	4		
5001	Control	4.9			
5001	Control	4.2			
5001	Control	2.8			
5001	Control	3.7			
5001	Control	3			
5001	Control	2.7			
5001	Control	4.1			
5001	Control	12.8			
5001	Control	2.6			
5001	Control	5.4			
5001	Control	3.4			
5001	Control	9.3			
5001	Control	3.5			
5001	Control	3.9			
5001	Control	4			
5001	Control	2.7			
5001	Control	2.8			
5001	Control	3.3	4.8		
5001	Control	8.5	6.2		
5001	Control	5.2			
5001	Control	5.7			
5001	Control	5	7.5		

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
5001	Control	5			
5001	Control	5			
5001	Control	2.8			
5001	Control	7.6			
5001	Control	4	2.5		
5203	Control	2.2	1.8	2.6	
5203	Control	2.9			
5203	Control	3.1			
5203	Control	4.2	2.4		
5203	Control	3.7			
5203	Control	6.6	4.3		
5203	Control	2.8			
5203	Control	10.4			
5203	Control	2.7			
5203	Control	6			
5203	Control	8.6			
5203	Control	3.2			
5203	Control	6			
5203	Control	4.3			
5203	Control	4.7			
5203	Control	5.7			
5203	Control	7.9			
5203	Control	3.6			
5203	Control	4			
5203	Control	3.8			
5203	Control	3.9			
5203	Control	11	2.5		
5203	Control	9.5			
5203	Control	13.3			
5203	Control	2.7			
5203	Control	2.6			
5203	Control	5.4			
5203	Control	9.3			
5203	Control	3.7			
5203	Control	2.8			
5203	Control	4.6			
5203	Control	2.8			
5203	Control	3.1			
5203	Control	3.6			
5203	Control	3.7			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
5203	Control	2.6	2.9		
5203	Control	4.4			
5203	Control	2.9			
5203	Control	3.1			
5203	Control	4.1			
5203	Control	4.1			
5203	Control	2.8			
5203	Control	5.2			
5203	Control	3.3			
5203	Control	2.6	2.5		
5203	Control	3.2			
5203	Control	2.6			
5203	Control	5.4			
5203	Control	3.9			
5203	Control	3.7			
5203	Control	4.4			
5203	Control	3.3			
5203	Control	9.5			
5203	Control	13			
5203	Control	4			
5203	Control	2.6			
5203	Control	3.3			
5203	Control	5.6			
51001	Control	2.6			
51001	Control	6.2			
51001	Control	3.7			
51001	Control	2.6			
51001	Control	2.5			
51001	Control	5			
51001	Control	3.2			
51001	Control	5.6			
51001	Control	3.2			
51001	Control	3.7			
51001	Control	3.2			
51001	Control	5.9			
51001	Control	6.6			
51001	Control	6.4			
51001	Control	2.8			
51001	Control	4.3	2.8		
51001	Control	3.8			

Plot	Plot type	dbh1	dbh2	dbh3	dbh4
51001	Control	2.8			
51001	Control	6.1			
51001	Control	8.8			
51001	Control	4.2			
51001	Control	9.5			
51001	Control	4.5			
51001	Control	2.6			
51001	Control	4.3			
51001	Control	4.1			
51001	Control	3.4			
51001	Control	3.1			
51001	Control	7.3			
51001	Control	4.6	5.3		
51001	Control	5.8			
51001	Control	2.6			
51001	Control	2.9			
51001	Control	3.5			
51001	Control	4			
51001	Control	5.7			
51001	Control	2.6			
51001	Control	2.9			
51001	Control	4.8			
51001	Control	3.8			
51001	Control	5			
51001	Control	3.7			
51001	Control	3.4			
51001	Control	3.2			
51001	Control	2.8			
51001	Control	2.7			
51001	Control	2.7			
51001	Control	3.5			
51001	Control	3.1			
51001	Control	2.5			
51001	Control	6.1			
51001	Control	2.9			
51001	Control	4.6			
51001	Control	3.8			
51001	Control	3.2			
51001	Control	4.8			

Appendix E. Percent transmittance of light on treatment and control subplots in 2012 and 2014.

Values were determined from analysis of canopy photos using Gap Light Analyzer software.

Subplot	Plot type	% T (2012)	% T (2014)
801	Treatment	40.31	40.68
802	Treatment	49.93	38.08
803	Treatment	39.64	48.26
804	Treatment	52.71	51.32
805	Treatment	51.72	51.35
806	Treatment	55.2	49.6
807	Treatment	47.3	50.05
808	Treatment	53.3	52.57
809	Treatment	52.88	53.54
810	Treatment	46.25	38.18
811	Treatment	49	51.45
812	Treatment	37.09	38.14
813	Treatment	50.64	44.73
814	Treatment	57.76	55.13
815	Treatment	53.73	50
816	Treatment	48.59	52.35
817	Treatment	41.24	41.19
818	Treatment	44.09	47.91
819	Control	27.4	26.84
820	Control	33.1	31.29
821	Control	21.93	24.42
822	Control	36.36	34.43
823	Control	29.73	30.6
824	Control	40.41	29.72
825	Control	32.53	35.19
826	Control	29.94	25.7
827	Control	32.47	32.86
828	Control	31.95	39.61
829	Control	34.3	33.94
830	Control	33.14	32
831	Control	33.72	41.47
832	Control	30.97	32.96
833	Control	42.53	40.31
834	Control	25.1	29.14
835	Control	26.53	24.12
836	Control	27.79	32.53

Appendix F. Sprouting data from 2012 for all girdled *P. borbonia* trees on treatment plots. Each row represents a different individual.

Plot	Tree ID	# of sprouts	Longest Sprout			Initial Tree Basal Area (cm ²)
			BD (cm)	DBH (cm)	Length (cm)	
1303	1203	6	0.7		41	15.21
1303	1302	4	0.8	0.5	72	17.35
1303	1303	11	0.7	0.3	56	81.08
1303	1304	35	0.6		34	13.20
1303	1402	10	0.5		34	11.34
1303	1303x1	27	0.9	0.5	72	35.89
1303	1303x2	23	0.4		31	16.85
1303	1303x3	8	0.4		33	6.16
1303	1303x4	15	1	0.3	87	19.63
1303	1303x5	7	0.6		64	28.27
1303	1303x6	12	0.6	0.3	56	19.63
1504	1403	12	0.5		40	6.16
1504	1501	33	1.2	0.5	113	136.11
1504	1502	12	1	0.3	49	66.48
1504	1503	29	0.5		48	15.21
1504	1504	48	0.8	0.4	58	184.79
1504	1601	15	1.2	0.5	129	60.82
1504	1602	3	0.8		79	19.63
1504	1603	14	0.7		88	27.17
1504	1504x1	6	1	0.4	77	5.73
1504	1504x2	37	0.8	0.4	65	32.81
1504	1504x3	10	0.5		47	9.96
1504	1504x4	15	0.9	0.3	71	4.91
1504	1504x5	18	0.5		43	6.61
1504	1504x6	12	0.6		49	5.73
1504	1504x7	11	0.5		45	8.04
1703	1702	40	1	0.3	75	176.25
1703	1703	4	0.8	0.3	77	15.90
1703	1704	7	0.4		52	6.61
1703	1802	14	1.1	0.7	116	13.85
1703	1703x1	8	1	0.3	71	33.18
1703	1703x10	9	0.8		78	8.55
1703	1703x2	18	0.8		54	14.52
1703	1703x3	20	0.9	0.5	84	13.85

1703	1703x5	6		0.7		61		10.75
1703	1703x6	3		0.5		31		11.34
1703	1703x8	8		0.9		60		12.57
1703	1703x9	16		1	0.3	92		60.82
4104	4101	36		0.7	0.4	76		105.68
4104	4102	15		0.6		42		7.07
4104	4103	26		0.6	0.3	37		18.86
4104	4104	24		0.6		49		14.52
4104	4201	4		0.7		56		21.24
4104	4202	17		0.9	0.3	62		106.01
4104	4204	4		1.1	0.3	105		307.91
4104	4104x1	6		0.7	0.3	45		27.34
4104	4104x2	8		0.5		49		11.34
4104	4104x3	7		0.6	0.3	47		4.52
4104	4104x4	19		0.7		59		5.31
4104	4104x5	9		1.1	0.3	65		16.62
4104	4104x6	8		0.8		45		10.18
4104	4104x7	4		0.4		17		19.63
4502	4402	39		0.7	0.2	66		37.52
4502	4403	6		1.4		62		82.83
4502	4404	11		0.8	0.4	63		16.65
4502	4501	4		0.5		39		12.57
4502	4502	23		0.6		52		16.62
4502	4503	15		1.1		88		31.17
4502	4502x1	11		0.5		42		17.35
4502	4502x2	12		1.3	0.4	84		128.68
4502	4502x3	12		0.6		45		4.15
4502	4502x4	13		0.8		41		22.06
4502	4502x5	13		0.9		56		8.04
4502	4502x6	8		1.2	0.4	88		21.24
11103	11001	19		1.1		47		94.85
11103	11003	3		0.6		66		13.85
11103	11004	10		0.9		71		36.10
11103	11102	20		0.9		57		29.04
11103	11103	7		1.1		77		14.52
11103	11201	15		1.2	0.8	95		17.35
11103	11202	31		0.6		58		10.75
11103	11103x1	5		1		70		50.27
11103	11103x10	10		0.7	0.2	55		6.61
11103	11103x11	32		1	0.3	53		44.71
11103	11103x12	10		0.7	0.2	73		10.18

11103	11103x13	12		0.7	0.3	60		12.57
11103	11103x2	8		0.4		29		6.16
11103	11103x3	10		0.7		57		15.90
11103	11103x4	7		0.9		80		9.62
11103	11103x5	12		0.7	0.2	57		7.07
11103	11103x7	5		0.9	0.7	117		13.85
11103	11103x8	11		0.5		34		33.89
11103	11103x9	4		0.4		30		6.16

Appendix G. Sprouting data from 2013 for all girdled *P. borbonia* trees on treatment plots. Each row represents a different individual.

Plot	Tree ID	# of sprouts	Longest Sprout					Initial Tree Basal Area
			BD	DBH1	DBH2	DBH3	DBH 4	
1303	1203	6	1	0.3				15.21
1303	1302	4	1.6	0.7	0.7			17.35
1303	1303	11	1.2	0.7				81.08
1303	1304	22	0.9	0.3				13.2
1303	1402	15	0.7	0.4				11.34
1303	1303x1	17	1.2	0.3				35.89
1303	1303x2	3	0.9					16.85
1303	1303x3	10	0.5					6.16
1303	1303x4	10	1.7	0.7				19.63
1303	1303x5	9	1.3	0.4				28.27
1303	1303x6	12	0.8	0.5				19.63
1504	1403	8	0.6					6.16
1504	1501	18	1.8	1.2	0.7	0.5		136.11
1504	1502	10	1.3	0.6				66.48
1504	1503	22	1.6	0.6	0.6	0.5		15.21
1504	1504	22	1.6	1.2				184.79
1504	1601	12	2.5	1.2	0.8	0.9		60.82
1504	1602	4	0.9					19.63
1504	1603	9	1.4	0.7				27.17
1504	1504x1	7	1.1	0.6				5.73
1504	1504x2	30	1.5	0.7				32.81
1504	1504x3	6	0.6					9.96
1504	1504x4	11	1.2	0.6				4.91
1504	1504x5	13	1	0.5				6.61
1504	1504x6	7	1	0.5				5.73
1504	1504x7	9	0.5					8.04
1703	1702	30	2.2	0.5	0.6			176.25
1703	1703	5	1.3	0.5	0.5			15.9
1703	1704	10	0.9					6.61
1703	1802	8	1.3	1.3				13.85
1703	1703x1	8	1.6	0.5				33.18
1703	1703x10	7	1.3	0.4				8.55
1703	1703x2	12	1.9	0.8	0.7	0.6		14.52
1703	1703x3	14	1.1	0.4				13.85

1703	1703x4	6		1.6	0.6				7.55
1703	1703x5	4		1.3	0.5				10.75
1703	1703x6	5		1.3	0.4				11.34
1703	1703x7	5		2.4	1.2	0.5	0.5		8.04
1703	1703x8	6		2	0.3				12.57
1703	1703x9	14		1.9	1	0.6			60.82
4104	4101	24		2.2	1.4	0.7			105.68
4104	4102	18		0.9					7.07
4104	4103	23		0.8	0.3				18.86
4104	4104	17		1.2	0.5	0.5			14.52
4104	4201	5		1.7	0.7				21.24
4104	4202	17		1.9	1.2	0.5			106.01
4104	4204	11		2.9	1.2	1.3			307.91
4104	4104x1	5		1.4	1	0.7			27.34
4104	4104x2	6		1.4	0.3				11.34
4104	4104x3	5		1	0.5				4.91
4104	4104x4	15		1.2	0.3				5.31
4104	4104x5	8		1.7	0.7	0.6	0.5		16.62
4104	4104x6	7		1.2	0.4				10.18
4104	4104x7	14		1.2	0.6				19.63
4502	4402	35		1.7	0.9				37.52
4502	4403	7		2.1	1.2	0.9	0.6		82.83
4502	4404	16		1.5	0.9	0.5	0.5		16.65
4502	4501	4		0.6					12.57
4502	4502	24		1.2					16.62
4502	4503	8		2.1	0.9	0.9	0.6		31.17
4502	4502x1	15		0.5					17.35
4502	4502x2	9		2.8	1	0.7	1.1	0.6	128.68
4502	4502x3	10		1.3	0.5				4.91
4502	4502x4	24		1.4	0.5				22.06
4502	4502x5	13		1.5	0.6				8.04
4502	4502x6	8		2.1	1	1	1.2	0.5	21.24
11103	11003	2		1					13.85
11103	11101	15		2.2	0.9	0.9	1		94.85
11103	11102	21		1.2	0.7				29.04
11103	11103	5		1.5	0.4				14.52
11103	11104	7		1.5	0.7	0.5			36.1
11103	11201	15		1.7	1	1.1			17.35
11103	11202	28		1.1					10.75
11103	11103x1	3		1.9	0.6				50.27
11103	11103x10	7		1	0.4				6.61

11103	11103x11	30		0.6					44.71
11103	11103x12	10		1.1	0.5				10.18
11103	11103x13	9		1.1	0.3				12.57
11103	11103x2	7		0.7					6.16
11103	11103x3	6		1.2	0.4				15.90
11103	11103x4	5		1.5	0.6	0.6	0.5		9.62
11103	11103x5	9		1.4	0.6	0.5			7.07
11103	11103x6	1		0.6					5.73
11103	11103x7	4		1.8	1.2	0.7			13.85
11103	11103x8	26		1	0.6				33.89
11103	11103x9	4		0.4					6.16

Appendix H. Sprouting data from 2014 for all girdled *P. borbonia* trees on treatment plots. Each row represents a different individual.

