Spring 5-7-2022

Restoration through reassembly: evaluating the role of native plants in combatting Chinese tallow

Olaniyi Ajala
ajalaoo@jacks.sfasu.edu

Repository Citation
Ajala, Olaniyi, "Restoration through reassembly: evaluating the role of native plants in combatting Chinese tallow" (2022). *Electronic Theses and Dissertations*. 433.
https://scholarworks.sfasu.edu/etds/433

Restoration through reassembly: evaluating the role of native plants in combatting Chinese tallow

RESTORATION THROUGH REASSEMBLY: EVALUATING THE ROLE OF NATIVE PLANTS IN COMBATTING CHINESE TALLOW

By

OLANIYI O. AJALA, B.S., M.S.

Presented to the Faculty of the Graduate School of
Stephen F. Austin State University
In Partial Fulfillment
Of the Requirements

For the Degree of
Doctor of Philosophy in Forestry

Stephen F. Austin State University
May 2022

RESTORATION THROUGH REASSEMBLY: EVALUATING THE IMPORTANCE OF NATIVE PLANTS IN COMBATTING CHINESE TALLOW

By

OLANIYI O. AJALA, B.S., M.S.

APPROVED:

Jeremy Stovall, Ph.D., Dissertation Director

Brian Oswald, Ph.D., Committee Member

Kathryn R. Kidd, Ph.D., Committee Member

Yuhui Weng, Ph.D., Committee Member

James Van Kley, Ph.D., Committee Member

Freddie Avant, Ph.D.
Interim Dean of Research and Graduate Studies

ABSTRACT

Non-native, invasive species disrupt ecological processes and functions, posing a serious threat to natural ecosystems. By examining the growth metrics of the non-native, invasive tree, Chinese tallow (*Triadica sebifera* [L.] Roxb.), hereafter tallow, across different flooding and light regimes, I investigated how restructuring native communities with valuable native species will prevent the reestablishment of tallow. I studied the changes in morphological and physiological traits of tallow when growing with water tupelo (*Nyssa aquatica* L.), sugarberry (*Celtis occidentalis* L.), and green ash (*Fraxinus pennsylvanica* Marshall). I found that in the non-flooded and high irradiance treatments, tallow's growth metrics were highest when growing with sugarberry and water tupelo, but decreased when competing with green ash. I concluded that tallow may be less competitive with certain native species and underplanting may be a possible opportunity for improving the success rates of native trees species establishment in areas prone to tallow invasion.

I also investigated the interactive effect of light, flooding, and community types on the growth, dominance, and competitive ability of tallow and water tupelo, sugarberry, green ash, and baldcypress (*Taxodium distichum* [L.] Rich). I found that mixed community depressed the dominance of tallow in the flooded and low irradiance treatment, however, leaf area and leaf biomass of tallow increased in the mixed community in the non-flooded and high irradiance treatment. I concluded that establishing an appropriate native community in flooded and low irradiance environments may reduce future dominance of tallow.

I additionally tested the competitive ability of tallow, water tupelo, sugarberry, green ash, and baldcypress using the relative interaction index, taking into account the competition of native taxa growing with tallow (effect of natives as competitors) and competition of tallow growing with native taxa (effect of competition on natives). I concluded that with the exception of water tupelo, tallow had no significant impact on the biomass of the native species studied.

Finally, I investigated the growth and survival of water tupelo, baldcypress, water oak (*Quercus nigra* L.), and loblolly pine (*Pinus taeda* L.) across the Green Bayou Wetland Mitigation Bank (GBWMB) in Harris County, TX. I found that baldcypress had the highest survival rates that baldcypress and water tupelo had greater tree heights than loblolly pine, and that only loblolly pine and water tupelo had significant increases in tree heights between establishment and final measurements. I concluded that baldcypress is better adapted to the microenvironmental conditions across GBWMB. Overall, the results show that restructuring a native community by planting valuable native hardwood species can be a potential means of reducing future dominance of tallow.

DEDICATION

This dissertation is dedicated to my family, friends, and creator.

ACKNOWLEDGEMENTS

“*If you want to go fast, go alone. If you want to go far, go together*.”

The path to completing doctoral requirements has been filled with opportunities and experiences that have required me to step outside of my comfort zone. This journey was accomplished with the help and input of different individuals whose efforts I truly appreciate.

I would like to appreciate my supervisor and dissertation advisor, Dr. Jeremy Stovall for accepting and believing in me. I sincerely thank you for allowing me to develop my skill sets as a researcher, forester, and natural resource manager. Thank you for your support and encouragement throughout this research project. I also thank my committee members: Drs. Brian Oswald, Rebecca Kidd, Yuhui Weng, and James Van Kley. Thank you all for providing mentorship, guidance, and constructive feedback through the process of proposing, writing, and revising this dissertation. A special thank you to Dr. Williams Forbes who served as the Graduate School representative on this committee.

I also thank the funding source and collaborators for this research project: Harris County Soil and Water Conservation District, Harris County Flood Control District, the Arthur Temple College of Forestry and Agriculture at Stephen F. Austin State University, National Institute of Food and Agriculture, U.S. Department of Agriculture, and McIntire

Stennis Project (226427). This project could not have been completed without your generosity.

Much of science is done in collaboration and this is not an exception. Field assistance was provided by Justin Blakeley, Daniel Fichtel, Naria Torres, Ryan Burns, Taylor Massey, Thomas Dimmitt, Abby Dixon, and Tyler Jones. I am very grateful for your assistance. Greenhouse assistance was provided by Lana Welford, I am grateful for your assistance while using the growth chambers and greenhouse. I also want to say thank you to my colleagues and friends at Arthur Temple College of Forestry and Agriculture, both past, and present. I extend my thanks to Hannah Angel, Cassie Phillips, Cassey Edwards, Mike Tiller, Naria Torres, and Lais Machado.

Thank you to my family at Grace Bible Church, especially for grabbing coffee with me to check in on my progress. I am grateful to the leadership, elders, members of the church, and the Powell small group. Thank you to the Knowles, Powell, Walley, and Barham families for welcoming me into your homes. Thank you to Grace Bible Church's audiovisual and sound team; our weekly conversations were always a nudge for me in the right direction.

This acknowledgment would be incomplete without my heartfelt appreciation for my family. My parents have sacrificed everything for me and without your sacrifices, I would not be here today. Words would fail to express my gratitude to you, but I pray you would live long to reap the rewards of your sacrifices. To my mother, who is my biggest cheerleader and has constantly supported, encouraged, and prayed for me, I say thank you ma. To my father whose academic career inspired this journey of excellence, I say thank

you, sir. To my siblings, Olaoluwapo, Olalere, and Tomike thank you for your unrelenting love through the highs and lows. To my Nigerian community at Stephen F. Austin State University (Efosa Egharevba, Ayomide Odugbesi, Ayodeji Opeyemi, Femi Alakija, Dami Fateru, Seun Mofikaya, and Udeme Ekanem), thank you for making my stay in Nacogdoches worth it.

TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER 1

INTRODUCTION

Invasion by highly aggressive, non-native, invasive species (hereafter invasive plants) poses a serious threat to the ecological processes and functions in natural ecosystems. Non-native plants do not all pose the same threats to ecosystems, only about 1% of introduced plants become invasive and have a measurable impact on the communities (Rejmánek et al. 2005; Lockwood et al. 2013). These plants, however, are a major concern because they have an impact on ecosystem function and require a significant amount of effort to manage once established. Chinese tallow (*Triadica sebifera* [L.] Roxb.), hereafter tallow, is the most pervasive non-native tree species in the southern U.S. forests (Nowak et al. 2005; Wheeler and Ding 2014; Camarillo et al. 2015). Since its introduction in Savannah, Georgia in the late 18th century, the population of tallow has increased along the Gulf Coast from Florida to Texas, and it has been recorded in ten states, including Alabama, Arkansas, California, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Texas (Bruce et al. 1997; Wheeler and Ding 2014; Enloe et al. 2015).

Tallow is the most common and abundant nonnative tree species throughout the Mississippi Alluvial Flood plain. Tallow's rapid growth has had a significant impact on the southeastern United States' coastal prairies, riparian areas, floodplains, wetlands, forestlands, and natural areas. Tallow displaces native graminoids and forbs in the coastal prairies of South Houston's Galveston and Brazoria counties, forming monospecific stands that alter community structure and initiate new woodland types (Nowak et al. 2005). Tallow alters stand structure and composition in East Texas bottomland hardwoods by reducing overstory species diversity and stocking (Camarillo et al. 2015).

In natural ecosystems, effective management of invasive plants requires an integrated approach that manages both the invader and the ecological community. Herbicides effectively suppress growth and are frequently used as the primary control treatment in the management of invasive plants. In addition to herbicides, mechanical treatments and fire are used to suppress the growth of invasive plants while biological control reduces their vigor. Following invasive plants removal, actively promoting native plant diversity and abundance through regeneration can improve community resistance to invasion. Many studies have determined effective methods of controlling tallow. Herbicide application timing has a significant impact on herbicide efficacy for controlling tallow and should be correlated with leaf fall (when total nonstructural carbohydrate concentrations in tallow were found to be highest) and leaf and seed development (when total nonstructural carbohydrate concentrations in tallow were found to be lowest, Conway et al. 1999; Pile et al. 2017). Injection appears to be a more effective method of herbicide application when targeting large individuals of tallow, and herbicide assimilation into perennating buds and organs results in the highest plant mortality (Pile et al. 2017). Tallow is susceptible to fire when young and can be killed by fire when small (Richardson 2011; Pile et al. 2017b). However, the invader’s ability to resprout aggressively allows it to survive fire as root-sprouts after top-kill (Grace 1998). With age, the bark of tallow thickens, indicating increased fire resistance (Pile et al. 2017b). Mastication may reduce seed germination by reducing the variation in day-night temperature at the soil surface only when mulch depths exceed 5 cm (Donahue et al. 2004). On the other hand, the seeds of tallow are large with ample nutritional resources that can emerge from deep mulch depths before requiring energy from photosynthesis (Pile et al. 2017b). Tallow has several potential biological control agents with high host specificity and plant fitness impacts, including foliage feeders, root feeders, and gall formers (Pile et al. 2017b). Because invasive ecotypes of tallow have weaker defense mechanisms but a higher damage tolerance, biocontrol agents may reach high densities but fail to control invasive populations (Wang et al. 2011).

After any control method reduces tallow coverage, promoting the growth of fast-growing native trees can increase the resistance of the ecological community by filling the resulting gaps and preventing the re-establishment of tallow. The objective of this research was to determine the role of biotic resistance in the control of tallow by examining the growth, survival, and performance of tallow in interaction with native hardwood species. The dissertation is organized into five chapters. Chapter 1 provides a general introduction. Chapter 2 gives a detailed synthesis of the current body of knowledge on the interactions between tallow and native species. By reviewing the competitive interactions between tallow and co-occurring native species in the southern United States, I was able to identify the factors that contribute to the invasiveness of tallow and select native species that belong to the same functional group as tallow. In chapter 3, the growth, survival, and physiological responses of tallow in competition with native hardwood species under a range of flooding and light availability conditions that are typical of floodplain forests is evaluated. The fluctuating resources hypothesis states that a community is more vulnerable to invasion after a disturbance displaces native species and increases the availability of limited resources. I compared the growth and survival of tallow in native, mixed, and invasive communities under a range of flooding and light conditions representative of natural conditions in floodplain forests (Chapter 4). Tallow compromises the overall integrity of the bottomland hardwood forest restoration process in the Southern United States. In chapter 5, an investigation of the growth and survival of one evergreen and three deciduous species as they varied along natural gradients of light, soil water content, and soil texture in a bottomland hardwood forest where tallow populations were suppressed is presented.

LITERATURE CITED

Bruce, K.A., G.N. Cameron, P.A. Harcombe, and G. Jubinsky. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) Roxb. Natural Areas Journal. 17, 255–260.

Camarillo, S.A., J.P. Stovall, and C.J. Sunda. 2015. The impact of Chinese tallow (*Triadica sebifera*) on stand dynamics in bottomland hardwood forests. Forest Ecology and Management. 344, 10–19.

Conway, W.C., L.M. Smith, R.E. Sosebee, and J.F. Bergan. 1999. Total Nonstructural Carbohydrate Trends in Chinese Tallow Roots. Journal of Range Management. 52(5):539–542.

Donahue, C., W.E. Rogers, and E. Siemann. 2004. Effects of temperature and mulch depth on Chinese tallow tree (*Sapium sebiferum*) seed germination. Texas Journal of Science. 56, 347–356.

Enloe, S.F., N.J. Loewenstein, D. Streett, and D.K. Lauer. 2015. Herbicide treatment and application method influence root sprouting in Chinese tallowtree (*Triadica sebifera*). Invasive Plant Science and Management. 8, 160–168.