Plot	Tree ID	# of sprouts	Longest Sprout					Initial Tree Basal Area
			BD	DBH1	DBH2	DBH3	DBH 4	
1303	1203	5	1.8	1				15.21
1303	1302	3	2.1	1.1				17.35
1303	1303	11	1.7	1.2				81.08
1303	1304	19	1.5	0.9				13.2
1303	1402	10	1.2	0.5				11.34
1303	1303x1	23	1.7	0.7				35.89
1303	1303x2	1	1.7	0.7				16.85
1303	1303x3	7	0.9					6.16
1303	1303x4	10	2.3	1.4				19.63
1303	1303x5	7	1.2	0.7				28.27
1303	1303x6	11	1.2	0.9				19.63
1504	1403	9	1.4	0.4				6.16
1504	1501	20	2.8	2	1.2			136.11
1504	1502	11	2.3	1.3	1.1			66.48
1504	1503	14	2.5	1.8				15.21
1504	1504	16	2.1	1.5				184.79
1504	1601	13	3.3	1.6				60.82
1504	1602	4	1.2					19.63
1504	1603	10	1.9	1.2				27.17
1504	1504x1	5	1.7	1.1				5.73
1504	1504x2	18	2.4	1.3	0.8			32.81
1504	1504x3	6	1.2	0.4				9.96
1504	1504x4	13	1.6	0.8	0.8			4.91
1504	1504x5	9	1.6	0.8				6.61
1504	1504x6	7	1.1	0.7				5.73
1504	1504x7	7	1.1					8.04
1703	1702	9	2.3	1.6				176.25
1703	1703	3	1.5	1				15.9
1703	1704	3	1.4	0.5				6.61
1703	1802	5	2.1	1.4				13.85
1703	1703x1	6	2.3	1				33.18
1703	1703x10	6	1.6	0.6	0.5			8.55
1703	1703x2	10	2.6	1.6				14.52

1703	1703x3	12		2	1.1				13.85
1703	1703x4	4		2.5	1.4				7.55
1703	1703x5	3		1.9	1	0.7			10.75
1703	1703x6	2		2	0.7	0.6			11.34
1703	1703x7	3		2.8	1.6				8.04
1703	1703x8	6		2.5	0.6				12.57
1703	1703x9	8		2.8	1.9				60.82
4104	4101	13		3	2.2				105.68
4104	4102	13		1.4	0.7	0.6			7.07
4104	4103	21		1.3	0.8				18.86
4104	4104	13		2.3	1.3				14.52
4104	4201	3		2.3	1.4				21.24
4104	4202	16		2.7	2				106.01
4104	4204	9		4.3	2.2	2.2			307.91
4104	4104x1	3		2.1	1.6				27.34
4104	4104x2	7		1.9	1.2				11.34
4104	4104x3	4		1.6	0.9	0.7			4.91
4104	4104x4	7		2	0.9	1			5.31
4104	4104x6	6		1.9	1.3				10.18
4104	4104x7	13		1.9	1.3				19.63
4502	4402	22		2.5	1.6				37.52
4502	4403	7		2.6	1.8	1.1			82.83
4502	4404	13		2.3	1.7				16.65
4502	4501	2		0.7					12.57
4502	4502	20		2.2	1.1				16.62
4502	4503	1		3.1	1.8	1.8			31.17
4502	4502x1	13		1.6					17.35
4502	4502x2	8		3.9	2.3	2	1.7		128.68
4502	4502x3	7		1.9	1.2	0.6			4.91
4502	4502x4	24		2.2	1.2	0.8	0.6		22.06
4502	4502x5	7		1.7	0.9				8.04
4502	4502x6	8		2.8	1.7	1.2	1.5		21.24
11103	11003	2		1.3	0.4				13.85
11103	11101	12		3.4	2.4				94.85
11103	11102	14		1.8	1.4				29.04
11103	11103	6		2.2	1.2				14.52
11103	11104	6		2.3	1.2	1.1			36.1
11103	11201	7		2	1.5				17.35
11103	11202	9		1.7	1				10.75
11103	11103x1	3		2.4	1.4				50.27
11103	11103x10	7		1.2	0.4				6.61

11103	11103x11	22		0.7	0.3					44.71
11103	11103x12	8		1.9	1.3					10.18
11103	11103x13	8		1.7	1					12.57
11103	11103x2	7		1.3	0.7					6.16
11103	11103x3	5		1.3	0.6					15.90
11103	11103x4	3		2.1	1.3	0.7				9.62
11103	11103x5	5		2	1.3					7.07
11103	11103x6	1		0.7						5.73
11103	11103x7	3		2.4	2					13.85
11103	11103x8	23		1.4	1					33.89
11103	11103x9	3		0.3						6.16

Appendix I. Percent cover of herbaceous plant species on composition plots during each survey year.

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
2301	834	A	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
2301	834	A	Control	<i>Smilax bona-nox</i>	5	2.5	5
2301	834	A	Control	<i>Spartina patens</i>	35	2.5	2.5
2301	834	B	Control	<i>Euthamia sp.</i>	5	0	0
2301	834	B	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
2301	834	B	Control	<i>Panicum virgatum</i>	5	2.5	2.5
2301	834	B	Control	<i>Smilax bona-nox</i>	5	2.5	2.5
2301	834	B	Control	<i>Spartina patens</i>	25	10	5
2301	835	A	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
2301	835	A	Control	<i>Spartina patens</i>	5	2.5	2.5
2301	835	B	Control	<i>Juncus roemerianus</i>	0	0	2.5
2301	835	B	Control	<i>Panicum virgatum</i>	5	5	5
2301	835	B	Control	<i>Rubus argutus</i>	10	2.5	7.5
2301	835	B	Control	<i>Spartina patens</i>	0	5	2.5
2301	836	A	Control	<i>Euthamia sp.</i>	5	0	2.5
2301	836	A	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
2301	836	A	Control	<i>Rubus argutus</i>	5	2.5	5
2301	836	A	Control	<i>Smilax bona-nox</i>	5	2.5	5
2301	836	A	Control	<i>Spartina patens</i>	15	10	7.5
2301	836	B	Control	<i>Andropogon virginicus</i>	5	2.5	2.5
2301	836	B	Control	<i>Dichanthelium sp.</i>	5	0	0
2301	836	B	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
2301	836	B	Control	<i>Rubus argutus</i>	5	2.5	2.5
2301	836	B	Control	<i>Solidago sp.</i>	0	2.5	2.5
2301	836	B	Control	<i>Spartina patens</i>	25	15	12.5
2301	836	B	Control	<i>Toxicodendron radicans</i>	5	2.5	5
5001	825	A	Control	<i>Centella asiatica</i>	5	2.5	2.5
5001	825	A	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
5001	825	A	Control	<i>Panicum virgatum</i>	5	0	2.5
5001	825	A	Control	<i>Rhynchospora sp.</i>	5	0	2.5
5001	825	A	Control	<i>Rubus argutus</i>	5	2.5	2.5
5001	825	A	Control	<i>Spartina patens</i>	5	2.5	2.5
5001	825	B	Control	<i>Panicum virgatum</i>	5	0	2.5
5001	825	B	Control	<i>Rubus argutus</i>	5	2.5	2.5
5001	825	B	Control	<i>Spartina patens</i>	0	2.5	2.5
5001	826	A	Control	<i>Euthamia sp.</i>	5	2.5	0

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
5001	826	A	Control	<i>Panicum virgatum</i>	5	2.5	0
5001	826	A	Control	<i>Rubus argutus</i>	0	2.5	0
5001	826	A	Control	<i>Spartina patens</i>	15	10	5
5001	826	B	Control	<i>Panicum virgatum</i>	5	0	2.5
5001	826	B	Control	<i>Rubus argutus</i>	0	0	2.5
5001	826	B	Control	<i>Smilax bona-nox</i>	5	2.5	5
5001	826	B	Control	<i>Spartina patens</i>	15	20	7.5
5001	827	A	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
5001	827	A	Control	<i>Panicum virgatum</i>	5	2.5	2.5
5001	827	A	Control	<i>Rubus argutus</i>	5	0	0
5001	827	A	Control	<i>Solidago odora</i>	10	5	5
5001	827	A	Control	<i>Spartina patens</i>	15	5	5
5001	827	A	Control	<i>Toxicodendron radicans</i>	5	0	0
5001	827	B	Control	<i>Andropogon virginicus</i>	10	10	7.5
5001	827	B	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
5001	827	B	Control	<i>Panicum virgatum</i>	5	0	0
5001	827	B	Control	<i>Rubus argutus</i>	5	2.5	2.5
5001	827	B	Control	<i>Solidago odora</i>	0	2.5	0
5001	827	B	Control	<i>Solidago odora</i>	5	0	2.5
5001	827	B	Control	<i>Spartina patens</i>	10	10	2.5
5203	822	A	Control	<i>Panicum virgatum</i>	5	2.5	
5203	822	A	Control	<i>Rhynchospora sp.</i>	5	0	2.5
5203	822	A	Control	<i>Rubus argutus</i>	10	2.5	5
5203	822	A	Control	<i>Solidago stricta</i>	0	0	2.5
5203	822	A	Control	<i>Spartina patens</i>	10	5	2.5
5203	822	A	Control	<i>Toxicodendron radicans</i>	5	2.5	2.5
5203	822	B	Control	<i>Dichanthelium sp.</i>	5	0	0
5203	822	B	Control	<i>Panicum virgatum</i>	5	2.5	2.5
5203	822	B	Control	<i>Rubus argutus</i>	5	2.5	2.5
5203	822	B	Control	<i>Setaria geniculata</i>	5	5	5
5203	822	B	Control	<i>Solidago stricta</i>	0	2.5	2.5
5203	822	B	Control	<i>Spartina patens</i>	20	10	12.5
5203	823	A	Control	<i>Andropogon virginicus</i>	5	5	5
5203	823	A	Control	<i>Dichanthelium sp.</i>	5	0	0
5203	823	A	Control	<i>Rubus argutus</i>	5	0	0
5203	823	A	Control	<i>Spartina patens</i>	10	5	5
5203	823	B	Control	<i>Andropogon virginicus</i>	5	2.5	2.5
5203	823	B	Control	<i>Dichanthelium sp.</i>	0	0	2.5
5203	823	B	Control	<i>Rubus argutus</i>	5	2.5	2.5
5203	823	B	Control	<i>Smilax bona-nox</i>	5	2.5	2.5

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
5203	823	B	Control	<i>Solidago stricta</i>	5	0	2.5
5203	823	B	Control	<i>Spartina patens</i>	5	2.5	2.5
5203	824	A	Control	<i>Rubus argutus</i>	5	2.5	5
5203	824	A	Control	<i>Spartina patens</i>	35	10	7.5
5203	824	A	Control	<i>Toxicodendron radicans</i>	5	2.5	2.5
5203	824	B	Control	<i>Rubus argutus</i>	5	2.5	2.5
5203	824	B	Control	<i>Spartina patens</i>	35	15	12.5
5203	824	B	Control	<i>Toxicodendron radicans</i>	5	2.5	2.5
21001	831	A	Control	<i>Andropogon virginicus</i>	5	10	7.5
21001	831	A	Control	<i>Panicum virgatum</i>	5	5	5
21001	831	A	Control	<i>Spartina patens</i>	15	25	7.5
21001	831	B	Control	<i>Ampelopsis arborea</i>	0	0	2.5
21001	831	B	Control	<i>Andropogon virginicus</i>	10	10	10
21001	831	B	Control	<i>Dichanthelium sp.</i>	0	2.5	2.5
21001	831	B	Control	<i>Panicum virgatum</i>	5	0	2.5
21001	831	B	Control	<i>Solidago stricta</i>	0	2.5	2.5
21001	831	B	Control	<i>Spartina patens</i>	10	5	2.5
21001	832	A	Control	<i>Juncus roemerianus</i>	10	5	5
21001	832	A	Control	<i>Panicum virgatum</i>	5	2.5	2.5
21001	832	A	Control	<i>Rubus argutus</i>	5	2.5	2.5
21001	832	A	Control	<i>Spartina patens</i>	20	5	2.5
21001	832	B	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
21001	832	B	Control	<i>Panicum virgatum</i>	5	2.5	2.5
21001	832	B	Control	<i>Smilax bona-nox</i>	0	2.5	2.5
21001	832	B	Control	<i>Smilax laurifolia</i>	5	0	0
21001	832	B	Control	<i>Spartina patens</i>	15	5	5
21001	833	A	Control	<i>Andropogon virginicus</i>	5	2.5	5
21001	833	A	Control	<i>Dichanthelium aciculare</i>	5	0	0
21001	833	A	Control	<i>Dichanthelium ensifolium</i>	5	2.5	2.5
21001	833	A	Control	<i>Juncus roemerianus</i>	5	2.5	2.5
21001	833	A	Control	<i>Spartina patens</i>	20	15	5
21001	833	B	Control	<i>Andropogon virginicus</i>	5	0	2.5
21001	833	B	Control	<i>Panicum virgatum</i>	5	0	2.5
21001	833	B	Control	<i>Rubus argutus</i>	0	0	2.5
21001	833	B	Control	<i>Spartina patens</i>	5	2.5	2.5
21001	833	B	Control	<i>Toxicodendron radicans</i>	5	0	2.5
21201	828	A	Control	<i>Andropogon virginicus</i>	0	0	2.5
21201	828	A	Control	<i>Dichanthelium sp.</i>	0	2.5	2.5
21201	828	A	Control	<i>Juncus roemerianus</i>	5	5	2.5
21201	828	A	Control	<i>Spartina patens</i>	40	10	2.5

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
21201	828	A	Control	<i>Toxicodendron radicans</i>	5	2.5	2.5
21201	828	B	Control	<i>Andropogon virginicus</i>	10	15	15
21201	828	B	Control	<i>Dichanthelium sp.</i>	0	2.5	2.5
21201	828	B	Control	<i>Spartina patens</i>	30	15	5
21201	828	B	Control	<i>Toxicodendron radicans</i>	5	2.5	2.5
21201	829	A	Control	<i>Andropogon virginicus</i>	0	0	2.5
21201	829	A	Control	<i>Dichanthelium sp.</i>	5	2.5	2.5
21201	829	A	Control	<i>Dichanthelium sp.</i>	5	0	0
21201	829	A	Control	<i>Spartina patens</i>	10	5	5
21201	829	A	Control	<i>Toxicodendron radicans</i>	0	0	2.5
21201	829	B	Control	<i>Andropogon virginicus</i>	0	2.5	2.5
21201	829	B	Control	<i>Rubus argutus</i>	5	0	0
21201	829	B	Control	<i>Spartina patens</i>	0	2.5	2.5
21201	829	B	Control	<i>Toxicodendron radicans</i>	0	2.5	2.5
21201	830	A	Control	<i>Dichanthelium aciculare</i>	5	0	0
21201	830	A	Control	<i>Dichanthelium sp.</i>	0	2.5	2.5
21201	830	A	Control	<i>Juncus roemerianus</i>	5	5	5
21201	830	A	Control	<i>Panicum virgatum</i>	5	5	5
21201	830	A	Control	<i>Solidago sp.</i>	0	2.5	5
21201	830	A	Control	<i>Spartina patens</i>	35	45	5
21201	830	B	Control	<i>Dichanthelium sp.</i>	0	2.5	2.5
21201	830	B	Control	<i>Juncus roemerianus</i>	5	2.5	5
21201	830	B	Control	<i>Juncus sp.</i>	0	2.5	0
21201	830	B	Control	<i>Panicum virgatum</i>	5	5	2.5
21201	830	B	Control	<i>Rhynchospora sp.</i>	5	0	0
21201	830	B	Control	<i>Rubus argutus</i>	10	2.5	5
21201	830	B	Control	<i>Spartina patens</i>	15	35	20
51001	819	A	Control	<i>Dichanthelium sp.</i>	5	2.5	5
51001	819	A	Control	<i>Panicum virgatum</i>	5	2.5	2.5
51001	819	A	Control	<i>Rubus argutus</i>	5	2.5	2.5
51001	819	A	Control	<i>Smilax bona-nox</i>	0	0	2.5
51001	819	A	Control	<i>Spartina patens</i>	10	5	5
51001	819	B	Control	<i>Dichanthelium aciculare</i>	0	0	2.5
51001	819	B	Control	<i>Rubus argutus</i>	5	2.5	2.5
51001	819	B	Control	<i>Spartina patens</i>	5	2.5	2.5
51001	820	A	Control	<i>Rubus argutus</i>	10	2.5	7.5
51001	820	A	Control	<i>Spartina patens</i>	15	2.5	2.5
51001	820	B	Control	<i>Euthamia sp.</i>	5	2.5	2.5
51001	820	B	Control	<i>Panicum virgatum</i>	5	2.5	2.5
51001	820	B	Control	<i>Rubus argutus</i>	10	2.5	5

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
51001	820	B	Control	<i>Spartina patens</i>	30	5	5
51001	821	A	Control	<i>Panicum virgatum</i>	0	2.5	2.5
51001	821	A	Control	<i>Rubus argutus</i>	5	2.5	2.5
51001	821	A	Control	<i>Spartina patens</i>	25	2.5	2.5
51001	821	B	Control	<i>Panicum virgatum</i>	15	0	2.5
51001	821	B	Control	<i>Rubus argutus</i>	5	2.5	2.5
51001	821	B	Control	<i>Smilax laurifolia</i>	5	0	0
51001	821	B	Control	<i>Solidago stricta</i>	5	2.5	5
51001	821	B	Control	<i>Spartina patens</i>	5	2.5	2.5
1303	807	A	Removal	<i>Imperata cylindrica</i>	5	0	40
1303	807	A	Removal	<i>Ipomea sagitata</i>	5	2.5	2.5
1303	807	A	Removal	<i>Juncus roemerianus</i>	5	0	0
1303	807	A	Removal	<i>Rubus argutus</i>	5	2.5	2.5
1303	807	A	Removal	<i>Spartina patens</i>	15	10	2.5
1303	807	A	Removal	<i>Toxicodendron radicans</i>	10	2.5	2.5
1303	807	B	Removal	<i>Imperata cylindrica</i>	20	45	60
1303	807	B	Removal	<i>Ipomea sagitata</i>	5	2.5	2.5
1303	807	B	Removal	<i>Rubus argutus</i>	5	2.5	2.5
1303	807	B	Removal	<i>Spartina patens</i>	5	2.5	2.5
1303	807	B	Removal	<i>Toxicodendron radicans</i>	10	0	2.5
1303	817	A	Removal	<i>Andropogon glomeratus</i>	0	0	2.5
1303	817	A	Removal	<i>Imperata cylindrica</i>	0	2.5	0
1303	817	A	Removal	<i>Panicum virgatum</i>	5	2.5	2.5
1303	817	A	Removal	<i>Rubus argutus</i>	5	2.5	2.5
1303	817	A	Removal	<i>Spartina patens</i>	30	2.5	2.5
1303	817	B	Removal	<i>Imperata cylindrica</i>	0	40	0
1303	817	B	Removal	<i>Juncus roemerianus</i>	5	2.5	2.5
1303	817	B	Removal	<i>Panicum virgatum</i>	5	0	0
1303	817	B	Removal	<i>Spartina patens</i>	45	15	7.5
1303	818	A	Removal	<i>Imperata cylindrica</i>	15	45	35
1303	818	A	Removal	<i>Ipomea sagitata</i>	5	0	2.5
1303	818	A	Removal	<i>Juncus roemerianus</i>	5	2.5	2.5
1303	818	A	Removal	<i>Rubus argutus</i>	5	2.5	5
1303	818	A	Removal	<i>Spartina patens</i>	5	2.5	2.5
1303	818	A	Removal	<i>Toxicodendron radicans</i>	5	2.5	2.5
1303	818	B	Removal	<i>Euthamia sp.</i>	5	0	0
1303	818	B	Removal	<i>Imperata cylindrica</i>	35	55	37.5
1303	818	B	Removal	<i>Ipomea sagitata</i>	5	2.5	5
1303	818	B	Removal	<i>Juncus roemerianus</i>	0	2.5	2.5
1303	818	B	Removal	<i>Rubus argutus</i>	5	2.5	2.5

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
1303	818	B	Removal	<i>Solidago odora</i>	5	0	2.5
1303	818	B	Removal	<i>Spartina patens</i>	10	2.5	2.5
1504	804	A	Removal	<i>Andropogon virginicus</i>	0	0	2.5
1504	804	A	Removal	<i>Dichanthelium sp.</i>	0	2.5	2.5
1504	804	A	Removal	<i>Rubus argutus</i>	0	5	2.5
1504	804	A	Removal	<i>Solidago odora</i>	0	5	5
1504	804	A	Removal	<i>Spartina patens</i>	30	15	7.5
1504	804	B	Removal	<i>Ampelopsis arborea</i>	0	0	2.5
1504	804	B	Removal	<i>Dichanthelium sp.</i>	0	2.5	0
1504	804	B	Removal	<i>Rubus argutus</i>	10	5	2.5
1504	804	B	Removal	<i>Spartina patens</i>	25	25	10
1504	804	B	Removal	<i>Toxicodendron radicans</i>	0	2.5	0
1504	808	A	Removal	<i>Andropogon virginicus</i>	0	0	2.5
1504	808	A	Removal	<i>Dichanthelium sp.</i>	0	5	5
1504	808	A	Removal	<i>Dichanthelium sp.</i>	0	2.5	0
1504	808	A	Removal	<i>Juncus roemerianus</i>	10	15	5
1504	808	A	Removal	<i>Panicum virgatum</i>	0	0	2.5
1504	808	A	Removal	<i>Rubus argutus</i>	5	0	2.5
1504	808	A	Removal	<i>Spartina patens</i>	20	10	12.5
1504	808	A	Removal	<i>Toxicodendron radicans</i>	0	0	2.5
1504	808	B	Removal	<i>Juncus roemerianus</i>	0	5	5
1504	808	B	Removal	<i>Solidago odora</i>	0	2.5	2.5
1504	808	B	Removal	<i>Spartina patens</i>	5	5	5
1504	813	A	Removal	<i>Panicum virgatum</i>	5	2.5	5
1504	813	A	Removal	<i>Spartina patens</i>	60	20	12.5
1504	813	B	Removal	<i>Dichanthelium aciculare</i>	5	0	0
1504	813	B	Removal	<i>Dichanthelium sp.</i>	5	2.5	2.5
1504	813	B	Removal	<i>Eupatorium serotinum</i>	0	0	2.5
1504	813	B	Removal	<i>Ipomea sagittata</i>	5	2.5	2.5
1504	813	B	Removal	<i>Juncus roemerianus</i>	10	10	7.5
1504	813	B	Removal	<i>Juncus sp.</i>	0	0	2.5
1504	813	B	Removal	<i>Panicum virgatum</i>	5	0	2.5
1504	813	B	Removal	<i>Rubus argutus</i>	5	0	2.5
1504	813	B	Removal	<i>Smilax bona-nox</i>	5	2.5	0
1504	813	B	Removal	<i>Spartina patens</i>	10	40	40
1703	806	A	Removal	<i>Andropogon virginicus</i>	0	2.5	5
1703	806	A	Removal	<i>Centella asiatica</i>	0	2.5	2.5
1703	806	A	Removal	<i>Dichanthelium sp.</i>	5	2.5	2.5
1703	806	A	Removal	<i>Eupatorium serotinum</i>	5	0	2.5
1703	806	A	Removal	<i>Euthamia sp.</i>	0	2.5	0

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
1703	806	A	Removal	<i>Panicum virgatum</i>	5	15	5
1703	806	A	Removal	<i>Rubus argutus</i>	5	2.5	2.5
1703	806	A	Removal	<i>Spartina patens</i>	50	20	17.5
1703	806	A	Removal	<i>Toxicodendron radicans</i>	5	2.5	2.5
1703	806	B	Removal	<i>Dichanthelium sp.</i>	0	0	2.5
1703	806	B	Removal	<i>Panicum virgatum</i>	5	5	2.5
1703	806	B	Removal	<i>Spartina patens</i>	10	15	5
1703	806	B	Removal	<i>Toxicodendron radicans</i>	15	2.5	5
1703	814	A	Removal	<i>Dichanthelium sp.</i>	5	5	2.5
1703	814	A	Removal	<i>Panicum virgatum</i>	5	10	17.5
1703	814	A	Removal	<i>Scleria sp.</i>	0	0	2.5
1703	814	A	Removal	<i>Smilax bona-nox</i>	5	2.5	5
1703	814	A	Removal	<i>Spartina patens</i>	5	5	7.5
1703	814	A	Removal	<i>Toxicodendron radicans</i>	5	2.5	2.5
1703	814	B	Removal	<i>Dichanthelium sp.</i>	5	2.5	2.5
1703	814	B	Removal	<i>Panicum virgatum</i>	5	5	5
1703	814	B	Removal	<i>Scleria sp.</i>	0	2.5	2.5
1703	814	B	Removal	<i>Spartina patens</i>	0	15	7.5
1703	814	B	Removal	<i>Toxicodendron radicans</i>	10	2.5	5
1703	816	A	Removal	<i>Centella asiatica</i>	0	2.5	2.5
1703	816	A	Removal	<i>Dichanthelium sp.</i>	5	0	0
1703	816	A	Removal	<i>Euthamia sp.</i>	0	5	0
1703	816	A	Removal	<i>Juncus roemerianus</i>	5	2.5	2.5
1703	816	A	Removal	<i>Panicum virgatum</i>	0	5	5
1703	816	A	Removal	<i>Rubus argutus</i>	5	2.5	2.5
1703	816	A	Removal	<i>Solidago odora</i>	25	0	5
1703	816	A	Removal	<i>Spartina patens</i>	10	5	5
1703	816	B	Removal	<i>Dichanthelium sp.</i>	5	2.5	2.5
1703	816	B	Removal	<i>Euthamia sp.</i>	0	5	0
1703	816	B	Removal	<i>Juncus roemerianus</i>	0	2.5	2.5
1703	816	B	Removal	<i>Panicum virgatum</i>	5	5	2.5
1703	816	B	Removal	<i>Rubus argutus</i>	5	2.5	5
1703	816	B	Removal	<i>Solidago odora</i>	15	0	7.5
1703	816	B	Removal	<i>Spartina patens</i>	5	5	5
1703	816	B	Removal	<i>Toxicodendron radicans</i>	10	2.5	2.5
4104	801	A	Removal	<i>Dichanthelium sp.</i>	0	0	2.5
4104	801	A	Removal	<i>Spartina patens</i>	10	5	5
4104	801	B	Removal	<i>Panicum virgatum</i>	5	2.5	5
4104	801	B	Removal	<i>Spartina patens</i>	5	5	2.5
4104	801	B	Removal	<i>Toxicodendron radicans</i>	10	0	2.5

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
4104	802	A	Removal	<i>Andropogon virginicus</i>	0	2.5	2.5
4104	802	A	Removal	<i>Panicum virgatum</i>	5	2.5	0
4104	802	A	Removal	<i>Spartina patens</i>	35	10	5
4104	802	A	Removal	<i>Toxicodendron radicans</i>	0	2.5	0
4104	802	B	Removal	<i>Andropogon virginicus</i>	5	5	2.5
4104	802	B	Removal	<i>Dichanthelium sp.</i>	0	2.5	2.5
4104	802	B	Removal	<i>Solidago stricta</i>	15	2.5	2.5
4104	802	B	Removal	<i>Spartina patens</i>	20	15	15
4104	802	B	Removal	<i>Toxicodendron radicans</i>	15	2.5	2.5
4104	803	A	Removal	<i>Andropogon virginicus</i>	0	0	2
4104	803	A	Removal	<i>Dichanthelium sp.</i>	5	5	5
4104	803	A	Removal	<i>Eleocharis sp.</i>	0	0	2.5
4104	803	A	Removal	<i>Juncus roemerianus</i>	0	5	5
4104	803	A	Removal	<i>Panicum virgatum</i>	5	2.5	2.5
4104	803	A	Removal	<i>Rubus argutus</i>	0	2.5	0
4104	803	A	Removal	<i>Spartina patens</i>	20	5	5
4104	803	A	Removal	<i>Toxicodendron radicans</i>	0	2.5	2.5
4104	803	B	Removal	<i>Juncus roemerianus</i>	5	5	2.5
4104	803	B	Removal	<i>Panicum virgatum</i>	5	0	0
4104	803	B	Removal	<i>Rubus argutus</i>	5	2.5	5
4104	803	B	Removal	<i>Spartina patens</i>	20	5	5
4104	803	B	Removal	<i>Toxicodendron radicans</i>	5	2.5	2.5
4502	805	A	Removal	<i>Panicum virgatum</i>	5	0	0
4502	805	A	Removal	<i>Solidago odora</i>	0	2.5	2.5
4502	805	A	Removal	<i>Spartina patens</i>	60	20	20
4502	805	A	Removal	<i>Toxicodendron radicans</i>	0	0	2.5
4502	805	B	Removal	<i>Spartina patens</i>	30	25	17.5
4502	805	B	Removal	<i>Toxicodendron radicans</i>	0	2.5	2.5
4502	809	A	Removal	<i>Dichanthelium ensifolium</i>	5	0	0
4502	809	A	Removal	<i>Dichanthelium sp.</i>	5	20	30
4502	809	A	Removal	<i>Panicum virgatum</i>	10	5	5
4502	809	A	Removal	<i>Rubus argutus</i>	10	2.5	2.5
4502	809	A	Removal	<i>Spartina patens</i>	35	15	10
4502	809	A	Removal	<i>Toxicodendron radicans</i>	5	0	2.5
4502	809	B	Removal	<i>Dichanthelium ensifolium</i>	5	0	0
4502	809	B	Removal	<i>Dichanthelium sp.</i>	5	15	7.5
4502	809	B	Removal	<i>Panicum virgatum</i>	15	5	5
4502	809	B	Removal	<i>Rubus argutus</i>	5	0	2.5
4502	809	B	Removal	<i>Spartina patens</i>	15	10	30
4502	809	B	Removal	<i>Toxicodendron radicans</i>	5	2.5	5

Plot	Subplot	Comp plot	Treatment	Species	Cover '11	Cover '12	Cover '13
4502	811	A	Removal	<i>Andropogon virginicus</i>	25	35	37.5
4502	811	A	Removal	<i>Panicum virgatum</i>	5	2.5	2.5
4502	811	A	Removal	<i>Spartina patens</i>	10	10	5
4502	811	B	Removal	<i>Panicum virgatum</i>	5	2.5	5
4502	811	B	Removal	<i>Spartina patens</i>	40	30	17.5
4502	811	B	Removal	<i>Toxicodendron radicans</i>	5	2.5	2.5
11103	810	A	Removal	<i>Rubus argutus</i>	5	0	2.5
11103	810	A	Removal	<i>Spartina patens</i>	5	2.5	2.5
11103	810	A	Removal	<i>Toxicodendron radicans</i>	15	5	10
11103	810	B	Removal	<i>Dichanthelium sp.</i>	0	2.5	0
11103	810	B	Removal	<i>Rubus argutus</i>	0	2.5	2.5
11103	810	B	Removal	<i>Spartina patens</i>	10	5	10
11103	810	B	Removal	<i>Toxicodendron radicans</i>	15	2.5	7.5
11103	812	A	Removal	<i>Dichanthelium sp.</i>	0	0	2.5
11103	812	A	Removal	<i>Panicum virgatum</i>	15	15	2.5
11103	812	A	Removal	<i>Rubus argutus</i>	5	2.5	5
11103	812	A	Removal	<i>Setaria geniculata</i>	0	0	2.5
11103	812	A	Removal	<i>Spartina patens</i>	5	5	2.5
11103	812	B	Removal	<i>Dichanthelium ensifolium</i>	5	0	0
11103	812	B	Removal	<i>Dichanthelium sp.</i>	5	2.5	0
11103	812	B	Removal	<i>Juncus roemerianus</i>	0	2.5	2.5
11103	812	B	Removal	<i>Panicum virgatum</i>	5	5	0
11103	812	B	Removal	<i>Rubus argutus</i>	0	2.5	2.5
11103	812	B	Removal	<i>Setaria geniculata</i>	0	0	2.5
11103	812	B	Removal	<i>Solidago stricta</i>	5	2.5	2.5
11103	812	B	Removal	<i>Spartina patens</i>	5	5	5
11103	815	A	Removal	<i>Panicum virgatum</i>	0	5	2.5
11103	815	A	Removal	<i>Spartina patens</i>	15	10	10
11103	815	B	Removal	<i>Juncus roemerianus</i>	5	2.5	2.5
11103	815	B	Removal	<i>Setaria geniculata</i>	0	0	2.5
11103	815	B	Removal	<i>Spartina patens</i>	25	2.5	2.5
11103	815	B	Removal	<i>Toxicodendron radicans</i>	5	2.5	2.5

Appendix J. Density of woody seedlings (m⁻²) on composition plots during each survey year.