Grace, J.B., 1998. Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion? Endangered Species Update 15, 70–76.

Leonard, N., 2005. Tadpoles of early breeding amphibians are negatively affected by leaf litter from invasive Chinese tallow trees. In: American Geophysical Union, Spring Meeting 2005, abstract #NB14A-05, p. 05.

Lockwood, J.L., M.F. Hoopes, and M.P. Marchetti. 2013. Invasion Ecology. John Wiley & Sons, West Sussex, UK.

Nowak, D.J., Smith, P.D., Merritt, M., Giedraitis, J., Walton, J.T., Hoehn, R.E., Stevens, J.C., Crane, D.E., Estes, M., Stetson, S., Burditt, C., Hitchcock, D., and W. Holtcamp. 2005. Houston's regional forests: Structure, function, and values. Texas Forest Service, Houston, Texas.

Pile, L.S., G.G. Wang, T.A. Waldrop, J.L. Walker, W.C. Bridges, Jr., and P.A. Layton. 2017. Managing an Established Tree Invader: Developing Control Methods for Chinese Tallow (*Triadica sebifera*) in Maritime Forests. Journal of Forestry. 115 (6): 522-529.

Pile, L.S., G.G. Wang, J.P. Stovall, E. Siemann, G.S. Wheeler, and C.A. Gabler. 2017b. Mechanisms of Chinese tallow (*Triadica sebifera*) invasion and their management implications – A review. Forest Ecology and Management. 404:1-13.

Rejmánek, M., D.M. Richardson, and P. Pysek. 2005. Plant invasions and invasibility of plant communities. Pages 332-354 in E. van Der Maarel, editor. Vegetation Ecology. Blackwell Publishing, Malden, MA.

Richardson, D.M., 2011. Trees and shrubs. In: Simberloff, D., Rejmánek, M. (Eds.), Encyclopedia of Biological Invasions. University of California Press, Berkeley, CA, pp. 670–677.

Wang, Y., W. Huang, E. Siemann, J.W. Zou, G.S. Wheeler, J. Carrillo, and J.Q. Ding. 2011. Lower resistance and higher tolerance of invasive host plants: biocontrol agents reach high densities but exert weak control. Ecological Applications. 21:729–738.

Wheeler, G.S. and J. Ding. 2014. Is Chinese tallowtree, *Triadica sebifera*, an appropriate target for biological control in the United States? Invasive Plant Science and Management. 7: 345–359.

CHAPTER 2

COMPETITIVE INTERACTIONS BETWEEN CHINESE TALLOW (*TRIADICA SEBIFERA*) AND CO-OCCURRING NATIVE SPECIES IN THE SOUTHERN UNITED STATES – A REVIEW

INTRODUCTION

The southern United States (US) forest region is one of the most productive forests in the world, accounting for 2% of the total forest area, yet producing 63% of US timber volume, 18% of the global pulpwood, and 7% of global industrial wood (Gan et al. 2009; Oswalt et al. 2012; Sharma et al. 2021). The introduction and spread of highly competitive non-native plants have the potential to reduce forest economic value, productivity, and biodiversity (Jones and McLeod 1990; Miller et al. 2003). The most influential invasive plant species can transform the communities they invade and form monospecific stands (Rejmánek et al. 2005). Chinese tallow tree (*Triadica sebifera* [L.] Roxb.), hereafter tallow, is one such species. It is the most recognized, forest-stand-replacing, non-native tree species in the southern US forests (Miller et al. 2008; Gan et al 2009). Tallow has become naturalized from the Gulf Coast of Texas to the Atlantic Coast of North Carolina where it occupies the edges and openings of coastal prairies, floodplains, wetlands, forestlands, and natural areas (Siemann and Rogers 2003; Pile et al. 2017). It has been shown to convert coastal prairies to woodland thickets where it displaces federally endangered bird species, impacts amphibian lifecycles, and suppresses fire regimes (Bruce et al. 1997; Leonard 2005; Pile et al. 2017).

Hypotheses that explain the dominance of invasive plants can be grouped into two broad categories: (1) those focused on the attributes of the community being invaded, and (2) those focused on the characteristics of the invasive plants (Pratt and Black 2006). One hypothesis focused on the community suggests that species-rich plant communities are resistant to invasion, while another suggests that the spread of invasive plants is facilitated by their release from specialist herbivores or diseases from their native range and avoidance of generalist herbivores in their new habitat (Elton 1958). A third hypothesis posits that natural and anthropogenic disturbances facilitate the invasion of communities (Lockwood et al. 2013). Invasions occur in communities based on their susceptibility to invasion; certain characteristics make communities susceptible to biological invasion.

Hypotheses focused on the characteristics of invasive plants highlight the biological traits of species that contribute to their invasive nature (Pratt and Black 2006). Most species perish upon introduction into a new range and according to the rule of tens, only 10% of species introduced into a new range successfully transit an invasion stage (Williamson 1996; Lockwood et al. 2013). According to this rule, only 10% of introduced species pass through the transport stage, 10% of transported species pass through the establishment stage, 10% of established species pass through the spread stage, and 10% of species that become widespread and abundant cause some kind of ecological or economic harm, earning the label "invasive" (Williamson 1996; Lockwood et al. 2013). Identifying the traits common among successful invaders enhances the ability to better manage invasive plants (Pratt and Black 2006).

Tallow’s success in the southern US can be attributed to community susceptibility to invasion and the biological features that enable the invader to overcome the invasion stages. These biological features include an unusual combination of fast growth, high tolerance to environmental stress, and phenotypic plasticity (Rogers and Siemann 2002; Butterfield et al. 2004; Gan et al. 2009). Phenotypic plasticity of a trait refers to the property of a given genotype to express different phenotypes in different environments (Zou et al. 2009). Some studies suggest that phenotypic plasticity plays an important role in the success of tallow in North America. For instance, in response to the lack of attack from herbivores in North America, tallow has evolved reduced allocation to defense with increased allocation to growth and/or reproduction (Siemanns and Rogers 2001; Siemanns and Rogers 2003c; Siemanns and Rogers 2003d). Invasive ecotypes of tallow (invasive populations in North America) have greater phenotypic plasticity than native ecotypes (native populations in China), suggesting increased plasticity in invaded range (Zou et al. 2007; Huang et al. 2012; Chen et al. 2013). Phenotypic plasticity has been identified as a fundamental trait contributing to tallow’s invasiveness and may explain its superior performance and ability to displace native species (Jones and McLeod 1990; Rogers and Siemann 2002).

Much of the literature on tallow has been focused on studying the growth, survival, and competitiveness of tallow and co-occurring native species during juvenile stages. Tallow populations in the southern United States have increased by several orders of magnitude over the last few decades, displacing native species. In order to understand the functional traits that allow the invader to successfully displace specific native species, the interactions between tallow and native species must be synthesized. Functional traits are the ecological attributes of a species that are related to both resource acquisition tactics and the effect of the species on the overall pool of resources in the ecosystem (Lavorel and Garnier 2002; Funk et al. 2008). This review focused on the functional traits of native species and tallow because species with similar traits are generally more likely to be displaced through direct competition for resources (Funk et al. 2008).

This comprehensive review summarizes the species-specific interactions between tallow and co-occurring native species in the southern US. I conducted a literature search using the terms "Chinese tallow", "tallow", "*Triadica*", "*Triadica sebifera*", "*Sapium*", and "*Sapium sebiferum*". After the search, I focused on research in which tallow was grown with natives in the southern US to provide a synthesis of the current literature on tallow concerning its interactions with co-occurring native species in the southern US. Specifically, I described the silvics and functional traits of native species, reviewed their growth, survival, and physiological response when grown in competition with tallow along with a range of flooding and light-availability conditions, and identified the functional traits that contribute to the dominance of tallow in competition with specific native species.

Sugarberry

Sugarberry (*Celtis laevigata* Willd.) is a fast-growing, medium-sized tree commonly found on the broad flats and shallow sloughs within the floodplains of major southern rivers (Kennedy 1990a). Across the southern US, sugarberry ranges south from southern Virginia to southern Florida, west to central Texas, and north to southern Illinois (Kennedy 1990a). Sugarberry is ecologically similar to tallow: both species are medium, deciduous, fast-growing, and shade-tolerant trees that can attain a height of about 20 m at maturity (Kennedy 1990a; Bruce et al. 1997; Siemann and Rogers 2003). Both trees are insect-pollinated and tend to grow in wetter sites where their seeds are widely dispersed by water and birds (Siemann and Rogers 2003a). In floodplain forests, the mortality and growth rates of sugarberry saplings are most similar to those of tallow saplings (Harcombe et al. 1999). Because sugarberry and tallow are ecologically similar species, both have been paired in multiple studies to evaluate the mechanisms of invasion, and growth survival of tallow (Roger et al. 2000; Nijjer et al. 2002; Rogers &

Siemann 2002; Siemann & Rogers 2003a; Siemann & Rogers 2003b; Ajala et al. 2022). Pairing ecologically similar species is important in competition studies as species with similar traits are generally more likely to be displaced through direct competition for resources.

Both tallow and sugarberry are classified as shade tolerant, showing significantly lower growth in ambient light and rigorous stem growth in shaded conditions (Rogers and Siemann 2002). When compared with tallow in shaded conditions, sugarberry seedlings generally have a poor form with drooping branches with smaller diameters (Kennedy 1990; Rogers and Siemann 2002). This suggests that the invader may be more shade tolerant and able to compete for limiting light resources in shaded conditions. Shade-tolerant plants function optimally under low-light intensity conditions by efficiently trapping available light, maintaining a low rate of respiration, and partitioning large portions of their carbohydrate pool into leaf growth (Kozlowski and Pallardy 1996; Ruberti et al. 2012). Although both species are capable of establishing and surviving long-term in the forest understory, tallow may be more shade-tolerant than sugarberry.

Although the fruits of both species are similar in dimensions, sugarberry seeds are better adapted than tallow to a variety of germination conditions (Nijjer et al. 2002; Bonner and Karrfalt 2008). Fruits of both species are 6 – 13 mm in diameter. Sugarberry fruits are spherical drupes with a thin pulp enclosing a single bony nutlet while tallow fruits are rounded, three-lobed capsules with 1 – 3 waxy seeds per capsule (Bonner and Karrfalt 2008). Both species produce good seed crops every year which are eaten by wildlife, and the fruits persist on the branches into the winter. Seeds of both species have the same germination requirements, which are primarily influenced by fluctuating temperatures (Nijjer et al. 2002). Compared with sugarberry, tallow does not have a light requirement for germination as the invader has a higher occurrence of germination in darkness while germination in sugarberry increases with continuous light (Nijjer et al. 2002). Sugarberry seeds have less restrictive germination requirements, greater germination rates, and can germinate across a broader range of environmental conditions than tallow (Nijjer et al. 2002). Since sugarberry is better adapted to a variety of germination conditions, adaptation to a broader range of environmental germination tolerances may not explain the invader's dominance over this native.

Lack of herbivory may explain tallow's overperformance and invasiveness (Rogers and Siemann 2002). Tallow is attacked by more than 100 insects in China but in the southern US, tallow suffers less insect damage as a seedling than sugarberry and other native tree species (Rogers and Siemann 2003; Zheng et al. 2005). In the southern US, sugarberry seedlings are browsed by insects and vertebrates more frequently than tallow in both shade and ambient light conditions (Rogers and Siemann 2003). The lack of herbivory may have allowed tallow to evolve reduced allocation to defense and increased allocation to growth and/or reproduction. Relative to native populations of tallow, invasive populations have lower concentrations of phenolics, produce lower amounts of extrafloral nectar, have more rapid growth rates, suffer more herbivore attacks, and have a higher tolerance to herbivores (Siemann et al. 2017). Invasive populations of tallow outperformed sugarberry in all resource conditions, despite sugarberry being one of the fastest-growing native trees in Texas (Siemann and Rogers 2003a). Despite having higher survival rates than tallow, sugarberry seedlings were smaller in field experiments with manipulated nitrogen and light treatments (Siemann and Rogers 2003a). Despite the ecological similarity between the two species, the lack of herbivory may give tallow an advantage over sugarberry in southern US forests.

Baldcypress

Baldcypress (*Taxodium distichum* (L.) Rich.) is a slow-growing, very long-lived deciduous conifer that grows in the deep swamps and bottomland forests of the southern United States (Wilhite and Toliver 1990). The range of this native extends from southern Delaware to southern Florida and west to southeastern Texas, where it is one of the dominant forest wetland species (Wilhite and Toliver 1990; Conner 1994). Baldcypress is ranked as very tolerant to flooding; first and second-year growth is best under flooded conditions even though the native grows on sites characterized by intermittent, frequent, and prolonged flooding (Wilhite and Toliver 1990; Conner et al. 1997). Baldcypress requires saturated soils for seed germination, after which seedlings grow fast enough to keep their crown above floodwaters for most of the growing season (Wilhite and Toliver 1990). Early germination and emergence increase the survival of Baldcypress, allowing seedlings to escape stress or disturbance associated with late germination and flooding (Conner et al. 2001). Baldcypress also develops specialized aerial roots (pneumatophores) which grow vertically out of the ground and are often involved in gas exchange (Kozlowki and Pallardy 1996). Flooding induces the formation of aerenchyma in the lateral roots, adventitious roots, stems, and leaves of Baldcypress (Wang and Cao 2012). Aerenchyma formation allows Baldcypress to transport atmospheric oxygen to underground tissues and maintain aerobic respiration (Wang and Cao 2012).

Like Baldcypress, tallow is also highly tolerant of flooding. Bald cypress tolerates a wide hydrological regime ranging from well-drained to 3m depth of flooding for the entire growing season, but tallow can tolerate inundation for only 40% of the growing season (Vann and Megonigal 2002; Wang and Cao 2012). Tallow is becoming increasingly more common in wetlands areas of southern United States with morphological characteristics (development of adventitious roots, production of thicker feeder roots, and hypertrophy of lenticels) indicative of flood tolerance. Tallow will not germinate in flooded or saturated soils, but will germinate throughout the growing season with high survival and growth. The wider germination window gives tallow a competitive edge in moist lowland areas (Conner et al. 2001).

While tallow can thrive in wetland areas of Southern US, growth is significantly reduced when flooded with fresh or saline water (Conner et al. 1997; Conner et al. 2001). Biomass accumulation and photosynthesis of tallow and baldcypress seedlings were similar when watered, but significantly different when flooded (Conner et al. 2001). Tallow seedlings perform poorly with flooding, but their height, leaf biomass, and stem biomass are greatest in well-drained soil conditions (Conner et al. 2001). Compared to baldcypress, which grows best as a monoculture regardless of drainage or flooding, tallow grows best in well-drained conditions. In well-drained conditions, the total biomass of tallow seedlings was three times that of baldcypress (Conner 1997). This suggests it has a competitive advantage over baldcypress in well-drained conditions. Although tallow is flood-tolerant and capable of thriving in wetland areas, flooding as little as 5 cm above the surface has a pronounced negative effect on its growth (Conner et al. 2001). When flooded, seedlings of flood-tolerant species typically lose their root systems; however, Conner 1994 observed a greater reduction in root biomass in tallow compared to baldcypress. When baldcypress loses its original root systems, the native develops aquatic roots and changes its root distribution to improve growth when flooded (Conner et al. 1997). In contrast, when the roots of tallow die off, their stem develops hypertrophied lenticels indicating its capacity for partial oxygen stress avoidance (Conner 1994; Conner et al. 1997).

Tallow is tolerant of high salinity and has a competitive edge in coastal areas with high salinity levels. When flooded with saline water, baldcypress and tallow were able to survive fairly well before both species were killed. However, the tallow was able to withstand salinity longer than baldcypress. This ability to withstand flooding with saline water gives tallow an advantage over baldcypress and other native species in coastal areas with increasing salinity levels (Conner 1994).

Water tupelo

Water tupelo (*Nyssa aquatica* L.) is a large, long-lived, tree with anatomical and physiological adaptations that allow for survival in continuously flooded conditions during the growing season (Hook and Brown 1973; Johnson 1990). Water tupelo extends from southeastern Virginia to southern Georgia along the coastal plain, from northwestern Florida to southeastern Texas in the Gulf Coast, and up the Mississippi River Valley to southern Illinois (Johnson 1990). Saturated soils with moving, aerated, and shallow water are ideal conditions for water tupelo growth. Large trees produce good annual seed crops that are primarily dispersed by water and germinate in partially shaded poorly drained soils (Johnson 1990). Water tupelo is one of the few trees that can survive extended periods of inundation due to a shallow root system characterized by anatomical and physiological adaptations (Hook and Brown 1973). This native survives flooded conditions by developing new secondary roots which tolerate high concentrations of CO_2, oxidize the rhizosphere, and accelerate anaerobic respiration in N_2 (Hook and Brown 1973). These morphological and physiological root characteristics allow water tupelo to survive in regions where it is too wet for most other species (Johnson 1990).

Like water tupelo, tallow can survive in flooded conditions that would kill many flood-tolerant species (Jones and Sharitz 1990). In the basin regions of South Carolina, tallow saplings have been observed to survive more than 15 years of permanent flooding (Conner et al. 2001). Moderate root competition in flooded conditions may facilitate tallow success in these conditions

(Jones and Sharitz 1990). The stress imposed by flooding in coastal forests may decrease competition and create open niches for more flood-tolerant species by decreasing the height and diameter of their less flood-tolerant counterparts. Increased growth of flood-tolerant species in flooded conditions is often associated with increased soil moisture, an influx of nutrients, and decreased competition (Young et al. 1995). Tallow is classified as intermediate in tolerance of root competition and a significant reduction in growth has been observed when in competition with roots from surrounding vegetation (Jones and Sharitz 1990). In addition to its high flood tolerance, high shade tolerance, and high resistance to herbivores, stressful anoxic conditions may facilitate the invasion of tallow if these conditions result in low densities of roots (Jones and Sharitz 1990).

The high shade tolerance and growth rate of tallow may give it a competitive edge over water tupelo. Although both species have similar flood tolerances, their similarities are limited to dense canopies (Conner et al. 2001). In 20% sunlight, the flood tolerance of tallow was similar to water tupelo but in full sunlight, tallow was less tolerant to flooding (Jones and Sharitz 1990). Relative to water tupelo, tallow seedlings have a higher leaf to stem mass ratio indicating the invader may survive in flooded areas with dense canopies where water tupelo might not be able to capture enough light for growth (Butterfield et al. 2004). Early germination and emergence in water tupelo seedlings provide a competitive edge over tallow with increased seedling survival and taller seedlings whose tops are above the water level (Conner et al. 2001). In a greenhouse experiment examining the growth and performance of tallow and four native tree species (including water tupelo), water tupelo seedlings were two to four times taller than all other species at emergence (Butterfield et al. 2004). Even though tallow may germinate later than water tupelo, rapid growth led to no difference in height between the two species at the end of the growing season (Conner et al. 2001). In well-drained conditions, tallow produced greater leaf and stem biomass than water tupelo (Conner et al. 2001). Overall, water tupelo has a competitive edge over tallow in flooded open canopies while tallow has a competitive edge in flooded closed canopies and well-drained conditions (Conner et al. 2001; Butterfield et al. 2004).

Green ash

Green ash (*Fraxinus pennsylvanica* Marsh.) is the most widely distributed and adaptable member of its genus in North America (Kennedy 1990b). This early successional and shade-tolerant species grows naturally across moisture-limited and flooded environments where it survives flooding for 40 % of the growing season (Kennedy 1990b). Certain root adaptations enable green ash to remain healthy when flooded, including the ability to develop adventitious roots, develop new secondary roots, oxidize the rhizosphere, and tolerate high concentrations of CO_2 (Hook and Brown 1973; Kennedy 1990b).

Green ash and tallow seedlings are both intermediate in their tolerance of root competition in flooded conditions (Jones and Sharitz 1990). Roots from surrounding forest vegetation significantly reduce seedling growth in both species, suggesting both species are sensitive to root competition in forest understory environments (Jones and Sharitz 1990). Compared to other woody plant species (including American sycamore [*Platanus occidentalis* L.], American elm [*Ulmus americana* L.], red maple [*Acer maple* L.], and cherrybark oak [*Quercus pagoda* Raf.]), tallow and green ash are intermediate in their tolerance to root competition. Among the woody species examined, American sycamore was the least sensitive, and cherrybark oak was the most sensitive (Jones and Sharitz 1990). Despite similarities in root competition tolerance, green ash partitions a greater proportion of its total biomass to its roots than tallow, allowing the native to have a larger root to shoot ratio than tallow (Jones and Sharitz 1990).

Green ash and tallow are both common and fast-growing tree species in the coastal forested wetlands of the southern US, but flooding affects green ash seedlings more (Jones and Sharitz 1990; Conner et al. 1997). To remain healthy in flooded conditions and avoid partial oxygen stress, both species develop hypertrophied lenticels (Jones and Sharitz 1990). Freshwater flooding reduces the height, diameter, and biomass of green ash seedlings when compared with well-watered treatments. In this flooded condition, the root biomass of tallow seedlings was 1.75 to 2.11 times larger than green ash, while stem biomass was 2.5 to 3 times greater than green ash (Conner et al. 1997). Similarly, in well-watered conditions total biomass of tallow seedlings was three times larger than green ash. Although green ash and tallow are flood-tolerant species, they are more sensitive to flooding when compared to other coastal forested wetland species (including water tupelo and baldcypress). Between tallow and green ash, the native is more sensitive to flooding with greater reductions in flooded conditions (Jones and Sharitz 1990; McLeod et al. 1996; Conner et al. 1997).

Reduced physiological activity, coupled with the presence of herbivores, may intensify biomass reductions in green ash seedlings. In contrast with well-drained conditions, flooded conditions significantly reduced photosynthetic CO_2 assimilation and stomatal conductance of green ash seedlings, but these values increased in tallow seedlings (McLeod et al. 1996). Reduced physiological activity in green ash may account for biomass reductions and increased sensitivity to flooding. Flooded conditions may reduce photosynthate production for tissue building by limiting oxygen uptake from soils (Infante-Mata et al. 2019). In coastal forests, herbivory pressure is low in tallow but higher in green ash. Tallow is rarely attacked by herbivores in North

America and has evolved increased allocation to growth, survival, and reproduction (Scheld and Cowles 1981; Bruce et al. 1997; Siemann and Rogers 2001). In contrast, many insects damage and feed occasionally on green ash (Kennedy 1990b). Several diseases are of importance, and young trees are subject to damage from deer and rabbit browsing (Jones and Sharitz 1990). Increased herbivory in green ash also results in linear decreases in seedling mass. Considering that the seedlings of flood-tolerant species tend to lose their original root systems when flooded, it is likely that green ash invested resources in developing new roots to compensate for losses instead of increasing the shoot height (Conner 1994; Mozo et al. 2021).

Carolina ash

Carolina ash (*Fraxinus caroliniana* Miller) is a subtropical ash tree native to the southeastern United States, from northern Florida to Texas and Oklahoma along the Gulf Coast, and to Virginia along the Atlantic coast (Nesom 2010). It is a small understory tree with several leaning trunks and a buttressed base that grows primarily in swampy or riverine habitats, often with their bases submerged (Nesom 2010). Because it is a native analog to tallow, Carolina ash has been used in comparative studies with tallow (Jones and McLeod 1990b). Both species are shade tolerant, grow steadily to a relatively small size, sprout profusely from the root collar, and thrive in waterlogged soils (Jones and McLeod 1990b).

Tallow had better growth metrics than Carolina ash in both deep shade and full sunlight (Jones and McLeod 1990b). In deep shade, the greater growth of tallow compared to Carolina ash was due to tallow's larger leaf area. Tallow partitioned more dry mass to leaves in deep shade, resulting in a higher leaf area ratio in tallow. Tallow’s success in full sunlight can be linked to a greater leaf area ratio once again. Higher photosynthetic efficiency, on the other hand, could be important. Even though both species exhibited suppressed net photosynthetic values at extremely high photosynthetic photon flux density, the average net photosynthesis in 100% light was higher in tallow than in Carolina ash. Greater overall morphological plasticity may account for the superior performance of tallow seedlings across a range of light environments, in addition to more leaf area per unit of total plant dry mass and potentially higher photosynthetic efficiency. Tallow had wider ranges in leaf area ratio and specific leaf area than Carolina ash. In addition, tallow was also able to spread its crown over a larger ground area due to its habit of forming branches and, as a result, a greater number of leaves. This could be a useful tool for maximizing the use of patchy light environments and reducing self-shading. In terms of the rate at which leaves develop maximum net photosynthesis, tallow may have had an advantage over Carolina ash. Other fast-growing angiosperms with simple, alternately arranged leaves show a pattern of rapid development of maximum net photosynthesis followed by a steady net photosynthesis decline.