Plot	Subplot	Comp plot	Treatment	Species	Density '11	Density '12	Density '13
2301	834	A	Control	<i>Persea borbonia</i>	1	2	3
2301	834	B	Control	<i>Cinnamomum camphora</i>	0	0	1
2301	834	B	Control	<i>Ilex vomitoria</i>	0	0	1
2301	835	A	Control	<i>Ilex glabra</i>	21	21	23
2301	835	B	Control	<i>Ilex glabra</i>	0	1	2
2301	836	A	Control	<i>Persea borbonia</i>	2	0	2
2301	836	B	Control	<i>Ilex vomitoria</i>	2	3	3
5001	825	A	Control	<i>Myrica cerifera</i>	0	1	2
5001	825	A	Control	<i>Persea borbonia</i>	3	1	1
5001	825	B	Control	<i>Ilex glabra</i>	3	1	3
5001	825	B	Control	<i>Morella cerifera</i>	1	0	2
5001	825	B	Control	<i>Persea borbonia</i>	9	10	8
5001	826	A	Control	<i>Ilex vomitoria</i>	0	1	1
5001	826	B	Control	<i>Ilex vomitoria</i>	5	8	6
5001	826	B	Control	<i>Morella cerifera</i>	1	0	1
5001	826	B	Control	<i>Persea borbonia</i>	2	2	3
5001	826	B	Control	<i>Pinus elliottii</i>	4	1	0
5001	827	A	Control	<i>Ilex vomitoria</i>	1	1	1
5001	827	B	Control	<i>Ilex vomitoria</i>	4	1	3
5001	827	B	Control	<i>Morella cerifera</i>	1	1	0
5001	827	B	Control	<i>Persea borbonia</i>	1	1	1
5203	822	A	Control	<i>Ilex vomitoria</i>	2	0	1
5203	822	A	Control	<i>Persea borbonia</i>	1	1	1
5203	822	A	Control	<i>Pinus elliottii</i>	1	0	1
5203	822	B	Control	<i>Myrica cerifera</i>	0	1	0
5203	822	B	Control	<i>Persea borbonia</i>	0	1	1
5203	823	A	Control	<i>Ilex glabra</i>	7	6	4
5203	823	A	Control	<i>Ilex vomitoria</i>	0	1	1
5203	823	A	Control	<i>Persea borbonia</i>	2	0	0
5203	823	B	Control	<i>Ilex vomitoria</i>	1	1	1
5203	823	B	Control	<i>Morella cerifera</i>	2	0	2
5203	823	B	Control	<i>Persea borbonia</i>	1	1	0
5203	824	A	Control	<i>Ilex vomitoria</i>	0	1	1
5203	824	B	Control	<i>Morella cerifera</i>	1	0	0
5203	824	B	Control	<i>Persea borbonia</i>	2	2	2
21001	831	A	Control	<i>Acer rubrum</i>	1	1	8
21001	831	A	Control	<i>Ilex glabra</i>	4	2	2

Plot	Subplot	Comp plot	Treatment	Species	Density '11	Density '12	Density '13
21001	831	A	Control	<i>Ilex vomitoria</i>	1	1	2
21001	831	A	Control	<i>Morella cerifera</i>	6	6	8
21001	831	A	Control	<i>Persea borbonia</i>	1	4	4
21001	831	B	Control	<i>Acer rubrum</i>	1	0	1
21001	831	B	Control	<i>Ilex glabra</i>	0	0	1
21001	831	B	Control	<i>Ilex vomitoria</i>	3	3	0
21001	831	B	Control	<i>Morella cerifera</i>	7	2	1
21001	831	B	Control	<i>Persea borbonia</i>	0	1	0
21001	832	A	Control	<i>Ilex glabra</i>	6	6	8
21001	832	A	Control	<i>Ilex vomitoria</i>	0	1	2
21001	832	A	Control	<i>Myrica cerifera</i>	0	0	3
21001	832	A	Control	<i>Persea borbonia</i>	0	1	0
21001	832	B	Control	<i>Acer rubrum</i>	1	1	2
21001	832	B	Control	<i>Ilex vomitoria</i>	3	1	2
21001	832	B	Control	<i>Morella cerifera</i>	1	0	1
21001	832	B	Control	<i>Persea borbonia</i>	1	1	0
21001	833	A	Control	<i>Ilex glabra</i>	22	30	30
21001	833	A	Control	<i>Ilex vomitoria</i>	1	0	2
21001	833	A	Control	<i>Morella cerifera</i>	2	0	1
21001	833	A	Control	<i>Persea borbonia</i>	1	2	4
21001	833	B	Control	<i>Ilex glabra</i>	15	13	18
21001	833	B	Control	<i>Ilex vomitoria</i>	3	1	2
21001	833	B	Control	<i>Morella cerifera</i>	1	0	0
21001	833	B	Control	<i>Persea borbonia</i>	1	0	0
21201	828	A	Control	<i>Ilex vomitoria</i>	0	0	1
21201	828	A	Control	<i>Myrica cerifera</i>	0	0	1
21201	828	A	Control	<i>Persea borbonia</i>	0	1	2
21201	828	A	Control	<i>Pinus elliottii</i>	0	1	0
21201	828	B	Control	<i>Persea borbonia</i>	1	0	0
21201	829	A	Control	<i>Acer rubrum</i>	1	0	0
21201	829	A	Control	<i>Ilex glabra</i>	8	5	5
21201	829	A	Control	<i>Ilex vomitoria</i>	3	1	0
21201	829	A	Control	<i>Morella cerifera</i>	2	2	0
21201	829	A	Control	<i>Persea borbonia</i>	1	1	0
21201	829	A	Control	<i>Pinus elliottii</i>	0	2	2
21201	829	B	Control	<i>Ilex glabra</i>	9	6	6
21201	829	B	Control	<i>Ilex vomitoria</i>	3	2	1
21201	829	B	Control	<i>Myrica cerifera</i>	0	2	1
21201	830	A	Control	<i>Ilex glabra</i>	1	0	0
21201	830	A	Control	<i>Ilex vomitoria</i>	0	1	1

Plot	Subplot	Comp plot	Treatment	Species	Density '11	Density '12	Density '13
21201	830	A	Control	<i>Persea borbonia</i>	0	1	1
21201	830	B	Control	<i>Ilex vomitoria</i>	2	3	2
21201	830	B	Control	<i>Persea borbonia</i>	1	2	1
21201	830	B	Control	<i>Pinus elliotii</i>	0	2	2
51001	819	A	Control	<i>Ilex glabra</i>	4	1	2
51001	819	A	Control	<i>Ilex vomitoria</i>	1	0	1
51001	819	A	Control	<i>Morella cerifera</i>	2	1	4
51001	819	A	Control	<i>Persea borbonia</i>	1	2	2
51001	819	A	Control	<i>Pinus elliotii</i>	1	0	0
51001	819	B	Control	<i>Ilex glabra</i>	12	3	7
51001	819	B	Control	<i>Ilex vomitoria</i>	1	2	6
51001	819	B	Control	<i>Myrica cerifera</i>	0	2	3
51001	819	B	Control	<i>Quercus virginiana</i>	1	2	2
51001	820	A	Control	<i>Ilex vomitoria</i>	2	1	2
51001	820	A	Control	<i>Persea borbonia</i>	1	1	1
51001	820	A	Control	<i>Pinus elliotii</i>	0	0	1
51001	820	B	Control	<i>Ilex vomitoria</i>	2	1	1
51001	820	B	Control	<i>Persea borbonia</i>	2	1	2
51001	820	B	Control	<i>Pinus elliotii</i>	1	0	0
51001	820	B	Control	<i>Quercus virginiana</i>	0	0	1
51001	821	A	Control	<i>Bacharris halimifolia</i>	1	0	0
51001	821	A	Control	<i>Ilex vomitoria</i>	2	1	1
51001	821	A	Control	<i>Myrica cerifera</i>	0	2	2
51001	821	A	Control	<i>Persea borbonia</i>	1	0	3
51001	821	B	Control	<i>Morella cerifera</i>	4	3	4
51001	821	B	Control	<i>Persea borbonia</i>	0	0	2
51001	821	B	Control	<i>Quercus virginiana</i>	0	1	0
1303	807	A	Removal	<i>Cinnamomum camphora</i>	0	1	0
1303	807	A	Removal	<i>Ilex vomitoria</i>	1	1	3
1303	807	A	Removal	<i>Persea borbonia</i>	1	0	2
1303	807	B	Removal	<i>Persea borbonia</i>	3	2	3
1303	817	A	Removal	<i>Cinnamomum camphora</i>	0	1	1
1303	818	A	Removal	<i>Cinnamomum camphora</i>	0	0	1
1303	818	B	Removal	<i>Ilex vomitoria</i>	0	1	1
1303	818	B	Removal	<i>Persea borbonia</i>	0	1	1
1504	804	A	Removal	<i>Persea borbonia</i>	0	7	9
1504	804	A	Removal	<i>Pinus elliotii</i>	0	1	1
1504	804	B	Removal	<i>Ilex vomitoria</i>	0	0	2
1504	804	B	Removal	<i>Persea borbonia</i>	3	11	8
1504	808	A	Removal	<i>Bacharris halimifolia</i>	0	0	1

Plot	Subplot	Comp plot	Treatment	Species	Density '11	Density '12	Density '13
1504	808	A	Removal	<i>Ilex vomitoria</i>	1	0	0
1504	808	A	Removal	<i>Pinus elliottii</i>	0	1	0
1504	808	B	Removal	<i>Ilex vomitoria</i>	3	4	5
1504	808	B	Removal	<i>Persea borbonia</i>	1	0	0
1504	813	A	Removal	<i>Bacharris halimifolia</i>	2	0	0
1504	813	B	Removal	<i>Ilex vomitoria</i>	1	0	0
1504	813	B	Removal	<i>Morella cerifera</i>	3	0	0
1504	813	B	Removal	<i>Persea borbonia</i>	1	1	1
1703	806	A	Removal	<i>Ilex glabra</i>	1	0	0
1703	806	A	Removal	<i>Ilex vomitoria</i>	1	1	4
1703	806	A	Removal	<i>Morella cerifera</i>	2	0	0
1703	806	A	Removal	<i>Persea borbonia</i>	0	0	1
1703	806	A	Removal	<i>Pinus elliottii</i>	0	1	1
1703	806	B	Removal	<i>Ilex vomitoria</i>	2	2	0
1703	806	B	Removal	<i>Persea borbonia</i>	5	5	0
1703	814	A	Removal	<i>Acer rubrum</i>	0	0	1
1703	814	A	Removal	<i>Bacharris halimifolia</i>	1	1	0
1703	814	A	Removal	<i>Ilex glabra</i>	1	0	0
1703	814	A	Removal	<i>Ilex vomitoria</i>	0	1	2
1703	814	A	Removal	<i>Pinus elliottii</i>	1	1	4
1703	814	B	Removal	<i>Baccharis halimifolia</i>	0	1	0
1703	814	B	Removal	<i>Ilex vomitoria</i>	2	2	2
1703	814	B	Removal	<i>Morella cerifera</i>	1	1	1
1703	814	B	Removal	<i>Persea borbonia</i>	1	1	1
1703	814	B	Removal	<i>Pinus elliottii</i>	1	0	0
1703	814	B	Removal	<i>Triadica sebifera</i>	1	1	1
1703	816	A	Removal	<i>Bacharris halimifolia</i>	1	0	0
1703	816	A	Removal	<i>Persea borbonia</i>	3	3	1
1703	816	B	Removal	<i>Acer rubrum</i>	0	0	1
4104	801	A	Removal	<i>Ilex glabra</i>	6	9	9
4104	801	A	Removal	<i>Ilex vomitoria</i>	1	2	5
4104	801	A	Removal	<i>Morella cerifera</i>	1	2	1
4104	801	A	Removal	<i>Pinus elliottii</i>	0	1	0
4104	801	B	Removal	<i>Ilex glabra</i>	14	8	9
4104	801	B	Removal	<i>Ilex vomitoria</i>	0	1	0
4104	802	A	Removal	<i>Acer rubrum</i>	0	0	1
4104	802	A	Removal	<i>Persea borbonia</i>	1	1	2
4104	802	B	Removal	<i>Ilex glabra</i>	1	2	3
4104	802	B	Removal	<i>Ilex vomitoria</i>	0	1	1
4104	803	A	Removal	<i>Ilex glabra</i>	2	5	4

Plot	Subplot	Comp plot	Treatment	Species	Density '11	Density '12	Density '13
4104	803	A	Removal	<i>Morella cerifera</i>	1	1	3
4104	803	A	Removal	<i>Persea borbonia</i>	1	0	0
4104	803	A	Removal	<i>Pinus elliottii</i>	0	2	0
4104	803	B	Removal	<i>Ilex vomitoria</i>	1	0	0
4104	803	B	Removal	<i>Persea borbonia</i>	0	1	0
4104	803	B	Removal	<i>Triadica sebifera</i>	1	0	0
4502	805	B	Removal	<i>Persea borbonia</i>	0	3	2
4502	805	B	Removal	<i>Pinus elliottii</i>	0	2	1
4502	809	A	Removal	<i>Ilex glabra</i>	0	1	1
4502	809	A	Removal	<i>Myrica cerifera</i>	0	1	0
4502	809	B	Removal	<i>Ilex glabra</i>	0	1	0
4502	811	A	Removal	<i>Ilex vomitoria</i>	1	1	1
4502	811	A	Removal	<i>Persea borbonia</i>	7	8	6
4502	811	B	Removal	<i>Persea borbonia</i>	0	2	1
11103	810	A	Removal	<i>Ilex vomitoria</i>	3	1	2
11103	810	A	Removal	<i>Morella cerifera</i>	3	4	4
11103	810	A	Removal	<i>Persea borbonia</i>	0	2	0
11103	810	A	Removal	<i>Photinia pyrifolia</i>	1	0	1
11103	810	A	Removal	<i>Quercus virginiana</i>	2	0	1
11103	810	B	Removal	<i>Morella cerifera</i>	1	2	3
11103	810	B	Removal	<i>Persea borbonia</i>	0	5	2
11103	812	A	Removal	<i>Morella cerifera</i>	2	4	4
11103	812	A	Removal	<i>Persea borbonia</i>	1	2	1
11103	812	B	Removal	<i>Ilex glabra</i>	4	3	5
11103	812	B	Removal	<i>Ilex vomitoria</i>	1	1	1
11103	812	B	Removal	<i>Pinus elliottii</i>	1	0	0
11103	815	A	Removal	<i>Ilex glabra</i>	0	1	0
11103	815	A	Removal	<i>Myrica cerifera</i>	0	1	0
11103	815	B	Removal	<i>Ilex glabra</i>	4	6	5
11103	815	B	Removal	<i>Morella cerifera</i>	2	0	0

Appendix K. Basal diameter (BD (cm)) of all shrubs within 2 m² subplots during each survey year. Shrubs were defined as woody plants with multiple main stems ≥ 1.5 m above ground level.