Sweetgum

Sweetgum (*Liquidambar styraciflua* L.) is a common deciduous bottomland species tree growing in North and Central America (Kormanik 1990; Jeffries 2008). Sweetgum ranges west from Connecticut and southern Illinois, south to central Florida, southeastern Texas, and south to the Gulf of Mexico coast with scattered populations through Central America (Kormanik 1990; Adams et al. 2015). This fast-growing native is one of the most adaptable hardwood species in the southern US, with a broad tolerance to different soil and site conditions (Kormanik 1990). On well-drained sites, sweetgum rapidly develops a deep taproot with numerous well-developed laterals, but its root system is shallow and wide in wetter sites with poor drainage (Kormanik 1990). On drier soils, sweetgum tends to grow well, presumably due to greater ease in penetrating the soil, but growth rates decline in wetter soils (Jeffries 2008).

Sweetgum is exceptionally competitive with other species that may form monocultures. It enters a new site through its seeds which are small, winged, and widely dispersed by wind and many species of birds (Kormanik 1990; Bonner and Karrfalt 2008). This native grows best on alluvial swamp sites and imperfectly on poorly drained soils (Kormanik 1990). In abandoned agricultural areas, sweetgum is a pioneer species that may form monocultures (Kormanik 1990; Jeffries 2008). In the southeastern US, sweetgum can be considered a weed from a land management perspective. The presence of this fast-growing native often leads to greater competition for light, water, and space, reducing the survival and growth of desired pine trees (Adams et al. 2015).

In a greenhouse experiment examining the growth and performance of tallow and four native trees across a water gradient, sweetgum was the only species that grew faster than tallow in the drier treatments (Butterfield et al. 2004). Although tallow has high growth rates across a water gradient, the invader is less successful in dry upland sites that support sweetgum (Butterfield et al. 2004). In dry upland sites, tallow has traits similar to sweetgum, including high root to shoot ratios, intermediate leaf to stem ratios, and high growth rates. However, sweetgum allocated more resources to stem growth, giving it a competitive edge over the tallow. Maximizing shoot growth is an adaptation consistent with shade-tolerant species. While tallow shows low variability of total mass and mass allocation along a water gradient, sweetgum shows high variability indicating the native maximizes growth under relatively specific favorable conditions (Butterfield et al. 2004). Lack of herbivore damage could explain why tallow can maximize growth under different conditions and stress tolerance. The evolved capacity to allocate more resources to growth and reproduction may give tallow a competitive edge over sweetgum. In contrast, sweetgum suffers extremely high damage from insects (forest tent caterpillar [*Malacosoma disstria*], bark beetles

[*Dryocoetes betulae* and *Pityophthorus liquidambarus*], and the Luna moth [Actias *luna*]), diseases (including sweetgum blight caused by *Botryosphaeria ribis*), and herbivores (including hogs [*Sus scrofa domesticus*], goats [*Capra hircus*], and cattle [*Bos taurus*; Kormanik 1990]).

Compared to sweetgum, tallow gains benefits from mycorrhizal associations which improve plant performance, and in turn impact the outcome of plant competition (van der Heijden and Sanders 2002; Nijjer et al. 2004; Pile et al. 2017). Nijjer et al. (2004) examined the effects of mycorrhizal inoculation on the growth of tallow and native tree species, including sweetgum. When inoculated with endo- and ecto- mycorrhizae, the growth and performance of tallow seedlings were enhanced when compared to seedlings without inoculation (Davis and Call 1990). Tallow had a positive growth response (65% increase) that was significantly different from the negative response of sweetgum (24% decrease). Unlike sweetgum, tallow was able to gain a large benefit from mycorrhizal associations with North American mycorrhizae species in conditions where sweetgum could not. This suggests that sweetgum may not benefit from the North American mycorrhizae species, and higher rates of mycorrhizal associations may give tallow a competitive advantage over sweetgum and other native trees in the US.

Black gum

Black gum (*Nyssa sylvatica* Marshall) is an inherently slow-growing, long-lived species that is fire resistant, shade tolerant, and drought tolerant (McGee 1990; Abrams 2007). It has a large range that extends north from central Missouri, Illinois, central Michigan, New York to southwestern Maine, and south from eastern Oklahoma, eastern Texas to south Florida (McGee 1990). Black gum is flood and drought-tolerant, growing best in alluvial stream bottoms and becoming an important component in nutrient-poor xeric sites (McGee 1990; Abrams 2007). It is an important wildlife species with very palatable fruits (with high crude fat, fiber, phosphorus, and calcium content) that are eaten by many birds and mammals (McGee 1990). Despite its ecological breadth, black gum is usually found in a mixture with other species where it occupies the intermediate crown position and usually never attains overstory dominance (McGee 1990; Abrams 2007).

The combination of fast growth and high tolerance to stress gives tallow a competitive edge over black gum. When the growth and performance of tallow and four native trees (including black gum, sweetgum, loblolly pine, and water tupelo) were examined, tallow had the highest growth rates and total biomass while black gum had the highest root to shoot ratios and variability in biomass allocation (Butterfield et al. 2004). High variability in total mass and mass allocation under varying treatments may indicate that black gum maximizes growth under specific favorable conditions. High root to shoot ratios indicates that black gum seedlings may survive flooding and grow rapidly when the flood subsides. With increasing resources, black gum makes significant changes in root to shoot ratios reflecting its high degree of morphological plasticity (Abrams 2007). Like tallow, black gum can persist in the understory for decades pending release by gap events into the overstory (Abrams 2007; Pile et al. 2017). Although the slow growth rate and low height potential of black gum may relegate it to an intermediate or codominant canopy position, its ability to find a safe site (occasional temporal or spatial opportunity), out persist and outlive the competition due to its ecological tolerances and longevity, and gradually grow into the forest canopy suggests that it may outperform the invader in permanently flooded conditions (Butterfield et al. 2004; Abrams 2007).

Tallow is less successful in extremely droughty, nutrient-poor, xeric sites where black gum obtains greater importance (Butterfield et al. 2004). Tallow grows most rapidly in wet conditions, but mortality rises, and growth slows in droughty conditions (Barrilleaux and Grace

2000). Drought intolerant seedlings are the main factors limiting tallow’s spread into more elevated habitats in the western portion of its range (Bower et al. 2009). In contrast, black gum thrives in low resource and low tree density sites (including swamps, mine spoils, and xeric uplands) due to its unusual combination of wind resistance, and tolerance of drought, shade, wind, flood, and fire (Abrams 2007). Due to its low nutrient requirements, black gum can avoid the negative effects of moisture stress in xeric soils by quickly closing its stomata and eventually abscising its leaf early (Abrams 2007). The success of black gum on xeric sites can be attributed to its ability to avoid drought by physiologically shutting down in the face of mild or moderate drought (Abrams 2007).

Cherrybark oak

Cherrybark oak (*Quercus pagoda* Raf.) is one of the hardiest and fastest-growing oak species, outgrowing most bottomland oak species on more sites (Krinard 1990). Across the bottomland hardwood forests of southern US, cherrybark oak is a common overstory species, favored by land managers for its superior form, excellent wood quality, and mast production (Gardiner and Hodges 1998). Its natural range extends from southeastern Virginia to northwestern Florida; west to eastern Texas; and north in the Mississippi Valley to extreme southeastern Oklahoma, southeastern Missouri, southern Illinois, and southwestern Indiana (Krinard 1990). Cherrybark oak is frequently found in its range on very productive alluvial sites, where it grows in combination with numerous other hardwood tree species, forming stands with multi-storied canopies (Krinard 1990). Being intolerant of flooding, saturated soils, and shade, cherrybark oak requires full sunlight and well-drained loamy soils for its best development, which in turn induces heavy competition from annual weeds, vines, briars, and brush (Krinard 1990; Gardiner and Hodges 1998).

Relative to cherrybark oak, tallow can grow rapidly in both deep shade and full sunlight environments. Jones and McLeod (1989) measured growth, biomass partitioning, and net photosynthesis for first-year seedlings of tallow and cherrybark oak grown in shade and full sunlight. Total biomass, height, and diameter for both species were greater in full sunlight than in shade, but tallow was larger in both shade and sunlight, supporting more stem plus root mass per unit of leaf mass. In shade tallow produced two times the total biomass and ground diameter, and nearly three times the total height of cherrybark oak. If tallow continues partitioning more stem plus root mass per unit of foliage mass over more than one growing season, this biomass allocation pattern would continue to give tallow a competitive edge over cherrybark oak (Jones and McLeod 1989).

High net photosynthesis may account for the growth advantages of tallow in both low and high light environments (Jones and McLeod 1989). In full sunlight and shade, tallow exceeded cherrybark oak in net photosynthesis while the stomatal conductance of tallow exceeded the native in shade. Tallow's ability to sustain high net photosynthetic values in shade and full sunlight suggests the invader does not conform to the traditional classifications of shade-tolerant vs. shade-intolerant species. In Jones and McLeod (1990), tallow grew fast in high irradiance (typical with shade-tolerant species) and maintained moderately fast growth in low irradiance (typical with shade-intolerant species). Photosynthetic performance has been identified as a major predictor of biomass output in C_3 plants and the rank order among species in net photosynthesis matches the rank in dry mass (Reddy and Mas 1986; Jones and McLeod 1990).

American sycamore

American sycamore (*Platanus occidentalis* L.), hereafter sycamore, is a large, fast-growing, and long-lived tree of lowlands and old fields (Wells and Schmidtling 1990). Except for

Minnesota, sycamore grows in all states east of the Great Plains where only a few species (including cottonwood) grow faster (Wells and Schmidtling 1990). The tree grows singly or in small groups with other trees, but rarely in extensive pure stands. Sycamore is most common in alluvial soils along streams and in bottomlands, where it grows to its largest size (Wells and Schmidtling 1990). Although tolerant of wet soil conditions, sycamore is relatively sensitive to flooding during the growing season and will die if the entire tree is inundated for more than two weeks (Wells and Schmidtling 1990). Under favorable conditions, seedlings develop a strong, spreading root system, and grow fast throughout their life. Sycamore is classified as intermediate in tolerance to shade and competition, as seedlings require direct sunlight to survive and compete effectively (Wells and Schmidtling 1990).

When the growth metrics of tallow and sycamore were compared, both species were similar in full sunlight, but tallow outgrew sycamore in shaded conditions (Jones and McLeod 1990). Full sunlight provided more favorable conditions for both species, as total dry mass, total height, and basal diameter were much greater (Jones and McLeod 1990). In shaded conditions, tallow had a higher net photosynthetic value which accounted for the taller seedlings with larger biomass and basal diameters. Relative to sycamore, tallow can grow rapidly in deep shade and is more shade tolerant than the native. In full sunlight, the growth metrics of both species are similar (Jones and McLeod 1990). Net photosynthesis and stomatal conductance are similar allowing both species to grow rapidly, producing stems with similar height, total biomass, and diameter (Jones and McLeod 1990). Within its natural range, sycamore is one of the fastest-growing tree species where only cottonwood (*Populus deltoides* W. Bartram ex Marshall), a few pines, silver maple (*Acer saccharinum* L.), and black willow (*Salix nigra* M.) grow faster (Wells and Schmidtling 1990). The ability of tallow to equal sycamore's growth in full sunlight indicates the rapid growth potential of the invader. The ability to grow rapidly in shaded and full sunlight conditions also indicates that the invader exhibits characteristics of both shade-tolerant and shade-intolerant species.

Red maple

Red maple (*Acer rubrum* L.) is one of the most abundant and widespread deciduous trees in eastern and central North America (Walters and Yawney 1990). Red maple is generally very fruitful, producing small, winged fruits that disperse well in the wind. Given the right temperature and moisture, the seed can germinate with very little light (Walters and Yawney 1990). This pioneer or subclimax is shade tolerant, longer-lived, and capable of growing well or better in more soil types, textures, moistures, pHs, and elevations than other forest species in North America (Walters and Yawney 1990). Root systems develop differently in response to varied surroundings, allowing them to survive in a variety of conditions, from swamp to dry upland (Walters and Yawney 1990). As the trees age, their root systems retain their inherent plasticity. Many adventitious roots form during floods, but the root systems recover rapidly once the water recedes (Walters and Yawney 1990). Seedlings grow short taproots with long, well-developed laterals in flooded conditions. Red maple appears to tolerate drought by developing long taproots with shorter laterals, ceasing to grow in dry conditions and releasing a second growth flush when conditions improve, even after growth has been halted for two weeks. Red maple increases in stocking as a result of disturbances such as fire, disease, hurricanes, and harvesting, where it formerly only existed as scattered trees (Walters and Yawney 1990). Both red maple and tallow form pure to nearly pure stands in poorly drained areas and are abundant species in lowland forests of the Atlantic Coastal Plain where they are able to tolerate shade and flooding.

Tallow appears to be more tolerant to shade, flooding, and salinity than red maple. Conner and Askew (1993) summarized the response of both species to salinity, reporting that increased flooding and saltwater significantly reduced the growth and vigor of both species. Tallow seedlings are more flood-tolerant and can withstand flooding for up to five days. Flooding killed 100% of red maple seedlings in one day of freshwater flooding and 80% of red maple seedlings in two weeks of saltwater flooding. After one day of flooding, red maple biomass values tended to stabilize, but tallow biomass values continued to decline for up to four days. Tallow root and stem biomass increased slightly in dry weight when seedlings were flooded for five days. Although both species are tolerant to shade, flooding, and salinity, tallow's greater tolerance to a wider range of environmental conditions gives it an advantage over red maple (Conner and Askew 1993).

Wax myrtle

Wax myrtle (*Morella cerifera* L.) is a small (1 to 3m tall) evergreen plant native to the southeastern United States Coastal Plain (Kalmbacher et al. 1993). Wax myrtle is often multi-stemmed and grows in clusters. It does not grow well in extremely dry or wet soils, nor does it grow well in nutrient-deficient soils (Kalmbacher et al. 1993). Wax myrtle seeds are abundant in the fall and winter, when many bird species disperse them across the coastal plains of southern North America (Kalmbacher et al. 1993; Borgmann et al. 2004). Its fruits are considered a "keystone" resource for overwintering birds (Borgmann et al. 2004).

Battaglia et al. (2009) assessed the effects of resident vegetation type in freshwater floating marshes on tallow's arrival and performance. Tallow was abundant and more likely to be found in dense wax myrtle shrub thickets than in surrounding floating marsh vegetation, implying that wax myrtle may have an overall facilitative influence on tallow invasion in comparable habitats (Battaglia et al. 2009; Pile et al. 2017). The wax myrtle's woody canopy provides perches and food for birds, and it may aid in the dispersal of tallow seeds and other bird-dispersed species, providing foci for tallow recruitment (Battaglia et al. 2009; Pile et al. 2017). The co-occurrence of tallow and wax myrtle may also be influenced by overlapping fruit ripening seasons. However, once grown, wax myrtle reduced tallow growth by competing for light (Battaglia et al. 2009; Pile et al. 2017).

Red bay

Red bay (*Persea borbonia* L.) is a small aromatic evergreen tree or shrub native to the southeastern Coastal Plains (Brendemuehl 1990). It is a common but rarely abundant component of the swamp forests of the Atlantic and Gulf Coastal Plains, ranging from southern Delaware to Florida and west to the lower Texas Gulf Coast. Red bay is shade tolerant, but it also grows well in the open, in young stands, and in old stands (Brendemuehl 1990). Overstory competition could explain the scarcity and poor quality of red bay growing in certain forest conditions (Brendemuehl 1990). Red bay is of significant importance to wildlife; the annual crops of fruits are eaten by several forms of wildlife including songbirds, white-tailed deer (*Odocoileus virginianus*), bobwhite (*Colinus virginianus*), wild turkey (*Meleagris gallopavo*), and black bear (*Ursus americanus*; Brendemuehl 1990).

Although both red bay and tallow are shade tolerant, red bay is typically found growing on the edges of swampy areas, whereas tallow can grow in conditions ranging from extremely dry to extremely wet (Conner and Askew 1993). Tallow seedlings are more tolerant of saltwater flooding than red bay seedlings; red bay seedlings were unable to survive one day of flooding, whereas tallow seedlings survived five days (Conner and Askew 1993). After a day of freshwater flooding, red bay biomass values tended to stabilize, whereas tallow biomass values continued to decline for up to four days (Conner and Askew 1993). For seedlings flooded for five days, both tallow and red bay root and stem biomass showed a slight increase in dry weight (Conner and Askew 1993). Tallow can withstand flooding, shade, salinity, and stress better than red bay, which may give the invader a competitive advantage over the native.

Loblolly pine

Loblolly pine (*Pinus taeda* L.) is the most extensively planted commercial pine species in the southern US, where commercial timber accounts for 60% of the nation's timber production (Fox et al. 2007). Its native range spans 14 states, from southern New Jersey to central Florida and west to eastern Texas (Baker and Langdon 1990). Loblolly pine is a very adaptable species that has been successfully planted on the outskirts of its natural range and with varying degrees of success on other continents (Baker and Langdon 1990). Rooting habits are strongly influenced by soil environment, on deep, sandy, or loamy soils, taproots are long, but they are stout and short on heavier clay soils. Loblolly grows in pure stands, in mixtures with other pine or hardwoods, and in combination with other vegetation types (Baker and Langdon 1990).

Gresham (1994) measured seed germination and seedling growth after applying several aqueous extracts of tallow leaves to loblolly pine seed in both potting media and forest soil. Tallow's allelochemical was extracted at a high enough concentration to have an impact on loblolly pine seed germination and seedling growth (Gresham 1994). Seedling height, top weight, and total weight were all reduced by the tannic acid dry leaf solution. Tallow allelochemicals can be extracted in cold water, and such solutions reduce loblolly pine seed germination and seedling growth, according to these experiments. In addition, the allelochemical is present in sufficient concentration in forest soil below tallow to affect loblolly pine seed germination and seedling growth (Gresham 1994). This allelopathy report in tallow contradicts all experimental studies to date, which show that allelopathy does not play a role in tallow invasion success (Conway et al. 1997; Keay et al. 2000; Conway et al. 2002; Rua et al. 2008). When Butterfield et al. (2004) compared the growth and performance of tallow and loblolly pine under a variety of water conditions, they discovered that tallow grew faster in all water treatments and only experienced minor growth reductions in response to water stress. Tallow appears to have a higher stress tolerance than loblolly pine, which may have contributed to its faster growth rate.

Conclusion

With the exception of Pile et al. (2019), who investigated the long-term growth dynamics and competitive interactions between tallow and native tree species, most studies on tallow growth have been conducted using short-term manipulative studies that account for competition with native fast-growing species during the early recruitment stage. This review synthesized the interactions between tallow and native species during the stand recruitment stage. These results indicate that tallow outcompetes native species in height growth due to functional traits that influence its survival, growth, and reproduction. However, when functionally similar native species are matched to the right site type, they may effectively compete with tallow.

LITERATURE CITED

Adams, J.P., J.M. Lingbeck, P.G. Crandall, E.M. Martin, and C.A. O'Bryan. 2015. Sweetgum: A new look. Biogeosciences and Forestry. 8:719–727.

Ajala, O.O., K.R. Kidd, B.P. Oswald, Y. Weng, and J.P. Stovall. 2022. Response of Chinese Tallow (*Triadica sebifera*) and Coexisting Natives to Competition, Shade, and Flooding. Forest Science. 68(1):17–26.

Baker, J.B., and O.G. Langdon 1990. Loblolly pine (*Pinus taeda* L.) In Silvics of North America: 1. Conifers. Edited by R.M. Burns and B.H. Honkala, 1018–1051. Washington, DC: USDA Forest Service. 1383 pages.

Barrilleaux, T.C., and J.B. Grace. 2000. Growth and invasive potential of *Sapium sebiferum* (Euphorbiaceae) within the coastal prairie region: the effects of soil and moisture regime. American Journal of Botany. 87(8):1099–1106.

Battaglia, L.L., J.S. Denslow, J.R. Inczauskis, and S.G. Baer. 2009. Effects of native vegetation on invasion success of Chinese tallow in a floating marsh ecosystem. Journal of Ecology. 97(2):239–246.

Bonner, F.T., and R.P. Karrfalt. 2008. The Woody Plant Seed Manual. United States Department of Agriculture. 1241 p.

Borgmann, K.L., S.F. Pearson, D.J. Levey, and C.H. Greenberg. 2004. Wintering yellow-rumped warblers (*Dendroica coronata*) track manipulated abundance of *Myrica cerifera* fruits. Auk. 121(1):74–87.

Bower, M.J., C.E. Aslan, and M. Rejmánek. 2009. Invasion Potential of Chinese Tallowtree (*Triadica sebifera*) in California's Central Valley. Invasive Plant Science and Management. 2(4):386–395.

Brendemuehl, R.H. 1990. Red bay (*Persea borbonia* L.) In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 503–506. Washington, DC: USDA Forest Service. 877 pages.

Bruce, K.A., G.H. Cameron, P.A. Harcombe, and G. Jubinsky. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) Roxb. Natural Areas Journal. 17:255–260.

Butterfield, B.J., W.E. Rogers, and E. Siemann. 2004. Growth of Chinese tallow tree (*Sapium sebiferum*) and four native trees under varying water regimes. Texas Journal of Science. 56(4):335–346.

Chen, L., C.J. Tiu, S. Peng, and E. Siemann. 2013. Conspecific plasticity and invasion: Invasive populations of Chinese tallow (*Triadica sebifera*) have performance advantage over native populations only in low soil salinity. PLoS One. 8(9): e74961.

Conner, W.H., L.W. Inabinette, and C.A. Lucas. 2001. Effects of Flooding on Early Growth and Competitive Ability of Two Native Wetland Tree Species and an Exotic. Castanea. 66(3):237–244.

Conner, W.H. 1994. The effect of salinity and waterlogging on growth and survival of bald cypress and Chinese tallow seedlings. Journal of Coastal Research. 10(4):1045–1049.

Conner, W.H., and G.R. Askew. 1993. Impact of saltwater flooding on red maple, redbay, and Chinese tallow seedlings. Castanea. 58(3):214–219.

Conner, W.H., K.W. McLeod, and J.K. McCarron. 1997. Flooding and salinity effects on growth and survival of four common forested wetland species. Wetlands Ecology and Management. 5(2):99–109.

Conway, W.C., L.M. Smith, and J.F. Bergan. 1997. The allelopathic potential of an exotic invasive tree: Chinese tallow. Bulletin of the Ecological Society of America. 78, 72.

Conway, W.C., L.M. Smith, and J.F. Bergan. 2002. Potential allelopathic interference by the exotic Chinese tallow tree (*Sapium sebiferum*). The American Midland Naturalist. 148:43–53.

Davies, F.T., and C.A. Call. 1990. Mycorrhizae, survival, and growth of selected woody plant species in lignite overburden in Texas. Agriculture, Ecosystems & Environment. 31(3):243–252.

Elton, C. 1958. The Ecology of Invasions by Animals and Plants. University of Chicago Press, Chicago. 181 p.

Fox, T.R., H.L. Allen, T.J. Albaugh, R. Rubilar, and C.A. Carlson. 2007. Tree Nutrition and Forest Fertilization of Pine Plantations in the Southern United States. Southern Journal of Applied Forestry. 31:5-11.

Funk, J.L., E.E. Cleland, K.N. Suding, and E.S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution. 23(12):695–703.

Gan, J., J.H. Miller, H. Wang, and J.W. Taylor. 2009. Invasion of tallow tree into southern US forests: Influencing factors and implications for mitigation. Canadian Journal of Forest Research. 39(7):1346–1356.

Gardiner, E.S., and J.D. Hodges. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. Forest Ecology and Management. 108(1):127–134.

Gioria, M., and B.A. Osborne. 2014. Resource competition in plant invasions: Emerging patterns and research needs. Frontiers in Plant Science. 5(SEP):1–21.

Gresham, G.A. 1994. Tallow tree (*Sapium sebiferum* L.) allelopathy affects loblolly pine seed germination and seedling growth. Eight Biennial Southern Silvicultural Research Conference. Auburn, AL, Nov 1–3.

Hook, D., and C. Brown. 1973. Root Adaptations and Relative Flood Tolerance of Five Hardwood Species. Forest Science. 19(3):225–229.

Huang, W., J. Carrillo, J.Q. Ding, and E. Siemann. 2012. Interactive effects of herbivory and competition intensity determine invasive plant performance. Oecologia. 170:373–382.

Infante-Mata, D., P. Moreno-Casasola, T. Valverde, and S. Maza-Villalobos. 2019. Effects of soil flooding, sunlight, and herbivory on seedlings of *Annona glabra* and *Pachira aquatica* in a tropical swamp. Wetlands Ecology and Management. 27(4):539–551 Available online at: https://doi.org/10.1007/s11273-019-09676-1.

Jeffries, T.M. 2008. Relationships of Growth Rate and Mechanical Properties in Sweetgum, *Liquidambar styraciflua*. Virginia Polytechnic Institute and State University, Electronic Theses and Dissertations.

Johnson, R.L. 1990. Water Tupelo (*Nyssa aquatica*). In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 474-478. Washington, DC: USDA Forest Service. 877 pages.

Jones, R.H., and K.W. McLeod. 1989. Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. Bulletin of the Torrey Botanical Club. 116(4):371–377.

Jones, R.H., and K.W. McLeod. 1990. Growth and photosynthetic responses to a range of light environments in Chinese tallow tree and Carolina ash seedlings. Forest Science. 36(4):851–862.