Plot	Subplot	Treatment	Species	BD '11	BD '12	BD '13
1303	807	Removal	<i>Baccharis halimifolia</i>	2.1	0	0
5001	825	Control	<i>Ilex glabra</i>	0	0	1.9
21001	832	Control	<i>Ilex glabra</i>	1.1	1.2	1.3
21001	833	Control	<i>Ilex glabra</i>	1.3	1.4	1.8
21001	833	Control	<i>Ilex glabra</i>	1.6	1.9	1.4
21001	833	Control	<i>Ilex glabra</i>	1.7	1.7	1.5
21201	829	Control	<i>Ilex glabra</i>	1	1.1	1.5
21201	829	Control	<i>Ilex glabra</i>	1	1.7	1.8
21201	829	Control	<i>Ilex glabra</i>	1.5	2.1	1.5
21201	829	Control	<i>Ilex glabra</i>	2	1.6	0.9
21201	829	Control	<i>Ilex glabra</i>	1.6	1	1.1
21201	829	Control	<i>Ilex glabra</i>	1.1	1.1	1.3
21201	829	Control	<i>Ilex glabra</i>	0	1.7	1.1
51001	819	Control	<i>Ilex glabra</i>	0	1.2	1.2
51001	819	Control	<i>Ilex glabra</i>	0	1.1	1.2
51001	819	Control	<i>Ilex glabra</i>	0	1.1	1.3
51001	819	Control	<i>Ilex glabra</i>	1.1	1.4	1.4
4104	801	Removal	<i>Ilex glabra</i>	1.6	2	1.1
4104	801	Removal	<i>Ilex glabra</i>	1.7	1.7	0.8
4104	801	Removal	<i>Ilex glabra</i>	1.6	0	1.4
11103	812	Removal	<i>Ilex glabra</i>	0	0	1.7
11103	812	Removal	<i>Ilex glabra</i>	1.4	1.7	1.1
11103	812	Removal	<i>Ilex glabra</i>	1.3	0	1.3
11103	815	Removal	<i>Ilex glabra</i>	1.2	0	0
4104	801	Removal	<i>Ilex glabra</i>	1.4	0	1.7
5001	825	Control	<i>Ilex vomitoria</i>	0.5	0	1.3
5001	826	Control	<i>Ilex vomitoria</i>	0	0	1.2
5001	826	Control	<i>Ilex vomitoria</i>	0	0	0.8
21001	831	Control	<i>Ilex vomitoria</i>	1.6	1.7	2
21001	831	Control	<i>Ilex vomitoria</i>	3.4	4	4.3
21001	831	Control	<i>Ilex vomitoria</i>	0	0	0.6
21001	831	Control	<i>Ilex vomitoria</i>	0	0	1.3
21001	833	Control	<i>Ilex vomitoria</i>	2	2.4	2.7
21201	829	Control	<i>Ilex vomitoria</i>	2.5	1.6	1.7

Plot	Subplot	Treatment	Species	BD '11	BD '12	BD '13
21201	829	Control	<i>Ilex vomitoria</i>	1.9	3.2	2.4
21201	829	Control	<i>Ilex vomitoria</i>	1.1	2.4	3.3
21201	830	Control	<i>Ilex vomitoria</i>	0.9	1	1
51001	820	Control	<i>Ilex vomitoria</i>	0	1.1	1.3
1504	808	Removal	<i>Ilex vomitoria</i>	1.1	2	1.5
1504	808	Removal	<i>Ilex vomitoria</i>	1	1.7	1.4
1504	808	Removal	<i>Ilex vomitoria</i>	1.3	0	2.3
1504	808	Removal	<i>Ilex vomitoria</i>	1	0	2.6
1504	813	Removal	<i>Ilex vomitoria</i>	0	1	1.3
1703	806	Removal	<i>Ilex vomitoria</i>	3.2	1.8	2.4
1703	806	Removal	<i>Ilex vomitoria</i>	1	4	4.4
1703	806	Removal	<i>Ilex vomitoria</i>	0.7	1.9	2.2
1703	806	Removal	<i>Ilex vomitoria</i>	0.7	2.3	3
1703	806	Removal	<i>Ilex vomitoria</i>	1.1	1.2	1.1
1703	806	Removal	<i>Ilex vomitoria</i>	1.9	0	0.9
4104	803	Removal	<i>Ilex vomitoria</i>	1.4	1.7	2.9
4104	803	Removal	<i>Ilex vomitoria</i>	1.3	2.3	3
4104	803	Removal	<i>Ilex vomitoria</i>	1.3	2.8	1.8
2301	835	Control	<i>Myrica cerifera</i>	2.2	2.4	3
2301	835	Control	<i>Myrica cerifera</i>	0	2.6	3.7
5001	825	Control	<i>Myrica cerifera</i>	4	2.2	2
5001	825	Control	<i>Myrica cerifera</i>	1.9	2.1	2.3
5001	825	Control	<i>Myrica cerifera</i>	2	1.1	1
5001	825	Control	<i>Myrica cerifera</i>	1.9	2.2	3.8
5001	825	Control	<i>Myrica cerifera</i>	2.6	0	2
5001	825	Control	<i>Myrica cerifera</i>	1.7	0	0
5001	825	Control	<i>Myrica cerifera</i>	1.9	0	0
5001	827	Control	<i>Myrica cerifera</i>	2.6	2.8	3.1
21201	829	Control	<i>Myrica cerifera</i>	3.2	1.6	3.6
21201	829	Control	<i>Myrica cerifera</i>	1.3	1.9	1.6
21201	829	Control	<i>Myrica cerifera</i>	0	3.1	1.8
51001	821	Control	<i>Myrica cerifera</i>	2.1	3.3	4.7
51001	821	Control	<i>Myrica cerifera</i>	4.7	5.2	2.3
51001	821	Control	<i>Myrica cerifera</i>	4.2	4.6	5.6
51001	821	Control	<i>Myrica cerifera</i>	0	1.6	3.2
4104	803	Removal	<i>Myrica cerifera</i>	1.1	1.6	1.7
11103	810	Removal	<i>Myrica cerifera</i>	0	0	1.6
11103	810	Removal	<i>Myrica cerifera</i>	2.8	3.5	3.2
11103	810	Removal	<i>Myrica cerifera</i>	2.7	2.4	2.5
11103	810	Removal	<i>Myrica cerifera</i>	1.9	2.8	2.2

Plot	Subplot	Treatment	Species	BD '11	BD '12	BD '13
11103	810	Removal	<i>Myrica cerifera</i>	2.4	3.4	3.9
11103	812	Removal	<i>Myrica cerifera</i>	1.3	1.5	1.7
11103	815	Removal	<i>Myrica cerifera</i>	1.7	1.8	1.6
11103	815	Removal	<i>Myrica cerifera</i>	1.4	0	2.4
11103	815	Removal	<i>Myrica cerifera</i>	1.4	0	0
11103	815	Removal	<i>Myrica cerifera</i>	2	0	0

					2011				2012				2013		
5001	826	Control	<i>Persea borbonia</i>	5001x10	2.8				3.6				3.8		
5001	826	Control	<i>Persea borbonia</i>		0.4				2.1	0.8			2.3		
5001	826	Control	<i>Persea borbonia</i>		1.8								0.5		
5001	826	Control	<i>Persea borbonia</i>		1.6										
5001	826	Control	<i>Pinus elliottii</i>		42.8				43.3				43.8		
5001	827	Control	<i>Persea borbonia</i>	5001	3				2.9	2			3.2		
5001	827	Control	<i>Pinus elliottii</i>		18.4				18.7				19.2		
21201	828	Control	<i>Persea borbonia</i>	21201x1	5.6				5.8				5.8		
21201	828	Control	<i>Persea borbonia</i>	21201x5	4.5				5.1				4.6		
21201	828	Control	<i>Persea borbonia</i>	21201x6	3				3				3.1		
21201	828	Control	<i>Persea borbonia</i>		2				2				2.1		
21201	828	Control	<i>Persea borbonia</i>		2										
21201	828	Control	<i>Pinus elliottii</i>		0.9				1.3				1.5		
21201	829	Control	<i>Persea borbonia</i>	21103	3.8				4.3				4.3		
21201	829	Control	<i>Persea borbonia</i>	21201x10	2.5				2.9				3		
21201	829	Control	<i>Persea borbonia</i>		1.1				1.8				1.3		
21201	829	Control	<i>Pinus elliottii</i>		31.4				32.2				32.4		
21201	830	Control	<i>Persea borbonia</i>	21201x7	2.5				3.1				3.3		
21201	830	Control	<i>Persea borbonia</i>	21201x9	2.5				2.7				2.7		
21001	831	Control	<i>Persea borbonia</i>	21001	2.8				3.1				3.2		
21001	831	Control	<i>Persea borbonia</i>	21001x1	3.9				4.5				4.5		
21001	832	Control	<i>Persea borbonia</i>	21001x10	4.2				4.7				4.6		
21001	832	Control	<i>Persea borbonia</i>	21001x11	3.2				3.2				3.3		
21001	832	Control	<i>Persea borbonia</i>	21001x12	4.3				3.9	2.1			4.2		
21001	832	Control	<i>Persea borbonia</i>	21001x8	3.9				4				3.8		
21001	832	Control	<i>Persea borbonia</i>	21001x9	5				5.1				5.1		
21001	832	Control	<i>Persea borbonia</i>		1.7				1.9	0.4			1.8	0.3	
21001	832	Control	<i>Persea borbonia</i>		2				2.1				2.1		
21001	833	Control	<i>Persea borbonia</i>	21001x5	2.6				3.1				3.2		

						2011				2012				2013		
21001	833	Control	<i>Persea borbonia</i>			1.1				1.8	1.6			1.3	1.2	
21001	833	Control	<i>Pinus elliottii</i>			40.7				41.4				41.3		
2301	834	Control	<i>Persea borbonia</i>	2301x17		2.7				3.4				3.6		
2301	834	Control	<i>Persea borbonia</i>			0.5				0.6				0.7		
2301	834	Control	<i>Pinus elliottii</i>			25.6				26.8				26.9		
2301	835	Control	<i>Persea borbonia</i>	2301x3		5.4				5.6				5.7		
2301	835	Control	<i>Persea borbonia</i>	2301x4		5.1				5.2				5.3		
2301	835	Control	<i>Persea borbonia</i>			2								2.3		
2301	835	Control	<i>Pinus elliottii</i>			29.9				30.1				30.5		
2301	836	Control	<i>Persea borbonia</i>	2301x10		2.6				2.5	2.8			3	3	
2301	836	Control	<i>Persea borbonia</i>			1.7				2				2.2		
2301	836	Control	<i>Pinus elliottii</i>			27.2				28.5				28.7		

Appendix M. Data from the greenhouse experiment testing the effects of light and nutrient levels (H = high, L = Low) on seedling biomass production. Columns labelled % Leaf and % Stem represent the final biomass as a percentage of the initial biomass.

Plant ID	Species	Shade house	Light	Nutrient	Initial biomass (g)		Final biomass (g)			
					Leaf	Stem	Leaf	% Leaf	Stem	% Stem
C1	<i>C. camphora</i>		H	L	2.12	0.83	0.75	0.354	0.9	1.084
C10	<i>C. camphora</i>	S2	L	L	1.45	0.32	2.35	1.621	1.09	3.406
C11	<i>C. camphora</i>	S4	L	H	4.43	1.38	5.97	1.348	4.17	3.022
C12	<i>C. camphora</i>	S4	L	H	9.41	4.64	8.94	0.950	5.69	1.226
C13	<i>C. camphora</i>		H	H	8.61	2.39	10.30	1.196	5.02	2.100
C14	<i>C. camphora</i>		H	H	8.32	3.09	9.25	1.112	4.64	1.502
C15	<i>C. camphora</i>		H	L	2.44	0.79	1.64	0.672	1.32	1.671
C16	<i>C. camphora</i>		H	H	11.99	3.76	10.80	0.901	5.4	1.436
C17	<i>C. camphora</i>		H	L	2.87	0.43	1.72	0.599	0.67	1.558
C18	<i>C. camphora</i>	S4	L	H	7.22	3.34	7.18	0.994	4.54	1.359
C19	<i>C. camphora</i>	S1	L	L	3.86	1.39	2.53	0.655	1.59	1.144
C2	<i>C. camphora</i>	S3	L	H	9.35	6.39	9.71	1.039	7.19	1.125
C20	<i>C. camphora</i>	S2	L	L	2.98	0.71	2.89	0.970	1.61	2.268
C21	<i>C. camphora</i>		H	H	6.63	3.14	7.02	1.059	3.5	1.115
C22	<i>C. camphora</i>	S1	L	L	2.8	0.88	2.14	0.764	1.24	1.409
C23	<i>C. camphora</i>		H	H	9.24	3.42	8.37	0.906	3.91	1.143
C24	<i>C. camphora</i>	S1	L	H	8.73	5.31	8.43	0.966	5.51	1.038
C25	<i>C. camphora</i>		H	H	10.44	3.68	8.86	0.849	5.36	1.457
C26	<i>C. camphora</i>	S2	L	L	1.92	0.41	2.41	1.255	1.3	3.171
C27	<i>C. camphora</i>		H	L	2.66	0.62	1.94	0.729	0.98	1.581
C28	<i>C. camphora</i>		H	H	6.67	1.97	8.21	1.231	4.06	2.061
C29	<i>C. camphora</i>		H	L	1.11	0.25	0.73	0.658	0.33	1.320
C3	<i>C. camphora</i>	S3	L	H	9.23	4.43	8.72	0.945	6	1.354

					Initial biomass (g)		Final biomass (g)			
C30	<i>C. camphora</i>	S3	L	L	4.11	1.02	3.67	0.893	2.38	2.333
C31	<i>C. camphora</i>	S3	L	H	7.88	4.72	9.29	1.179	7.96	1.686
C32	<i>C. camphora</i>	S1	L	L	2	0.43	2.66	1.330	1.09	2.535
C33	<i>C. camphora</i>	S3	L	H	9.39	5.49	8.12	0.865	4.47	0.814
C34	<i>C. camphora</i>		H	H	7.44	2.77	3.04	0.409	2.74	0.989
C35	<i>C. camphora</i>		H	L	2.25	0.43	1.94	0.862	0.76	1.767
C36	<i>C. camphora</i>	S2	L	L	3.83	1.25	3.10	0.809	1.9	1.520
C37	<i>C. camphora</i>	S2	L	L	2.35	0.52	1.93	0.821	0.99	1.904
C39	<i>C. camphora</i>	S1	L	L	2.82	0.69	2.53	0.897	1.46	2.116
C4	<i>C. camphora</i>		H	H	8.88	3.28	7.30	0.822	4.34	1.323
C40	<i>C. camphora</i>		H	H	8.88	1.86	7.74	0.872	2.61	1.403
C5	<i>C. camphora</i>		H	L	3.31	0.64	1.93	0.583	0.9	1.406
C6	<i>C. camphora</i>		H	L	0.78	0.21	0.98	1.256	0.47	2.238
C7	<i>C. camphora</i>	S4	L	H	7.78	4.03	7.72	0.992	5.37	1.333
C8	<i>C. camphora</i>		H	L	2	0.53	2.21	1.105	0.95	1.792
C9	<i>C. camphora</i>		H	L	2.34	0.59	1.72	0.735	0.78	1.322
CA1	<i>C. camphora</i>		H	L	2.46	0.73	3.04	1.236	1.31	1.795
CA11	<i>C. camphora</i>	S4	L	H	10.25	2.58	5.65	0.551	2.19	0.849
CA12	<i>C. camphora</i>	S4	L	H	6.98	3.93	6.46	0.926	5.54	1.410
CA13	<i>C. camphora</i>	S4	L	L	3.01	0.86	2.65	0.880	1.71	1.988
CA14	<i>C. camphora</i>	S1	L	H	9.07	2.86	8.12	0.895	3.89	1.360
CA15	<i>C. camphora</i>		H	H	9.78	3.25	7.45	0.762	3.29	1.012
CA16	<i>C. camphora</i>	S1	L	L	3.82	1.28	2.13	0.558	1.45	1.133
CA17	<i>C. camphora</i>		H	H	10.94	4.26	9.12	0.834	3.64	0.854
CA18	<i>C. camphora</i>	S3	L	L	3.67	1.15	2.21	0.602	1.12	0.974
CA19	<i>C. camphora</i>	S2	L	L	3.67	1.23	2.62	0.714	1.57	1.276
CA2	<i>C. camphora</i>		H	L	2.12	0.69	1.93	0.910	1.32	1.913
CA20	<i>C. camphora</i>		H	H	12.88	2.81	8.65	0.672	3.89	1.384
CA21	<i>C. camphora</i>	S4	L	H	15.07	5.25	10.06	0.668	4.19	0.798