Jones, R.H., and R.R. Sharitz. 1990. Effects of root competition and flooding on growth of Chinese tallow tree seedlings. Canadian Journal of Forest Research. 20:573–578.

Jones, R.H. and K.W. McLeod. 1990b. Growth and photosynthetic responses to a range of light environments in Chinese tallow tree and Carolina ash seedlings. Forest Science. 36(4):851-862.

Kalmbacher, R., J.E. Eger, Jr., and A.J. Rowland-Bamford. 1993. Response of Southern Wax Myrtle (*Myrica cerifera*) to Herbicides in Florida. Weed Science Society of America. 7(1):84–91 Available online at: https://www.jstor.org/stable/3987965.

Keay, J., W.E. Rogers, R. Lankau, and E. Siemann, E., 2000. The role of allelopathy in the invasion of the Chinese tallow tree (*Sapium sebiferum*). Texas Journal of Science. 52:57–64.

Kennedy, H.E. 1990a. Hackberry (*Celtis occidentalis*) In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 262–265. Washington, DC: USDA Forest Service. 877 pages.

Kennedy, H.E. 1990b. Green ash (*Fraxinus pennsylvanica*) In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 348–354. Washington, DC: USDA Forest Service. 877 pages.

Kormanik, P.P. 1990. Sweetgum (*Liquidambar styraciflua* L.) In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 399–405. Washington, DC: USDA Forest Service. 877 pages.

Kozlowski, T.T., and S.G. Pallardy. 1996. Physiology of Woody Plants. Elsevier Science.

Krinard, R.M. 1990. Cherrybark oak (*Quercus falcata* var. *pagodifolia* Ell.) In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 644–649. Washington, DC: USDA Forest Service. 877 pages.

Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology. 16:545–556

Leonard, N., 2005. Tadpoles of early breeding amphibians are negatively affected by leaf litter from invasive Chinese tallow trees. In: American Geophysical Union, Spring Meeting 2005, abstract #NB14A-05, p. 05.

Lockwood, J.L., M.F. Hoopes, and M.P. Marchetti. 2013. Invasion Ecology. John Wiley & Sons, West Sussex, UK. 313 p.

McGee, C.E. 1990. Black tupelo (*Nyssa sylvatica* Marsh.) In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 482–485. Washington, DC: USDA Forest Service. 877 pages.

McLeod, K.W., J.K. McCarron, and W.H. Conner. 1996. Effects of flooding and salinity on photosynthesis and water relations of four southeastern coastal plain forest species. Wetlands Ecology and Management. 4(1):31–42.

Miller, J.H. 2003. Nonnative invasive plants of southern forests: a field guide for identification and control. General Technical Report SRS-62. Asheville, NC. 93 p. Available online at: http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Nonnative+Invasive+Plants+of+Southern+Forests:+A+Field+Guide+for+Identification+and+Control#1.

Miller, J.H., E.B. Chambliss, and C.M. Oswalt. 2008. Maps of occupation and estimates of acres covered by nonnative invasive plants in southern forests using SRS FIA data were posted on March 15, 2008. [Available only on the internet: https://www.invasive.org/fiamaps/ Date accessed: 10-12-2021]

Mozo, I., M.E. Rodríguez, S. Monteoliva, and V.M.C. Luquez. 2021. Floodwater Depth Causes Different Physiological Responses During Post-flooding in Willows. Frontiers in Plant Science. 12:1–12.

Nesom, G.L. 2010, Taxonomy of the water ashes: *Fraxinus caroliniana*, *F. cubensis*, and *F. pauciflora* (Oleaceae). Phytoneuron 2010-39:1–13.

Nijjer, S., R.A. Lankau, W.E. Rogers, and E. Siemann. 2002. Effects of Temperature and Light on Chinese Tallow and Texas Sugarberry. Texas Journal of Science. 54(1):63–68.

Nijjer, S., W.R. Rogers, and E. Siemann. 2004. The effect of mycorrhizal inoculum on the growth of five native tree species and the invasive Chinese tallow tree (*Sapium sebiferum*). Texas Journal of Science. 56(4):357–368.

Oswalt, S.N., W.B. Smith, P.D. Miles, and S.A. Pugh. 2014. Forest Resources of the United States, 2012: a technical document supporting the Forest Service 2010 update of the RPA Assessment. General Technical Report WO- 91.

Pile, L.S., G.G. Wang, J.P. Stovall, E. Siemann, G.S. Wheeler, and C.A. Gabler. 2017. Mechanisms of Chinese tallow (*Triadica sebifera*) invasion and their management implications – A review. Forest Ecology and Management. 404:1–13.

Pile, L.S., Vickers, L., M. Stambaugh, C. Norman, and G.G. Wang. 2019. The tortoise and the hare: A race between native tree species and the invasive Chinese tallow. Forest Ecology and Management. 445:110–121.

Pratt, R.B., and R.A. Black. 2006. Do invasive trees have a hydraulic advantage over native trees? Biological Invasions. 8(6):1331–1341.

Reddy, A. G. R., and V. S. R. Das. 1986. Correlation between biomass production and net photosynthetic rates and kinetic properties of RuBP carboxylase in certain C_3 plants. Biomass. 10:157–164.

Rejmánek, M., D.M. Richardson, and P. Pysek. 2005. Plant invasions and invasibility of plant communities. P. 332–354 in Vegetation Ecology, van Der Maarel, E. (ed.). Blackwell Publishing, Malden, MA.

Rogers, W.E., and E. Siemann. 2002. Effects of simulated herbivory and resource availability on native and invasive exotic tree seedlings. Basic and Applied Ecology. 3(4):297–307.

Rua, M.A., S. Nijjer, A. Johnson, W.E. Rogers, and E. Siemann. 2008. Experimental approaches to test allelopathy: a case study using the invader *Sapium sebiferum*. Allelopathy Journal. 22:1–13.

Ruberti, I., G. Sessa, A. Ciolfi, M. Possenti, M. Carabelli, and G. Morelli. 2012. Plant adaptation to dynamically changing environment: the shade avoidance response. Biotechnology advances. 30(5):1047–1058.

Scheld, H.W., and J.R. Cowles. Woody biomass potential of the Chinese tallow tree. Economic Botany. 35:391–397.

Sharma, A., S.K. Ojha, L.D. Dimov, J.G. Vogel, and J. Nowak. 2021. Long-term effects of catastrophic wind on southern US coastal forests: Lessons from a major hurricane. PLoS One. 16(1 January):1–27 Available online at: http://dx.doi.org/10.1371/journal.pone.0243362.

Siemann, E., and W.E. Rogers. 2001. Genetic differences in growth of an invasive tree species. Ecology Letters. 4:514–518.

Siemann, E., and W.E. Rogers. 2003a. Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. Journal of Ecology. 91(6):923–931.

Siemann, E., and W.E. Rogers. 2003b. Herbivory, disease, recruitment limitation, and success of alien and native tree species. Ecology. 84(6):1489–1505.

Siemann, E., and W.E. Rogers. 2003c. Increased competitive ability of an invasive tree may be limited by an invasive beetle. Ecological Applications. 13:1503–1507.

Siemann, E., and W.E. Rogers. 2003d. Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. Oecologia 135, 451–457.

Siemann, E., S.J. DeWalt, J. Zou, and W.E. Rogers. 2017. An experimental test of the EICA hypothesis in multiple ranges: Invasive populations outperform those from the native range independent of insect herbivore suppression. AoB Plants. 9(1).

van der Heijden M.G.A. and I.R. Sanders. 2002. Mycorrhizal Ecology: Synthesis and Perspectives. In: van der Heijden M.G.A., Sanders I.R. (eds) Mycorrhizal Ecology. Ecological Studies (Analysis and Synthesis), vol 157. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-38364-2_17

Vann, C.D., and J.P. Megonigal. 2002. Productivity responses of *Acer rubrum* and *Taxodium distichum* seedlings to elevated CO_2 and flooding. Environmental Pollution. 116:31–36.

Walters, R.S. and H.W. Yawney. 1990. Red maple (*Acer rubrum* L.) In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 60–69. Washington, DC: USDA Forest Service. 877 pages.

Wang, G.B., and F.L. Cao. 2012. Formation and function of aerenchyma in baldcypress (*Taxodium distichum* (L.) Rich.) and Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) under flooding. South African Journal of Botany. 81:71–78.

Wear, D.N., and J.G. Greis. 2013. The southern forest futures project: Technical report. General Technical Report SRS-GTR- 178. Asherville, NC. 542 p.

Wells, O.O. and R.C. Schmidtling. 1990. American sycamore (*Platanus occidentalis* L.) In Silvics of North America: 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 511–517. Washington, DC: USDA Forest Service. 877 pages.

Wilhite, L.P. and J.R. Toliver. 1990. Bald cypress (*Taxodium distichum*) In Silvics of North America: 1. Conifers. Edited by R.M. Burns and B.H. Honkala, 1153-1164. Washington, DC: USDA Forest Service. 1164 pages.

Williamson, M.H. 1996. Biological invasions. Chapman & Hall, London, UK.

Williamson, M.H., and A. Fitter. 1996. The characters of successful invaders. Biological Conservation. 78:163–170.

Young, P.J., B.D. Keeland, and R.R. Sharitz. 1995. Growth response of baldcypress (*Taxodium distichum* (L.) Rich.) to an altered hydrologic regime. The American Midland Naturalist. 133(2):206–212.

Zheng, H., Y. Wu, J. Ding, D. Binion, W. Fu, and R. Reardon. 2005. Invasive Plants Established in the United States that are Found in Asia and Their Associated Natural Enemies. Forest Health Technology Enterprise Team. 2:1–175.

Zou, J., W.E. Rogers, and E. Siemann. 2007. Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. Functional Ecology. 21:721–730.

Zou, J., W.E. Rogers, and E. Siemann. 2009. Plasticity of *Sapium sebiferum* seedling growth to light and water resources: Inter- and intraspecific comparisons. Basic and Applied Ecology. 10(1):79–88.

CHAPTER 3

RESPONSE OF CHINESE TALLOW (TRIADICA SEBIFERA) AND COEXISTING NATIVES TO COMPETITION, SHADE, AND FLOODING

Published in Forest Science 68(1):17–26.

https://doi.org/10.1093/forsci/fxab046

ABSTRACT

A greenhouse experiment was designed to determine the interactive effect of light, flooding, and competition on the growth and performance of Chinese tallow (*Triadica sebifera* [L.] Roxb.) and three tree species native to the southeastern United States: water tupelo (*Nyssa aquatica* L.), sugarberry (*Celtis occidentalis* L.) and green ash (*Fraxinus pennsylvanica* Marshall). The experiment used a factorial design that received two treatments: light (low irradiance or high irradiance) and flood (non-flooded and flooded) regimes. In the non-flooded and high irradiance treatment, changes in the growth (ground diameter, number of leaves, and total biomass) indicated that growth metrics of tallow were highest when growing with sugarberry and water tupelo but decreased when tallow competed with green ash. In contrast, competition with tallow reduced the height, net photosynthetic rate, stomatal conductance, and transpiration rate of water tupelo. The results showed that tallow had lower growth metrics when in competition with green ash at no apparent decrease in the growth of green ash except for growth rate. The results suggest that tallow may be less competitive with certain native species and underplanting may be a possible opportunity for improving the success rates of native trees species establishment in areas prone to tallow invasion.

Keywords: Invasive species, Chinese tallow, competition, sugarberry, green ash, water tupelo

INTRODUCTION

Chinese tallow tree (*Triadica sebifera* [L.] Roxb.), hereafter tallow, is a medium-sized deciduous tree and native to China, Japan, and northern Vietnam (Zheng et al. 2005). Across its native range, the wax-coated seeds of tallow are important for the production of candle wax and fatty acids (Zheng et al. 2005; Gao et al. 2016). The tree also has extensive medicinal value as different chemicals with medicinal properties can be derived from its tissues (McCormick 2005). Since its introduction in Georgia in the 18th century, tallow has expanded its geographic range in the United States and has been reported in Alabama, Arkansas, California, Florida, Louisiana, Mississippi, North Carolina, South Carolina, and Texas (Wheeler and Ding 2014; Enloe et al. 2015). Between 1992 and 2007, tallow volume across East Texas increased from 21 million cubic feet to 87 million cubic feet, making the species one of the most successful invaders in East Texas (Oswalt 2010). Oswalt 2010 ranks tallow as the fifth most common tree species in Louisiana, only superseded by loblolly pine (*Pinus taeda* L.), sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), and water oak (*Quercus nigra* L.). In Florida, tallow is a naturalized tree species and has been recorded in more than half of the counties in the state (38 of 47 counties: Wheeler and Ding 2014). Across its current range in the Southeastern United States, tallow is expected to expand 334 km north at a rate of 1231 m / year (Wang et al. 2011a; Suriyamongkol et al. 2016).

Successful control of tallow requires an integrated pest management (IPM) plan, this involves an integration of biological, chemical, mechanical, and physical control techniques (McCormick 2005). Several potential biological control agents have been identified for tallow, however, reduced defense mechanisms and higher tolerance of damage observed in invasive ecotypes suggest that biological control agents may reach high densities without successful control (Wang et al. 2011b; Pile et al. 2017). Chemical treatments generally decrease foliar cover and sprout number during the first growing season, however, vigorous regrowth during the second growing season suggests that tallow can overcome chemical treatments (Enloe et al. 2015). Mechanical treatments aimed at reducing density and preventing germination of tallow are often ineffective and may exacerbate invasion in some situations (McCormick 2005). An IPM plan designed specifically for tallow based on its documented physiology was effective in reducing density (Pile et al. 2017). Mastication in the spring decreased tallow density while increasing the horizontal continuity of the fuel bed. Subsequently, foliar herbicide application in the fall and winter targeted regeneration from the seedbank and roots. Mastication and herbicide treatments were followed by prescribed fire treatment aimed at minimizing resprouting and regeneration. Even though this integrated approach was effective in reducing tallow covered, an open canopy may foster re-establishment. To prevent the re-establishment of tallow, invaded communities should be restructured with native species with similar functional traits. Based on the principle of limiting similarity, interspecific competition should be greatest between functionally similar species. Studies have proposed that invasive species are unlikely to establish in the presence of species with similar functional traits (Funk et al. 2008; Young et al. 2009).

Tallow often coexists with water tupelo (*Nyssa aquatica* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and sugarberry (*Celtis laevigata* Willd) in the floodplain forests of southeastern United States. Based on their growth rate, shade tolerance, and flood tolerance, these native species can be considered to belong to the same functional group as tallow. Water tupelo is a large, long-lived tree that grows in minor topographic positions in floodplains forests where the root system is periodically underwater. Seedlings survive flooded conditions by developing new secondary roots which tolerate high concentrations of CO_2, oxidize the rhizosphere, and accelerate anaerobic respiration in N_2 (Hook and Brown 1973). These morphological and physiological root characteristics allow water tupelo to survive in regions where it is too wet for most other species (Johnson 1990). In addition to its high flood tolerance, water tupelo is a prolific stump sprouter and is classified as moderately tolerant to intolerant of shade (Johnson 1990; Allen et al. 2001). Green ash is the most widely distributed member of the *Fraxinus* genus in America and can be commonly found on alluvial soils close to rivers and streams (Kennedy 1990). Green ash also has rooting habits and adaptations that enable seedlings to withstand flooding regimes that would kill other species (Kennedy 1990). Such habits include regeneration of secondary roots from primary roots, development of adventitious roots on submerged stems, accelerated anaerobic respiration rate in the absence of oxygen, and ability to oxidize its rhizospheres. Sugarberry is a medium-sized, fast-growing species with intermediate flood tolerance that grows well on moist well-drained soils (Krajicek and Williams 1990). Sugarberry is principally a bottomland species adapted to a wide range of soil and moisture conditions but grows best on bottomland soils where it grows fast and may live for 150 years (Krajicek and Williams 1990). Sugarberry can be propagated by stem cuttings, grafting and sprouts develop from stumps of small trees (Krajicek and Williams 1990).

Aside from the previously described characteristics, the three native species have traits that suggest they successfully occupy the open vegetation canopy left after the removal of tallow, hampering re-establishment by tallow regeneration. Water tupelo seedlings develop better in saturated soils and can survive continuous flooding provided seedlings are above water (Johnson 1990). The high flood tolerance of water tupelo allows this species to thrive in unshaded, wet, poorly drained soils where tallow may persist. Green ash is an early successional and fast-growing species with moderate tolerance to shade. Green ash is probably the most adaptable member of the genus *Fraxinus* in North America, where it grows on a range of soil types including frequently flooded soils, soils with limited available moisture, and highly acidic soils (Kennedy 1990). Sugarberry is classified as tolerant of shade and can become established in the understory of most floodplain forests (Kennedy 1990). Sugarberry is one of the fastest-growing native trees in Texas and like tallow, the native is insect-pollinated, bird-dispersed, and has the potential to grow rapidly on wetter sites (Siemann and Rogers 2003).

A greenhouse experiment was designed to investigate the changes in morphological and physiological traits of tallow in competition with each native species, and the changes in morphological and physiological traits of each native species in competition with tallow. The objective of this study was to determine the growth, survival, and physiological responses of tallow in competition with native hardwood species under a range of flooding and light availability conditions representative of natural conditions in floodplain forests.

METHODS

Seed germination and study area

This study was conducted in a temperature-controlled greenhouse at Stephen F. Austin State University, Nacogdoches, TX. This area is a subtropical zone with humid summers, mild winters, and average annual rainfall of 98 – 152 cm. Tallow seeds were collected from the limbs of randomly selected trees (lat. 31º37′N, long. 94º39′W) on the Stephen F. Austin State University (SFASU) campus during the winter of 2017. Tallow seeds were in the waxy capsule at the time of collection from two mother trees in the overstory and within 1 m of each other. Seeds of water tupelo, sugarberry, and green ash were purchased from the Louisiana Forest Seed Company, LA USA in early January 2018. All seeds were stored at 3-5 ℃ and subsequently stratified according to the instructions of Burns and Honkala (1990) in early February 2018. After stratification, seeds were sown (20 – 30 mm deep) on 3 – 5 March 2018 into containers measuring 10.5 × 15 × 11 cm filled with Miracle-Gro® Potting Mix. Seeds were germinated in a growth chamber (day: 30 ℃, 8 hr, 59% humidity; night: 20 ℃, 16 hr, 63% humidity) and watered every two days to avoid water stress. Seed germination was tracked for the first eight weeks in the growth chamber (Table 3.1).

Experimental design

On June 14, 2018, three months after sowing, bare-root seedlings were transplanted and randomly placed into containers (measuring 21 × 17 × 22 cm) filled with soil from the Kurth series (fine-loamy, siliceous, semiactive, and thermic Oxyaquic Glossudalfs). The soil was dug from the Gail Creek Property (lat. 31º12′N, long. 95º23′W), which is located in east Texas and representative of native soil from the region where all four species are found. The soil was not sterilized before use and no fertilizers were added for the duration of this experiment (June to October 2018: 134 days). Seedlings were placed in a temperature-controlled greenhouse on the SFASU campus in Nacogdoches, TX. The average daily temperature during the experimental period (June to October 2018) in the greenhouse was 28.5 ℃ (maximum temperature) and 21.2 ℃ (minimum temperature), and an evaporative cooler was used to maintain greenhouse temperatures.

The study design involved the following randomly assigned treatments and levels per treatment:

i. Light treatments: (1) high irradiance: containers were not shaded with a black polypropylene shade cloth, and the irradiance was not reduced, indicating a lack of forest overstory, indicated by *H,* and (2) low irradiance: containers were placed under a black polypropylene shade cloth that reduced irradiance simulating a shaded forest understory, indicated by *L*. Shade cloth was mounted on a frame measuring 303 × 123 × 110 cm.

ii. Flooding treatments: (1) non-flooded: containers were watered daily until water flowed out of the bottom of the container representing a well-drained floodplain site, indicated by *N*; (2) pulsed-flooded: containers received the non-flooded treatment for two weeks followed by permanent submergence in a plastic tub (27.9 × 42.2 × 60.3 cm) filled with water (1-3 cm above soil surface) for two weeks, representing a frequently flooded floodplain site, indicated by *F*. This four-week cycle was repeated for the 134 days. Losses by evaporation and transpiration were replaced with de-ionized water to avoid salt accumulations (Butterfield et al. 2004).

iii. Competition treatments included pair-wise combinations of intraspecific and interspecific competition were replicated four times, as follows: (1) four seedlings of sugarberry per container, indicated by *SBSB*; (2) four seedlings of green ash per container, indicated by *GAGA*; (3) four seedlings of water tupelo per container, indicated by *WTWT*; (4) four seedlings of tallow per container, indicated by *CTCT*; (5) two seedlings of sugarberry and two of tallow per container, indicated by *SBCT* or *CTSB*, *SBCT* means sugarberry growing with tallow under interspecific competition and *CBST* means tallow growing under interspecific competition with sugarberry; (6) two seedlings of green ash and two of tallow per container, indicated by *GACT* or *CTGA*, *GACT* means green ash growing under interspecific competition with tallow and *CTGA* means tallow growing under interspecific competition with green ash; (7) two seedlings of water tupelo and two of tallow per container, indicated by *WTCT* or *CTWT*, *WTCT* means water tupelo growing under interspecific competition with tallow and *CTWT* means tallow growing under interspecific competition with water tupelo.

Containers received two light treatments, two flooding treatments and seven competition treatments in a full factorial design (n = 112, 2 shade × 2 flooding × 7 competition × 4 replicates). The final number of containers were 112 (2 shade treatments × 2 flooding treatments × 7 competition treatments × 4 replicates) and each container had four seedlings, resulting in a total of 448 seedlings. There were four light and flooding treatments: flooded and high irradiance (FH), flooded and low irradiance (FL), non-flooded and high irradiance (NH), and non-flooded and low irradiance (NL). FH represented a frequently flooded floodplain site lacking a forest overstory, FL represented a frequently flooded floodplain site with a shaded overstory, NH represented a well-drained floodplain site lacking a forest overstory, and NL represented a well-drained floodplain site with a shaded overstory. Twenty-eight containers were included in each light and flooding treatment. Containers were randomly placed, maintained in one section of the greenhouse, and evenly spaced in the greenhouse to prevent overlap and container–container shading. Seedlings were spaced evenly within each container and watered daily for two weeks before initiation of treatments. Seedlings were grown under the treatments for 134 days.

Photosynthetic measurements

The leaf-level gas exchange parameters recorded in this study represent a point in time measurement and reflect the immediate condition of each seedling and the leaf. Leaf gas exchange was measured between August 22, 2018, and September 11, 2018, on clear-sky days between 1000- and 1400- hours of Central Daylight Time. Net photosynthetic rate (P_n; µ mol m^{-2} s^{-1}), stomatal conductance (G_s; mol m^{-2} s^{-1}), intercellular carbon dioxide (C_i; µ mol mol^{-1}), transpiration rate (T_{r}; m mol m^{-2} s^{-1}) and water-use efficiency (WUE; µ mol CO_2 / m mol H_2O) per leaf unit area were measured simultaneously using a single infrared gas analyzer (Li-Cor 6400, Lincoln, NE, USA). Measurements were made with the following chamber conditions: 800 µmol m^{-2} s^{-1} *PPFD* (under no shade; Li et al. 2015), 350 µmol m^{-2} s^{-1} *PPFD* (under shade; Wu et al. 2017), 380 µmol mol^{-1} reference CO_2 concentration (Li et al. 2015), ambient chamber temperature and humidity, and a flow rate of 200 µmol s^{-1}. Before taking measurements, the leaves were equilibrated in the leaf chamber for at least 9 minutes under artificial light conditions and each leaf took the entirety of the chamber. Each seedling was treated as a replicate and four separate measurements were taken from four different fully expanded leaves. The gas exchange parameters were computed as the average values for each seedling.

Growth measurements

Initial stem height, ground line diameter, and leaf count were recorded for each plant at treatment initiation to account for ontogenetic effects (Table 3.2). At the end of the experiment, the final seedling height, ground line diameters, and leaf counts were measured. Ground line diameter was measured with a digital caliper. Leaf length, width, and area were measured by scanning fresh leaves with a portable leaf area meter (LI-3000A, Li-COR Biosciences) at the end of the experiment. Morphological variables were measured from 10 fresh leaves sampled from each seedling before harvest. In October 2018, all seedlings were harvested, divided into roots, leaves, and stems, and dried at 60 °C for 96 hours to constant mass to calculate root, stem, and leaf biomass, and total biomass was the sum of these three. Based on seedling biomass and leaf area measurement, the following plant morphological traits were calculated: root: shoot ratio (RSR, ratio of root dry mass to leaf and stem dry mass, g g^{-1}) and specific leaf area (SLA; leaf area per unit leaf mass, cm^2 g^{-1}). Leaf mass fraction (LMF), stem mass fraction (SMF) and root mass fraction (RMF) were calculated as follows: LMF = (leaf dry mass / total biomass) × 100, SMF = (stem dry mass / total biomass) × 100, RMF = (root dry mass / total biomass) × 100 (Wu et al. 2017).