					Initial biomass (g)		Final biomass (g)			
CA22	<i>C. camphora</i>	S2	L	H	11.32	5.58	8.84	0.781	5.3	0.950
CA23	<i>C. camphora</i>	S3	L	H	14.8	5.86	8.63	0.583	6.79	1.159
CA24	<i>C. camphora</i>	S4	L	H	8.8	6.5	7.23	0.822	5.12	0.788
CA25	<i>C. camphora</i>		H	L	1.36	0.56	2.28	1.676	0.76	1.357
CA26	<i>C. camphora</i>		H	H	10.68	1.88	7.84	0.734	2.82	1.500
CA27	<i>C. camphora</i>		H	H	8.11	3.3	2.03	0.250	1.32	0.400
CA28	<i>C. camphora</i>		H	L	1.81	0.71	2.13	1.177	1.39	1.958
CA29	<i>C. camphora</i>		H	L	2.53	1.15	2.05	0.810	1.52	1.322
CA3	<i>C. camphora</i>		H	L	3.36	1.25	3.30	0.982	2.38	1.904
CA30	<i>C. camphora</i>	S3	L	L	3.62	1.31	2.54	0.702	1.43	1.092
CA31	<i>C. camphora</i>		H	L	2.7	0.65	1.08	0.400	5.01	7.708
CA32	<i>C. camphora</i>	S2	L	L	3.37	1.29	2.32	0.688	1.6	1.240
CA33	<i>C. camphora</i>		H	L	1.75	0.9	1.72	0.983	0.87	0.967
CA34	<i>C. camphora</i>		H	H	9.95	4.47	9.34	0.939	3.75	0.839
CA35	<i>C. camphora</i>		H	L	1.86	0.7	1.40	0.753	0.85	1.214
CA36	<i>C. camphora</i>	S4	L	H	9.27	6.54	8.10	0.874	4.5	0.688
CA37	<i>C. camphora</i>	S1	L	H	9.75	9.68	9.70	0.995	6.67	0.689
CA39	<i>C. camphora</i>		H	H	8.29	3.82	9.45	1.140	3.86	1.010
CA4	<i>C. camphora</i>	S4	L	L	3.33	1.11	2.55	0.766	1.72	1.550
CA40	<i>C. camphora</i>		H	H	14.27	3.84	11.18	0.783	4.21	1.096
CA41	<i>C. camphora</i>		H	H	7.82	2.88	8.94	1.143	2.61	0.906
CA42	<i>C. camphora</i>		H	L	1.6	0.58	1.90	1.188	1.16	2.000
CA5	<i>C. camphora</i>	S1	L	L	3	0.62	2.07	0.690	1.32	2.129
CA6	<i>C. camphora</i>		H	H	8.19	2.87	6.96	0.850	2.89	1.007
CA7	<i>C. camphora</i>	S3	L	H	8.42	3.82	8.03	0.954	7.26	1.901
CA8	<i>C. camphora</i>	S4	L	H	4.35	1.32	4.46	1.025	2.51	1.902
CA9	<i>C. camphora</i>	S3	L	L	3.35	1.14	2.84	0.848	1.36	1.193
R1	<i>P. borbonia</i>		H	L	0.23	0.14	0.38	1.652	0.49	3.500
R10	<i>P. borbonia</i>	S4	L	H	0.57	0.3	2.31	4.053	2.43	8.100

					Initial biomass (g)		Final biomass (g)			
R11	<i>P. borbonia</i>		H	H	2.78	1.11	6.89	2.478	6.73	6.063
R12	<i>P. borbonia</i>	S4	L	L	0.34	0.15	0.81	2.382	0.76	5.067
R13	<i>P. borbonia</i>		H	L	0.37	0.16	0.20	0.541	0.28	1.750
R14	<i>P. borbonia</i>		H	L	0.68	0.58	0.82	1.206	1.16	2.000
R15	<i>P. borbonia</i>	S4	L	L	0.43	0.28	0.60	1.395	0.8	2.857
R16	<i>P. borbonia</i>		H	H	1.65	0.64	5.70	3.455	4.95	7.734
R17	<i>P. borbonia</i>	S4	L	H	1.03	0.47	4.87	4.728	4.44	9.447
R18	<i>P. borbonia</i>	S2	L	L	0.33	0.2	0.40	1.212	0.59	2.950
R19	<i>P. borbonia</i>		H	L	0.32	0.13	0.29	0.906	0.27	2.077
R2	<i>P. borbonia</i>	S2	L	H	0.73	0.21	2.53	3.466	2.58	12.286
R20	<i>P. borbonia</i>		H	H	2.82	1.2	5.69	2.018	5.17	4.308
R21	<i>P. borbonia</i>		H	H	0.68	0.28	1.69	2.485	1.36	4.857
R22	<i>P. borbonia</i>		H	L	0.27	0.12	0.45	1.667	0.44	3.667
R23	<i>P. borbonia</i>		H	L	0.21	0.12	0.18	0.857	0.3	2.500
R24	<i>P. borbonia</i>	S4	L	L	0.47	0.18	0.81	1.723	0.71	3.944
R25	<i>P. borbonia</i>		H	H	1.09	0.43	2.99	2.743	3.46	8.047
R26	<i>P. borbonia</i>		H	H	1.58	0.68	5.51	3.487	5.87	8.632
R27	<i>P. borbonia</i>	S3	L	L	0.93	0.41	1.76	1.892	1.43	3.488
R28	<i>P. borbonia</i>	S4	L	L	0.31	0.13	0.19	0.613	0.27	2.077
R29	<i>P. borbonia</i>	S1	L	L	1.14	0.73	1.50	1.316	2.14	2.932
R3	<i>P. borbonia</i>	S3	L	H	0.3	0.22	2.13	7.100	2.97	13.500
R30	<i>P. borbonia</i>	S4	L	H	0.4	0.14	0.66	1.650	0.55	3.929
R32	<i>P. borbonia</i>		H	H	0.83	0.29	5.60	6.747	4.49	15.483
R33	<i>P. borbonia</i>	S1	L	L	0.12	0.06	0.08	0.667	0.14	2.333
R34	<i>P. borbonia</i>	S4	L	L	0.27	0.19	0.16	0.593	0.22	1.158
R35	<i>P. borbonia</i>		H	L	0.26	0.14	0.05	0.192	0.18	1.286
R36	<i>P. borbonia</i>		H	H	0.73	0.25	3.31	4.534	3.42	13.680
R37	<i>P. borbonia</i>	S1	L	L	0.35	0.17	0.59	1.686	0.8	4.706
R4	<i>P. borbonia</i>		H	L	0.88	0.29	0.76	0.864	0.52	1.793

					Initial biomass (g)		Final biomass (g)			
R5	<i>P. borbonia</i>	S2	L	H	0.93	0.46	3.47	3.731	3.53	7.674
R6	<i>P. borbonia</i>	S2	L	H	1.7	0.84	3.64	2.141	3.53	4.202
R7	<i>P. borbonia</i>		H	H	1.8	0.56	4.12	2.289	4.11	7.339
R8	<i>P. borbonia</i>		H	L	0.44	0.17	0.19	0.432	0.23	1.353
R9	<i>P. borbonia</i>	S1	L	H	3.28	1.97	2.15	0.655	3.17	1.609
RB10	<i>P. borbonia</i>	S4	L	H	9.19	5.75	6.95	0.756	5.94	1.033
RB11	<i>P. borbonia</i>	S4	L	L	5.3	4.35	2.50	0.472	1.47	0.338
RB12	<i>P. borbonia</i>	S2	L	H	11.33	8.15	6.37	0.562	5.03	0.617
RB13	<i>P. borbonia</i>	S3	L	L	5.02	3.85	2.06	0.410	1.26	0.327
RB15	<i>P. borbonia</i>		H	L	5.06	4.09	2.15	0.425	1.72	0.421
RB16	<i>P. borbonia</i>	S1	L	L	6.44	3.11	2.86	0.444	1.83	0.588
RB2	<i>P. borbonia</i>	S2	L	H	6.85	3.95	7.50	1.095	7.08	1.792
RB20	<i>P. borbonia</i>		H	H	12.52	7.07	7.82	0.625	4.51	0.638
RB21	<i>P. borbonia</i>	S3	L	L	5.2	2.45	4.31	0.829	3.26	1.331
RB22	<i>P. borbonia</i>		H	L	4.5	5.07	1.83	0.407	2.54	0.501
RB23	<i>P. borbonia</i>	S3	L	H	12.58	8.14	4.80	0.382	2.64	0.324
RB24	<i>P. borbonia</i>	S3	L	H	7.19	3.7	7.17	0.997	4.92	1.330
RB25	<i>P. borbonia</i>	S1	L	H	12.8	6.44	6.23	0.487	6.15	0.955
RB27	<i>P. borbonia</i>	S2	L	L	5.48	2.88	2.26	0.412	1.56	0.542
RB29	<i>P. borbonia</i>	S3	L	H	10.2	4.93	8.60	0.843	6.56	1.331
RB30	<i>P. borbonia</i>		H	L	6.07	4.43	2.27	0.374	1.77	0.400
RB31	<i>P. borbonia</i>	S3	L	L	5.3	3.04	2.09	0.394	1.64	0.539
RB32	<i>P. borbonia</i>		H	H	8.05	2.67	4.35	0.540	2.62	0.981
RB33	<i>P. borbonia</i>		H	L	4.69	4.91	2.24	0.478	1.57	0.320
RB34	<i>P. borbonia</i>		H	H	13.8	9.35	4.40	0.319	2.98	0.319
RB35	<i>P. borbonia</i>	S2	L	H	10.38	4.91	4.83	0.465	3.31	0.674
RB37	<i>P. borbonia</i>	S1	L	L	2.95	1.39	2.35	0.797	1.61	1.158
RB38	<i>P. borbonia</i>	S1	L	H	4.3	1.49	3.78	0.879	2.14	1.436
RB39	<i>P. borbonia</i>	S3	L	L	2.97	1.13	2.59	0.872	1.45	1.283

					Initial biomass (g)		Final biomass (g)			
RB4	<i>P. borbonia</i>		H	H	10.08	4.97	3.66	0.363	3	0.604
RB40	<i>P. borbonia</i>		H	L	2.84	1.57	1.51	0.532	0.85	0.541
RB41	<i>P. borbonia</i>		H	L	3.24	2.01	1.26	0.389	0.91	0.453
RB42	<i>P. borbonia</i>	S3	L	L	3.83	1.88	4.79	1.251	2.56	1.362
RB43	<i>P. borbonia</i>		H	H	9.62	4.54	7.62	0.792	3.87	0.852
RB45	<i>P. borbonia</i>		H	H	9.59	4.35	6.06	0.632	3.92	0.901
RB47	<i>P. borbonia</i>		H	H	15.33	6.98	5.52	0.360	2.76	0.395
RB48	<i>P. borbonia</i>		H	L	4.89	3.41	1.80	0.368	1.12	0.328
RB49	<i>P. borbonia</i>		H	H	10.23	4.62	6.67	0.652	4.39	0.950
RB5	<i>P. borbonia</i>		H	L	2.63	1.96	2.45	0.932	1.32	0.673
RB50	<i>P. borbonia</i>		H	H	10.01	5.77	4.82	0.482	4.09	0.709
RB6	<i>P. borbonia</i>		H	H	9.97	4.3	5.16	0.518	2.85	0.663
RB7	<i>P. borbonia</i>	S4	L	L	5.08	2.27	2.47	0.486	1.97	0.868
RB8	<i>P. borbonia</i>		H	L	3.35	2.62	1.14	0.340	1.1	0.420
RB9	<i>P. borbonia</i>	S2	L	H	10.78	5.03	6.05	0.561	3.21	0.638

Appendix N. Data from larval rearing (neonate – 4th instar) of *P. palamedes*. All mass is reported in grams. ☹ = instar during which mortality occurred. Date and time represent the beginning of each stage with the exception of 4th Instar Final which represents the end of a 7-day observation period.

[illegible]

			⊗		Neonate			2nd Instar			4th Instar Initial			4th Instar Final		
B	CC7	<i>C. camphora</i>	3rd		6/25/2012	14:55	0.0011		6/30/2012	14:30	0.0119					
B	CC8	<i>C. camphora</i>			6/25/2012	15:30	0.0015		6/30/2012	15:10	0.0107		7/21/2012	9:45	0.5155	7/28/2012 9:10 1.8885
B	CC9	<i>C. camphora</i>			6/25/2012	16:05	0.0011		6/30/2012	17:45	0.0073		7/21/2012	9:55	0.4659	7/28/2012 9:20 2.1384
C	RC1	<i>P. borbonia</i>			6/19/2012	15:00	0.001		6/23/2012	19:20	0.0068		7/10/2012	11:55	0.5834	7/17/2012 10:15 2.5837
B	RC10	<i>P. borbonia</i>			6/25/2012	16:30	0.0011		6/30/2012	18:10	0.0048		7/17/2012	11:00	0.442	7/24/2012 9:35 1.7319
B	RC11	<i>P. borbonia</i>	2nd		6/25/2012	17:05	0.0012		6/30/2012	18:35	0.006					
B	RC12	<i>P. borbonia</i>			6/25/2012	17:45	0.0011		6/30/2012	19:05	0.0077		7/18/2012	9:35	0.4662	7/25/2012 9:10 1.5856
K	RC13	<i>P. borbonia</i>			6/29/2012	9:45	0.001		7/5/2012	12:05	0.0106		7/24/2012	10:05	0.671	7/31/2012 9:30 2.3109
K	RC14	<i>P. borbonia</i>			6/29/2012	10:20	0.001		7/6/2012	11:20	0.0101		7/24/2012	10:15	0.5334	7/31/2012 9:35 2.0376
H	RC15	<i>P. borbonia</i>			6/29/2012	17:25	0.0013		7/6/2012	12:00	0.012		7/26/2012	10:20	0.5934	8/2/2012 9:55 1.8254
H	RC16	<i>P. borbonia</i>	2nd		6/29/2012	17:50	0.0014		7/5/2012	12:35	0.0101					
O	RC17	<i>P. borbonia</i>			6/30/2012	10:40	0.001		7/9/2012	13:20	0.0121		7/24/2012	10:35	0.444	7/31/2012 9:45 1.9665
O	RC18	<i>P. borbonia</i>	1st		6/30/2012	11:00	0.001									
O	RC19	<i>P. borbonia</i>			6/30/2012	11:25	0.001		7/6/2012	13:05	0.006		7/23/2012	11:10	0.5676	7/30/2012 10:10 2.2315
D	RC2	<i>P. borbonia</i>			6/20/2012	8:50	0.0011		6/24/2012	16:25	0.0069		7/10/2012	11:45	0.5665	7/17/2012 10:00 2.3149
O	RC20	<i>P. borbonia</i>			6/30/2012	11:50	0.001		7/7/2012	12:40	0.0068		7/24/2012	10:50	0.7043	7/31/2012 9:50 2.4962
L	RC21	<i>P. borbonia</i>			6/30/2012	13:05	0.0013		7/5/2012	14:25	0.0082		7/26/2012	10:35	0.499	8/2/2012 10:05 1.5652
M	RC22	<i>P. borbonia</i>			6/30/2012	13:40	0.0011		7/7/2012	12:55	0.0094		7/22/2012	11:15	0.5544	7/29/2012 10:05 2.2419
O	RC23	<i>P. borbonia</i>			7/3/2012	16:50	0.0011		7/9/2012	14:05	0.0083		7/26/2012	10:50	0.5294	8/2/2012 9:15 1.9993
F	RC3	<i>P. borbonia</i>			6/22/2012	8:50	0.001		6/28/2012	18:05	0.0069		7/14/2012	10:25	0.7577	7/21/2012 9:00 3.1058
F	RC4	<i>P. borbonia</i>			6/23/2012	8:20	0.0013		6/29/2012	18:25	0.0103		7/15/2012	10:00	0.5756	7/22/2012 10:25 2.335
G	RC5	<i>P. borbonia</i>			6/23/2012	9:40	0.0013		6/28/2012	19:00	0.0082		7/15/2012	10:05	0.6057	7/22/2012 10:30 2.4653
B	RC6	<i>P. borbonia</i>			6/24/2012	9:45	0.0011		6/29/2012	18:55	0.0092		7/16/2012	8:45	0.4168	7/23/2012 9:50 1.5916
B	RC7	<i>P. borbonia</i>			6/25/2012	14:45	0.001		6/30/2012	14:15	0.0095		7/17/2012	10:45	0.5585	7/24/2012 9:10 2.1615
B	RC8	<i>P. borbonia</i>			6/25/2012	15:15	0.0012		6/30/2012	15:00	0.0093		7/16/2012	16:20	0.5582	7/23/2012 9:55 2.0152
B	RC9	<i>P. borbonia</i>			6/25/2012	15:55	0.0009		6/30/2012	17:30	0.0073		7/16/2012	19:55	0.5513	7/23/2012 10:25 1.9953
F	RS1	<i>P. borbonia lwd</i>			6/21/2012	19:20	0.0014		6/28/2012	9:38	0.0205		7/13/2012	9:20	0.7538	7/20/2012 10:25 3.303
B	RS10	<i>P. borbonia lwd</i>			6/25/2012	16:50	0.001		6/30/2012	18:25	0.0086		7/17/2012	11:10	0.6736	7/24/2012 9:45 2.6991

			⊗		Neonate			2nd Instar			4th Instar Initial			4th Instar Final		
B	RS11	<i>P. borbonia lwd</i>			6/25/2012	17:25	0.0012	7/1/2012	13:20	0.0068	7/19/2012	11:10	0.5448	7/26/2012	9:50	2.0558
K	RS12	<i>P. borbonia lwd</i>			6/29/2012	9:35	0.0008	7/5/2012	11:25	0.016	7/20/2012	11:55	0.6677	7/27/2012	10:10	2.4815
K	RS13	<i>P. borbonia lwd</i>			6/29/2012	10:05	0.0005	7/5/2012	11:50	0.0156	7/19/2012	11:05	0.6678	7/26/2012	9:40	2.4082
H	RS14	<i>P. borbonia lwd</i>			6/29/2012	17:15	0.0011	7/5/2012	12:20	0.0141	7/22/2012	10:50	0.6214	7/29/2012	9:50	1.6703
H	RS15	<i>P. borbonia lwd</i>			6/29/2012	17:45	0.0013	7/6/2012	12:55	0.0085	7/29/2012	10:30	0.4678	8/5/2012	12:05	1.8553
H	RS16	<i>P. borbonia lwd</i>			6/29/2012	18:10	0.001	7/5/2012	12:45	0.0202	7/23/2012	10:50	0.8389	7/30/2012	10:05	2.3159
O	RS17	<i>P. borbonia lwd</i>			6/30/2012	10:55	0.001	7/5/2012	13:35	0.0165	7/20/2012	12:25	0.5804	7/27/2012	10:40	1.9141
O	RS18	<i>P. borbonia lwd</i>			6/30/2012	11:15	0.0007	7/5/2012	13:10	0.0084	7/21/2012	10:25	0.6995	7/28/2012	9:30	2.2612
O	RS19	<i>P. borbonia lwd</i>			6/30/2012	11:45	0.0009	7/5/2012	13:25	0.0162	7/21/2012	10:35	0.932	7/28/2012	9:40	2.6308
F	RS2	<i>P. borbonia lwd</i>			6/21/2012	21:45	0.0013	6/28/2012	9:45	0.0127	7/11/2012	12:45	0.725	7/18/2012	8:30	2.8095
O	RS20*	<i>P. borbonia lwd</i>			6/30/2012	12:10	0.0009	7/5/2012	14:10	0.0195	7/21/2012	10:45	0.7152	7/28/2012	9:50	1.9591
M	RS21	<i>P. borbonia lwd</i>			6/30/2012	13:25	0.0009	7/5/2012	13:45	0.0143	7/20/2012	12:15	0.708	7/27/2012	10:25	2.497
M	RS22	<i>P. borbonia lwd</i>			6/30/2012	13:55	0.001	7/6/2012	13:15	0.0122	7/22/2012	11:00	0.4898	7/29/2012	9:55	1.8761
O	RS23	<i>P. borbonia lwd</i>	1st		7/3/2012	16:20	0.0011									
O	RS24	<i>P. borbonia lwd</i>			7/3/2012	16:35	0.0013	7/9/2012	14:15	0.0114	7/26/2012	10:40	0.6979	8/2/2012	10:15	1.5965
O	RS25	<i>P. borbonia lwd</i>			7/3/2012	16:05	0.0014	7/9/2012	13:50	0.0071	7/24/2012	11:10	0.8052	7/31/2012	10:00	2.4466
F	RS3	<i>P. borbonia lwd</i>	1st		6/22/2012	11:45	0.0011									
G	RS4	<i>P. borbonia lwd</i>			6/23/2012	9:30	0.0011	6/28/2012	12:36	0.011	7/13/2012	9:50	0.5777	7/20/2012	10:50	2.5874
G	RS5	<i>P. borbonia lwd</i>			6/23/2012	10:05	0.0009	6/28/2012	19:35	0.0097	7/13/2012	9:40	0.7896	7/20/2012	11:00	3.3124
B	RS6	<i>P. borbonia lwd</i>	2nd		6/24/2012	17:00	0.0012	7/1/2012	12:55	0.0058						
B	RS7	<i>P. borbonia lwd</i>	2nd		6/25/2012	15:05	0.0009	6/30/2012	14:40	0.0067						
B	RS8	<i>P. borbonia lwd</i>			6/25/2012	15:40	0.0008	6/30/2012	15:25	0.0086	7/16/2012	20:00	0.3618	7/23/2012	10:10	1.6205
B	RS9	<i>P. borbonia lwd</i>			6/25/2012	16:15	0.0011	6/30/2012	17:55	0.0097	7/14/2012	10:40	0.598	7/21/2012	9:10	2.577

Appendix O. Data from larval rearing (pre-pupal – adult) of *P. palamedes*. Date and time represent the beginning of each stage. Mass is reported in grams (fresh weight).

	Pre-pupal		Pupal			Adult		
ID	Date	Time	Date	Time	Mass	Date	Time	Sex
CC1	7/24/2012	5:00	7/26/2012	5:00	1.4999	8/12/2012	5:00	M
CC10	8/6/2012	8:00	8/8/2012	5:00	1.0828	8/25/2012	5:00	M
CC12	8/9/2012	10:00	8/11/2012	5:00	1.1996	8/27/2012	5:00	F
CC13	8/12/2012	8:00	8/14/2012	5:00	1.3646	8/31/2012	5:00	F
CC16	8/15/2012	5:00	8/17/2012	5:00	1.4571	9/3/2012	5:00	F
CC18	8/15/2012	8:00	8/17/2012	5:00	1.3688	9/3/2012	5:00	M
CC24	8/15/2012	9:30	8/17/2012	5:00	1.0556	9/5/2012	5:00	M
CC4	7/27/2012	10:00	7/29/2012	5:00	1.3782	8/15/2012	5:00	M
CC5	8/2/2012	10:00	8/4/2012	5:00	0.9154	8/21/2012	5:00	F
CC8	7/31/2012	5:00	8/2/2012	5:00	1.3494	8/26/2012	5:00	F
CC9	7/31/2012	5:00	8/2/2012	5:00	1.3522	8/18/2012	5:00	M
RC1	7/18/2012	17:00	7/20/2012	8:00	1.3946	8/6/2012	5:00	M
RC10	7/26/2012	14:00	7/28/2012	5:00	1.2	8/13/2012	5:00	M
RC12	7/30/2012	5:00	8/1/2012	5:00	1.4571	8/19/2012	5:00	F
RC13	8/4/2012	9:00	8/6/2012	5:00	1.6514	8/23/2012	5:00	F
RC14	8/4/2012	12:00	8/6/2012	5:00	1.5714	8/23/2012	5:00	F
RC15	8/7/2012	12:00	8/9/2012	10:00	1.5152	8/26/2012	5:00	F
RC17	8/2/2012	15:00	8/4/2012	13:00	1.1858	8/24/2012	5:00	M
RC19	8/3/2012	9:30	8/5/2012	5:00	1.6291	8/22/2012	5:00	F
RC2	7/21/2012	5:00	7/22/2012	5:00	1.4334	8/24/2012	5:00	F
RC20	8/1/2012	8:00	8/3/2012	10:00	1.4532	8/22/2012	5:00	M
RC21	8/7/2012	10:00	8/9/2012	5:00	1.5107	8/26/2012	5:00	M
RC22	7/30/2012	16:00	8/1/2012	5:00	1.2345	8/19/2012	5:00	M
RC23	8/6/2012	12:00	8/8/2012	5:00	1.5015	8/28/2012	5:00	F
RC3	7/24/2012	9:00	7/26/2012	5:00	1.691	8/11/2012	5:00	F
RC4	7/26/2012	14:00	7/28/2012	5:00	1.534	8/14/2012	5:00	F
RC5	7/25/2012	13:00	7/27/2012	5:00	1.6923	8/14/2012	5:00	F
RC6	7/26/2012	14:00	7/28/2012	5:00	1.2188	8/14/2012	5:00	M
RC7	7/26/2012	14:00	7/28/2012	5:00	1.3442	8/13/2012	5:00	M

	Pre-pupal			Pupal				Adult		
RC8	7/26/2012	14:00		7/28/2012	5:00	1.3016		8/13/2012	5:00	M
RC9	7/26/2012	14:00		7/28/2012	5:00	1.3014		8/13/2012	5:00	M
RS1	7/24/2012	5:00		7/26/2012	5:00	1.7947		8/11/2012	5:00	F
RS10	7/27/2012	8:00		7/29/2012	5:00	1.5356		8/15/2012	5:00	F
RS11	7/30/2012	10:00		8/1/2012	5:00	1.2671		8/19/2012	5:00	F
RS12	7/30/2012	5:00		8/1/2012	5:00	1.3108		8/18/2012	5:00	M
RS13	7/30/2012	5:00		8/1/2012	5:00	1.5335		8/18/2012	5:00	F
RS14	8/4/2012	12:00		8/6/2012	9:30	1.4709		8/23/2012	5:00	F
RS15	8/10/2012	5:00		8/12/2012	5:00	1.2427		8/29/2012	5:00	M
RS16	8/4/2012	12:00		8/6/2012	5:00	1.4894		8/24/2012	5:00	F
RS17	7/31/2012	9:00		8/2/2012	5:00	1.3065		8/19/2012	5:00	M
RS18	7/31/2012	9:00		8/2/2012	5:00	1.3474		8/21/2012	5:00	M
RS19	7/31/2012	10:00		8/2/2012	5:00	1.4878		8/20/2012	5:00	F
RS2	7/21/2012	5:00		7/22/2012	16:30	1.5258		8/7/2012	5:00	M
RS20	7/30/2012	13:00		8/1/2012	5:00	1.1764		8/20/2012	5:00	M
RS21	7/29/2012	5:00		7/31/2012	5:00	1.3674		8/18/2012	5:00	M
RS22	8/2/2012	10:00		8/4/2012	5:00	1.2311		8/21/2012	5:00	M
RS24	8/8/2012	5:00		8/10/2012	5:00	1.3562		8/29/2012	5:00	M
RS25	8/4/2012	12:00		8/6/2012	5:00	1.5827		8/23/2012	5:00	F
RS4	7/23/2012	9:00		7/25/2012	5:00	1.5413		8/11/2012	5:00	M
RS5	7/23/2012	7:00		7/25/2012	6:00	1.6996		8/11/2012	5:00	F
RS8	7/27/2012	8:00		7/29/2012	5:00	1.099		8/14/2012	5:00	M
RS9	7/25/2012	9:00		7/27/2012	5:00	1.4331		8/13/2012	5:00	F

Appendix P. Oviposition data for *P. palamedes* showing the number of eggs laid by each female on two host plants (*P. borbonia* and *C. camphora*) and inanimate objects (*i.e.*, oviposition cage).

Treatments are no choice trials with either *P. borbonia*, *C. camphora*, or plastic foliage and choice trails with both *P. borbonia* and *C. camphora*.

Female	Treatment	Date		Eggs		
				<i>P.borbonia</i>	<i>C. camphora</i>	Inanimate
A	<i>P. borbonia</i>	6/21/13		0	na	0
B	<i>P. borbonia</i>	6/22/13		0	na	0
C	<i>P. borbonia</i>	6/23/13		17	na	1
D	<i>P. borbonia</i>	6/23/13		222	na	12
E	<i>P. borbonia</i>	6/24/13		8	na	0
F	<i>P. borbonia</i>	6/23/13		0	na	0
G	<i>P. borbonia</i>	6/23/13		30	na	5
H	<i>P. borbonia</i>	6/24/13		12	na	0
I	<i>P. borbonia</i>	6/24/13		32	na	0
J	<i>P. borbonia</i>	6/24/13		0	na	0
K	<i>P. borbonia</i>	6/25/13		8	na	4
L	<i>P. borbonia</i>	6/25/13		0	na	0
M	<i>P. borbonia</i>	6/25/13		0	na	0
N	<i>P. borbonia</i>	6/26/13		9	na	0
O	<i>P. borbonia</i>	6/27/13		36	na	0
P	<i>P. borbonia</i>	6/27/13		0	na	0
Q	<i>P. borbonia</i>	6/26/13		6	na	0
R	<i>P. borbonia</i>	6/26/13		13	na	0
S	<i>P. borbonia</i>	6/27/13		58	na	2
T	<i>P. borbonia</i>	6/27/13		0	na	0
U	<i>C. camphora</i>	6/25/13		na	0	0
V	<i>C. camphora</i>	6/26/13		na	0	0
W	<i>C. camphora</i>	6/28/13		na	0	0
X	<i>C. camphora</i>	6/28/13		na	0	0
Y	<i>C. camphora</i>	6/28/13		na	0	0
Z	<i>C. camphora</i>	6/29/13		na	0	0
AA	<i>C. camphora</i>	7/01/13		na	0	0
BB	<i>C. camphora</i>	7/03/13		na	0	0
CC	<i>C. camphora</i>	7/03/13		na	0	0
DD	<i>C. camphora</i>	7/04/13		na	0	0
EE	<i>C. camphora</i>	8/05/13		na	0	0

FF	<i>C. camphora</i>	8/07/13		na	0	0
GG	<i>C. camphora</i>	8/08/13		na	0	0
HH	<i>C. camphora</i>	8/26/13		na	0	0
II	<i>C. camphora</i>	8/30/13		na	0	0
JJ	<i>C. camphora</i>	8/30/13		na	0	20
KK	<i>C. camphora</i>	8/30/13		na	19	9
LL	<i>C. camphora</i>	8/30/13		na	3	26
MM	Choice	7/02/13		0	0	0
NN	Choice	7/02/13		0	0	0
OO	Choice	7/08/13		0	0	0
PP	Choice	7/09/13		10	1	0
QQ	Choice	7/12/13		0	0	0
RR	Choice	7/12/13		38	0	0
SS	Choice	7/16/13		0	0	0
TT	Choice	7/17/13		0	0	0
WW	Choice	7/17/13		0	0	0
XX	Choice	8/04/13		3	0	0
YY	Choice	8/04/13		0	0	0
ZZ	Choice	8/27/13		4	0	0
AAA	Choice	8/27/13		37	0	0
BBB	Choice	9/03/13		0	0	0
CCC	Choice	9/03/13		0	0	0
DDD	Choice	9/10/13		62	1	3
EEE	Choice	9/11/13		0	0	0
FFF	Choice	9/14/13		0	0	0
GGG	Choice	9/15/13		0	0	0
HHH	Plastic	9/04/13		na	na	0
III	Plastic	9/05/13		na	na	0
KKK	Plastic	9/12/13		na	na	0
LLL	Plastic	9/12/13		na	na	0
MMM	Plastic	9/12/13		na	na	0
NNN	Plastic	9/17/13		na	na	0
OOO	Plastic	9/24/13		na	na	0
PPP	Plastic	9/25/13		na	na	0

Appendix Q. Data from pollinator visitation surveys of *P. ciliaris*. Only those survey period for which pollinators were observed are shown. PAPA = *P. palamedes* and PHSE = *P. sennae*. Some individuals were observed visiting multiple plants before flying out of view.

Site	1			
Date	8/24/2012			
Time period	11:15-12:15			
Orchid	Flowers open	Flowers visited	Species	Individual
1	19	5	PAPA	1
2	22	2	PAPA	1
1	19	5	PAPA	2
1	19	3	PAPA	3
3	9	3	PAPA	4
2	22	2	PAPA	4
4	20	3	PAPA	5
1	19	3	PAPA	6
1	19	4	PAPA	7
Site	1			
Date	8/24/2012			
Time period	1:15-2:15			
Orchid	Flowers open	Flowers visited	Species	Individual
1	19	6	PAPA	1
2	22	4	PAPA	2
2	22	3	PAPA	3
1	19	5	PHSE	1
4	20	1	PHSE	2
2	22	2	PHSE	3
4	20	1	PHSE	3
6	5	5	PAPA	4
5	5	2	PAPA	4
Site	1			
Date	8/25/2012			
Time period	9:30-10:00			
Orchid	Flowers open	Flowers visited	Species	Individual

4	20	5	PAPA	1
2	22	1	PAPA	2
Site	4			
Date	8/25/2012			
Time period	10:05-11:05			
Orchid	Flowers open	Flowers visited	Species	Individual
1	10	5	PAPA	1
2	10	10	PAPA	1
3	5	2	PAPA	1
Site	1			
Date	8/25/2012			
Time period	12:00-1:00			
Orchid	Flowers open	Flowers visited	Species	Individual
4	20	10	PAPA	1
Site	4			
Date	8/26/2012			
Time period	9:40-10:10			
Orchid	Flowers open	Flowers visited	Species	Individual
7	14	13	PAPA	1
6	12	2	PAPA	1
5	11	2	PAPA	1
7	14	2	PAPA	2
2	10	10	PAPA	3
3	5	1	PAPA	3
Site	1			
Date	8/26/2012			
Time period	10:15-10:45			
Orchid	Flowers open	Flowers visited	Species	Individual
6	5	2	PAPA	1
1	19	1	PAPA	2
2	22	1	PAPA	2
4	20	3	PAPA	3
5	21	3	PAPA	3

1	19	2	PAPA	4
2	22	3	PAPA	4
4	20	2	PAPA	5
2	22	8	PAPA	6
1	19	3	PAPA	6
Site	2			
Date	8/26/2012			
Time period	11:00-12:00			
Orchid	Flowers open	Flowers visited	Species	Individual
2	9	3	PAPA	1
2	9	1	PAPA	2
Site	4			
Date	8/26/2012			
Time period	12:15-12:45			
Orchid	Flowers open	Flowers visited	Species	Individual
6	12	2	PAPA	1
7	14	3	PAPA	1
2	10	3	PAPA	2
4	9	4	PAPA	2
Site	3			
Date	8/26/2012			
Time period	1:25-1:55			
Orchid	Flowers open	Flowers visited	Species	Individual
1	19	1	PAPA	1
Site	4			
Date	8/26/2012			
Time period	2:00-2:30			
Orchid	Flowers open	Flowers visited	Species	Individual
7	14	1	PAPA	1

Appendix R. Nectar spur lengths of *P. ciliaris* plants. For two individuals, a nectar spur from only one flower was measured.

Plant	Flower	Length (mm)
1	1	30.48
1	2	30.27
2	1	27.97
2	2	27.64
3	1	30.41
3	2	31.11
4	1	28.25
4	2	28.17
5	1	29.54
5	2	29.41
6	1	31.48
6	2	32.59
7	1	28.93
7	2	27.79
8	1	30.49
8	2	
9	1	31.68
9	2	
10	1	27.64
10	2	26.56
11	1	27.3
11	2	27.29
12	1	26.57
12	2	28.69
13	1	27.78
13	2	27.62
14	1	27.14
14	2	26.29
15	1	30.23
15	2	28.92
16	1	33.17
16	2	29.25
17	1	27.57
17	2	26.66
18	1	30.8
18	2	28.16

Plant	Flower	Length (mm)
19	1	30.28
19	2	29.25
20	1	29.67
20	2	29.04
21	1	29.32
21	2	29.43
22	1	29.61
22	2	27.96

Appendix S. Proboscis lengths of *P. palamedes* and *P. sennae*.

<i>P. palamedes</i>				<i>P. sennae</i>		
Individual	Sex	Length (mm)		Individual	Sex	Length (mm)
1	F	27.07		1	F	29.93
2	F	28.15		2	F	29.49
3	F	29.78		3	F	28.05
4	F	28.8		4	F	30.8
5	F	31.11		5	F	29
6	F	26.98		6	F	29.4
7	F	26.3		7	F	27.9
8	F	28.55		8	F	27.56
9	F	29.64		9	F	30.13
10	F	29.07		10	F	30.46
11	M	30.24		11	M	27.94
12	M	31.23		12	M	27.97
13	M	30.02		13	M	28.85
14	M	30.41		14	M	29.85
15	M	28.68		15	M	28.12
16	M	30.37		16	M	29.64
17	M	29.17		17	M	29.4
18	M	28.88		18	M	28.94
19	M	28.6		19	M	28.55
20	M	28.22		20	M	30.4

Appendix T. Data from fruit selectivity experiments. For background tree ID's, T = *T. sebifera*, M = *M. cerifera* and the number represents the individual tree being used. Columns labelled "*P. borbonia*" and "*C. camphora*" show the number of fruits removed of each species for that day.

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>
12/11/2012	T1	3	7
12/11/2012	T2	0	1
12/11/2012	T3		
12/11/2012	T4		
12/11/2012	T5		
12/11/2012	M1		
12/11/2012	M2		
12/11/2012	M3		
12/11/2012	M4		
12/11/2012	M5		
12/12/2012	T1	1	10
12/12/2012	T5	1	0
12/12/2012	T2		
12/12/2012	T3		
12/12/2012	T4		
12/12/2012	M1		
12/12/2012	M2		
12/12/2012	M3		
12/12/2012	M4		
12/12/2012	M5		
12/13/2012	T1	5	0
12/13/2012	T5	1	0
12/13/2012	T2		
12/13/2012	T3		
12/13/2012	T4		
12/13/2012	M1		
12/13/2012	M2		
12/13/2012	M3		
12/13/2012	M4		
12/13/2012	M5		
12/14/2012	M4		
12/14/2012	M5		
12/14/2012	M1		
12/14/2012	M2		

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>
12/14/2012	M3		
12/14/2012	T1		
12/14/2012	T2		
12/14/2012	T3		
12/14/2012	T4		
12/14/2012	T5		
12/15/2012	T7	1	4
12/15/2012	T6		
12/15/2012	T8		
12/15/2012	T9		
12/15/2012	T10		
12/15/2012	M6		
12/15/2012	M7		
12/15/2012	M8		
12/15/2012	M9		
12/15/2012	M10		
12/16/2012	M10	1	1
12/16/2012	M8	1	0
12/16/2012	T7	3	10
12/16/2012	T6	0	1
12/16/2012	M6		
12/16/2012	M7		
12/16/2012	M9		
12/16/2012	T8		
12/16/2012	T9		
12/16/2012	T10		
12/18/2012	M11	0	5
12/18/2012	M12	9	10
12/18/2012	M13	10	2
12/18/2012	T11	1	8
12/18/2012	T12	2	10
12/18/2012	T13	8	10
12/18/2012	M14		
12/18/2012	M15		
12/18/2012	T14		
12/18/2012	T15		
12/18/2012	F1		
12/18/2012	F2		
12/18/2012	F3		
12/18/2012	F4		

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>
12/19/2012	M11	10	9
12/19/2012	M12	9	8
12/19/2012	M13	6	2
12/19/2012	T11	10	10
12/19/2012	T13	5	10
12/19/2012	T12		
12/19/2012	M14		
12/19/2012	M15		
12/19/2012	T14		
12/19/2012	T15		
12/19/2012	F1		
12/19/2012	F2		
12/19/2012	F3		
12/19/2012	F4		
12/20/2012	M11	1	6
12/20/2012	M12	1	1
12/20/2012	T11	7	10
12/20/2012	T12	5	3
12/20/2012	T13	5	5
12/20/2012	T14		
12/20/2012	T15		
12/20/2012	M13		
12/20/2012	M14		
12/20/2012	M15		
12/20/2012	F1		
12/20/2012	F2		
12/20/2012	F3		
12/20/2012	F4		
1/10/2013	M16	3	10
1/10/2013	M17	2	0
1/10/2013	T18	3	0
1/10/2013	M18		
1/10/2013	M19		
1/10/2013	M20		
1/10/2013	T19		
1/10/2013	T20		
1/10/2013	T16		
1/10/2013	T17		
1/11/2013	M16		
1/11/2013	M17		

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>
1/11/2013	T18		
1/11/2013	M18		
1/11/2013	M19		
1/11/2013	M20		
1/11/2013	T19		
1/11/2013	T20		
1/11/2013	T16		
1/11/2013	T17		
1/11/2013	F1		
1/11/2013	F2		
1/11/2013	F3		
1/11/2013	F4		
1/12/2013	M16		
1/12/2013	M17		
1/12/2013	T18		
1/12/2013	M18		
1/12/2013	M19		
1/12/2013	M20		
1/12/2013	T19		
1/12/2013	T20		
1/12/2013	T16		
1/12/2013	T17		
1/12/2013	F1		
1/12/2013	F2		
1/12/2013	F3		
1/12/2013	F4		
1/13/2013	F1		
1/13/2013	F2		
1/13/2013	F3		
1/13/2013	F4		
1/15/2013	M21	0	1
1/15/2013	M23	1	0
1/15/2013	M24	10	7
1/15/2013	M25	10	9
1/15/2013	T21	2	7
1/15/2013	T22	10	10
1/15/2013	T23	10	10
1/15/2013	T24	10	10
1/15/2013	T25	5	8
1/15/2013	M22		

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>
1/16/2013	M25	3	1
1/16/2013	T25	4	0
1/16/2013	M21		
1/16/2013	M22		
1/16/2013	M23		
1/16/2013	M24		
1/16/2013	T21		
1/16/2013	T22		
1/16/2013	T23		
1/16/2013	T24		
1/17/2013	M21	10	10
1/17/2013	M22	10	10
1/17/2013	M25	10	10
1/17/2013	T21	10	10
1/17/2013	T22	10	10
1/17/2013	T25	10	10
1/17/2013	M23		
1/17/2013	M24		
1/17/2013	T23	10	10
1/17/2013	T24		
1/6/2014	M1		
1/6/2014	M2		
1/6/2014	M3		
1/6/2014	T1		
1/6/2014	M4		2
1/6/2014	M5		
1/6/2014	T2		
1/6/2014	T3	2	10
1/6/2014	T4		3
1/6/2014	T5		
1/6/2014	T6	5	10
1/6/2014	M6		
1/6/2014	F1		
1/6/2014	F2		
1/7/2014	M1		
1/7/2014	M2	4	10
1/7/2014	M3		
1/7/2014	T1		
1/7/2014	M4		

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>
1/7/2014	M5		
1/7/2014	T2		
1/7/2014	T3	5	10
1/7/2014	T4	1	10
1/7/2014	T5	7	10
1/7/2014	T6		
1/7/2014	M6		
1/7/2014	F1		4
1/7/2014	F2		4
1/8/2014	M1	10	10
1/8/2014	M2		
1/8/2014	M3		
1/8/2014	T1		
1/8/2014	M4		
1/8/2014	M5		
1/8/2014	T2		4
1/8/2014	T3	8	10
1/8/2014	T4	10	10
1/8/2014	T5	4	10
1/8/2014	T6	2	10
1/8/2014	M6	4	10
1/8/2014	F1		2
1/8/2014	F2		
1/9/2014	M1		
1/9/2014	M2	4	10
1/9/2014	M3	10	10
1/9/2014	T1	4	10
1/9/2014	M4		
1/9/2014	M5		
1/9/2014	T2	2	9
1/9/2014	T3	10	10
1/9/2014	T4	3	10
1/9/2014	T5	4	8
1/9/2014	T6	3	10
1/9/2014	M6	3	7
1/9/2014	F1		1
1/9/2014	F2		
1/11/2014	M2	6	8
1/11/2014	F1		
1/11/2014	F2		1

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>
1/13/2014	T2	7	10
1/15/2014	M1		
1/15/2014	T1		
1/15/2014	T2		
1/15/2014	M2		
1/15/2014	M3		
1/15/2014	T3		
1/15/2014	M4		
1/15/2014	T4		
1/15/2014	M5		6
1/15/2014	T5		
1/15/2014	F1		
1/15/2014	F2		
1/16/2014	M1	3	10
1/16/2014	T1		
1/16/2014	T2		10
1/16/2014	M2		
1/16/2014	M3		
1/16/2014	T3		
1/16/2014	M4		
1/16/2014	T4	3	1
1/16/2014	M5	10	10
1/16/2014	T5		
1/16/2014	F1		
1/16/2014	F2		
1/17/2014	M1		5
1/17/2014	T1		
1/17/2014	T2		7
1/17/2014	M2		
1/17/2014	M3		2
1/17/2014	T3		
1/17/2014	M4		
1/17/2014	T4	3	1
1/17/2014	M5	7	10
1/17/2014	T5		
1/18/2014	M1	2	10
1/18/2014	T1		
1/18/2014	T2		10
1/18/2014	M2		
1/18/2014	M3	10	10

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>
1/18/2014	T3		
1/18/2014	M4		
1/18/2014	T4	10	10
1/18/2014	M5	6	10
1/18/2014	T5		3
1/19/2014	M1	6	10
1/19/2014	T1	8	2
1/19/2014	T2	10	10
1/19/2014	M2	10	10
1/19/2014	M3	10	10
1/19/2014	T3		
1/19/2014	M4		
1/19/2014	T4	10	9
1/19/2014	M5	10	8
1/19/2014	T5	1	10

Appendix U. Data from fruit accessibility experiments. For background tree ID's, $T = T.$
sebifera, $M = M. cerifera$ and the number represents the individual tree being used (E2 =
 experiment two). Columns labelled "*P. borbonia*" and "*C. camphora*" show the number of fruits
 removed of each species for that day. The column labelled "NA fruit" shows which fruit was on
 the non-accessible display.

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>	NA fruit
1/17/2014	E2T1		3	<i>C. camphora</i>
1/17/2014	E2T2			<i>C. camphora</i>
1/18/2014	E2T1	13	20	<i>C. camphora</i>
1/18/2014	E2T2		7	<i>C. camphora</i>
1/19/2014	E2T1	17	20	<i>P. borbonia</i>
1/19/2014	E2T2	5	16	<i>C. camphora</i>
1/20/2014	E2T2	17	20	<i>P. borbonia</i>
1/22/2014	E2M1	1	20	<i>C. camphora</i>
1/22/2014	E2T3	20	20	<i>C. camphora</i>
1/22/2014	E2M2	20	20	<i>C. camphora</i>
1/22/2014	E2T4	20	11	<i>C. camphora</i>
1/23/2014	E2M1	20	20	<i>C. camphora</i>
1/23/2014	E2T3	20	20	<i>C. camphora</i>
1/23/2014	E2M2	20	20	<i>C. camphora</i>
1/23/2014	E2T4	20	17	<i>C. camphora</i>
1/24/2014	E2M1	20	20	<i>P. borbonia</i>
1/24/2014	E2T3	20	20	<i>P. borbonia</i>
1/24/2014	E2M2	20	20	<i>P. borbonia</i>
1/24/2014	E2T4	20	20	<i>P. borbonia</i>
1/25/2014	E2M1	20	20	<i>P. borbonia</i>
1/25/2014	E2T3	20	20	<i>P. borbonia</i>
1/25/2014	E2M2	20	20	<i>P. borbonia</i>
1/25/2014	E2T4	20	20	<i>P. borbonia</i>
1/27/2014	E2M3			<i>C. camphora</i>
1/27/2014	E2T5			<i>C. camphora</i>
1/27/2014	E2M4	2	9	<i>C. camphora</i>
1/27/2014	E2T6			<i>C. camphora</i>
1/28/2014	E2M3	6		<i>C. camphora</i>
1/28/2014	E2T5	1		<i>C. camphora</i>
1/28/2014	E2M4	4	20	<i>C. camphora</i>
1/28/2014	E2T6	8	20	<i>C. camphora</i>

Date	Background tree ID	<i>P. borbonia</i>	<i>C. camphora</i>	NA fruit
1/29/2014	E2M3	20	20	<i>C. camphora</i>
1/29/2014	E2T5	20	20	<i>C. camphora</i>
1/29/2014	E2M4	5	20	<i>C. camphora</i>
1/29/2014	E2T6	20	20	<i>C. camphora</i>
1/30/2014	E2M3	11	20	<i>P. borbonia</i>
1/30/2014	E2T5	20	20	<i>P. borbonia</i>
1/30/2014	E2M4	2	20	<i>P. borbonia</i>
1/30/2014	E2T6	20	20	<i>P. borbonia</i>
1/31/2014	E2M3	13	20	<i>P. borbonia</i>
1/31/2014	E2T5	20	20	<i>P. borbonia</i>
1/31/2014	E2M4		8	<i>P. borbonia</i>
1/31/2014	E2T6	20	20	<i>P. borbonia</i>

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