Statistical analysis

All analyses were performed using the Statistical Analysis System (SAS 9.4, SAS Institute, Cary, NC). Pearson's correlation was used to examine the bivariate relationships between the different response variables (using PROC CORR). Since all morphological and physiological variables were moderately or highly correlated ($r \geq 0.5$), a multivariate analysis of variance (MANOVA) was conducted to examine the effects of light treatment, flooding treatment, competition treatment, and their interactions on the response variables. Because the

MANOVA results were significant, I conducted an Analysis of Variance (ANOVA) for each variable followed by pairwise comparison with the Tukey's test at $P < 0.05$ (using PROC GLM). The model assumptions of normality and homoscedasticity were verified using residual plots. Data did not need to be transformed to meet the assumptions of normality and homoscedasticity. I set the significance level at 5% *a priori* for all statistical tests. I considered any P value ≤ 0.05 as evidence of a significant difference. The following model was used to analyze the effects:

$$y_{ijkl} = \mu + S_i + L_j + F_k + S_i{*}L_j + S_i{*}F_k + L_j{*}F_k + S_i{*}L_j{*}F_k + \mathcal{E}_{ijkl}$$

Where, y was the value of a response variable of the l^{th} seedling of the i^{th} species, treated with the j^{th} shading and k^{th} flooding, S_i was the i^{th} species effect, L_j was the j^{th} light effect, F_k was the k^{th} flooding effect, $S_i{*}L_j$, $\mathrm{Si}{*}F_k$, $L_j{*}F_k$, and $S_i{*}L_j{*}F_k$ were the respective interaction between species and light, species and flooding, light, and flooding, and among species, light, and flooding (which basically is the effect among containers). All factors were treated as fixed. $\mathcal{E}_{ijkl}$ was random error, which is NID (0, σ^2), where σ^2 is the error variance.

RESULTS

Effects of species, light, and flooding

Among all the variables examined, most indicators showed significant interactions of species, light, and water effects, except for leaf dry mass per area (Table 3.1, MANOVA, F = 0.98, $P > 0.05$) and the physiological variables which were not significantly affected by the interaction (Table 3.3).

Seedling survivorship

Out of the 448 seedlings planted, 407 survived to the end of the 134 days experiment (Table 3.4). Survival was highest in NL where 98% (110 alive from the 112 planted) of the seedlings survived till the end of the experiment, but lowest in FH with 76% (85 alive from the 112 planted). Flooding induced the formation of adventitious roots in tallow and green ash. In FL, I observed 100% survival in all species combinations except for tallow (in interspecific competition with sugarberry) and green ash (Table 3.4). Sugarberry survival was lowest in FH with no seedlings surviving to the end of the experiment (Table 3.4). In NH, seedling survival was at a 100% in all species combinations except for sugarberry in intraspecific competition (Table 3.4). Seedling survivorship in NL was a 100% in all species combinations apart from tallow in intraspecific competition (Table 3.4).

Growth and morphological response

The morphological traits examined decreased with low irradiance and increased with high irradiance (Figure 3.1). Growth rate of the seedlings was highest in NH, in this treatment stems were tallest with the highest leaf count and leaf area (Figures 3.1A - E). Seedling biomass also increased in this treatment with seedlings producing the largest biomass in NH and lowest in FL (Figure 3.1F). LMF was highest in NL, intermediate in FH but lowest in FL and NH (Figure 3.1G). SMF was also highest in NL but intermediate in the high irradiance treatments and lowest in FL (Figure 3.1H). The highest RMF values were observed in high irradiance while the lowest in the while was in FL (Figure 3.1I). Root shoot ratio decreased with decreasing light, with the lowest values in FL (Figure 3.1J).

Gas exchange response

The gas-exchange parameters showed that with decreasing light levels, P_n and WUE decreased. P_n and WUE increased in high irradiance with a significant difference between FH and NH (Figure 3.1K and 3.1O). There was a significant difference in WUE in FL and NL (Figure 3.1O). G_s was highest in NH, intermediate in FL, and lowest in FH and NL (Figure 3.1L). C_i increased with decreasing irradiance and was lowest in the FH and NH with a significant difference between both treatments (Figure 3.1M). T_r was highest in NH with a significant difference between FL and NL, but no difference between FH, and NL (Figure 3.1N).

Response to competition

Morphological variables varied in response to competition across the different treatments (Figures 3.2 and 3.3). Among the native species growing in intraspecific competition, water tupelo seedlings were tallest in FH while sugarberry was the tallest in NH and NL (Figure 3.2 and 3.3A). There was no significant difference in seedling height, ground diameter, number of leaves, and leaf area in FL (Figure 3.2D, 3.3A, 3.3B, 3.3C, and 3.3D). Competition with the native species impacted the ground diameter of tallow in NH (Figure 3.2A and 3.3B). In NH, the ground diameter of tallow was largest when growing with sugarberry and water tupelo but smallest in intraspecific competition and when growing with green ash (Figure 3.3B). In NH, water tupelo had the largest ground diameter in intraspecific competition and was the only native species with a reduced ground diameter in interspecific competition (Figure 3.2A and 3.31 B). Sugarberry had the highest leaf count in NH and tallow produced more leaves in competition with sugarberry and water tupelo in the same treatment (Figure 3.2C). There was no significant difference in the number of leaves and leaf area in FH, FL, and NL (Figures 3.3C and 3.3D). Among the native species, green ash had the highest leaf area in NH (Figure 3.3 D). In this treatment, the leaf area of tallow was highest in competition with sugarberry but lowest in intraspecific competition and in competition with water tupelo and green ash (Figure 3.3D). In FH, interspecific competition did not impact the growth rate of any of the species and tallow had the highest growth rates in intraspecific competition (Figure 3.3E). Among the native species in FL, green ash and sugarberry had the highest growth rates while water tupelo had the lowest growth rates (Figure 3.3E). Water tupelo seedlings were on average two and three times taller than the other species at the beginning of the treatments, this may have contributed to the low final growth rate. In NH, sugarberry had the highest growth rate in intraspecific competition among the native species (Figure 3.3E). Green ash was the only native species to experience a reduction in growth rate when in competition with tallow in NH (Figure 3.3E).

The total biomass of the selected native species was not impacted by competition across the NH treatment (Figure 3.4A). In NH, the total biomass of tallow was highest in competition with sugarberry and water tupelo but lowest in intraspecific competition and in competition with green ash (Figure 3.4A). There was no significant difference in seedling total biomass in FL and NL (Figure 3.4A). There was also no significant difference in LMF and SMF in NL and FL (Figure 3.4B and 3.4C). Sugarberry also had the highest SMF among the native species in NH (Figure 3.4B). I also observed no significant differences in RMF in FL, NH, and NL (Figure

3.4D). There was no significant difference in root shoot ratio in NL and FL (Figure 3.4E). Among the native species in NH, green ash had the highest root shoot ratio under interspecific competition with tallow (Figure 3.4E).

With the gas-exchange parameters, there was no significant difference between P_n, G_s, and *WUE* in FH, FL, and NL (Figures 3.5A, 3.5B, and 3.5E). In NH, tallow recorded its highest P_n in competition with water tupelo but had its lowest P_n in competition with green ash, sugarberry, and under intraspecific competition (Figure 3.5A). Tallow had its lowest G_s value under intraspecific competition in NH, but G_s increased in competition with native species (Figure 3.5B). Among the native species in NH, green ash had the highest G_s in competition with tallow, sugarberry had the lowest G_s, and water tupelo was the only native species with reduced G_s under interspecific competition (Figure 3.5B). In NL and FH, C_i of green ash was lower under intraspecific competition but higher under interspecific competition with tallow (Figure 3.5C). In NL, where C_i of sugarberry was lower under interspecific competition with tallow and higher intraspecific competition (Figure 3.5C). Unlike sugarberry, C_i of green ash was lower in intraspecific competition but higher in interspecific competition (Figure 3.5C). Among the native species in interspecific competition, green ash had the highest C_i in FH (Figure 3.5C). There was no significant difference in C_i in FL and NH (Figure 3.5C). Sugarberry had the lowest T_r among native species under intraspecific competition in NH (Figure 3.5D). In NH and FL, T_r of tallow is lowest under intraspecific competition but significantly higher under interspecific competition (Figure 3.5D). Among the native species under interspecific competition, water tupelo had the lowest T_r in FL while sugarberry had the lowest T_r in NH (Figure 3.5D). There was no significant difference in WUE in NL and FL (Figure 3.5E). Among the native species in NH, sugarberry had the highest WUE in both intraspecific and interspecific competition (Figure 3.5E).

DISCUSSION AND CONCLUSION

Interspecific competition plays a crucial role in influencing the successful replacement of invasive plant species (Domènech and Vilà 2008; Li et al. 2015). For the selected native species to be competitive, I expect the growth metrics of tallow to be reduced in interspecific competition more than in intraspecific competition. This study showed that the growth metrics of the early recruitment stages of tallow in well-drained sites lacking forest overstory will differ greatly among native species. The non-flooded and high irradiance treatment (NH) attempted to stimulate a well-drained floodplain site lacking forest overstory. In this treatment, tallow had lower growth metrics when grown with green ash with no apparent decrease in the growth metrics of green ash except for growth rate. In contrast, tallow had higher growth metrics when grown with water tupelo and sugarberry with a significant decrease in the growth metrics of the two native species. Even though tallow is the only member of the Euphorbiaceae family in Texas that is a tree, underplanting may improve the success rate of functionally similar native species in areas prone to tallow invasion (Siemann and Rogers 2003).

Replacement control through planting functionally similar native species has been effective in suppressing the recruitment of invasive vines and perennials (Li et al. 2012; Li et al. 2015). Similarly, the competitive advantages of invasive tree species could be diminished with fast-growing native tree species (Pile et al. 2019). At 12 years, the higher growth rates and competitive ability of tallow reduced when growing with slash pine, a fast-growing conifer in the Southern Coastal Plain ecoregion (Pile et al. 2019). The study also provides evidence of reduced growth metrics in the early recruitment stages of tallow when grown with green ash. These metrics were observed in the non-flooded and high irradiance treatment (NH), which represents a well-drained floodplain site lacking forest overstory.

Despite being one of the fastest-growing native trees in Texas, flooding resulted in heavy mortality in sugarberry seedlings. Of the three natives, sugarberry was the least tolerant to flooding as evidenced by its poor survival. Green ash and water tupelo were the most tolerant to flooding with the highest survival and moderate growth reductions. Tallow was intermediate with moderate survival and growth reductions. Flooding induced the formation of adventitious roots in tallow and green ash which is typical of woody plants capable of surviving prolonged periods of flooding and low soil redox potentials (Jones and McLeod 1989; Jones and Sharitz 1990; Wang and Cao 2012). The relative flood tolerance of the selected native species has been identified and they are similar to the results of this study (Hosner 1959; Hosner and Boyce 1962; Gabler and Siemann 2013).

As has been reported, shade lowered seedling height, ground diameter, number of leaves, leaf area, total biomass, and root mass fraction, but the highest LMF and SMF values were recorded in the shade. Increased LMF and SMF suggest that seedlings of all species adapted to the limited light conditions by allocating more photosynthates to produce organs that are able to acquire the resources (Guo et al. 2013). This explains why more biomass was allocated to the leaves and stems in the shaded conditions. Based on the total biomass, height, ground diameter, tallow seedlings exhibited modest growth in shade conditions, but I observed the superior competitive ability of the invasive in full light conditions.

Changes in growth metrics relative to competition underpin the competitiveness of the selected species in this study. Changes in ground diameter and number of leaves in NH indicated that tallow stems were larger with a higher leaf count when tallow competed with sugarberry and water tupelo, as compared to when tallow competed with green ash and itself. By contrast, the ground diameter of water tupelo decreased when the native competed with tallow, as compared with growth in intraspecific competition. Similarly, tallow stems had higher growth rates when in competition with sugarberry and water tupelo, as compared to when tallow was under intraspecific competition. Together, these results suggest that the growth metrics of the invasive species will vary depending on the native species that tallow is in competition with.

Another factor that increased the competitiveness of the invasive species, tallow, is that interspecific competition increased the gas-exchange parameters of the invasive. Gas exchange parameters showed that the rate of photosynthesis per unit leaf area was lower when tallow was in the presence of competition from green ash and sugarberry but increased in the presence of competition from water tupelo. By contrast, the rate of photosynthesis per unit area of water tupelo decreased when the native was in competition with tallow compared to intraspecific competition. The lower rates of photosynthesis may account for the reduced ground diameter of water tupelo when in competition with tallow. Tallow has been reported to have an ability to spread its crown over a larger area due to the formation of large branches with a greater number of leaves, competition for light with tupelo may have resulted in partial shading of water tupelo leaves by tallow (Jones and McLeod 1990). Changes in the stomatal conductance and transpiration rate of tallow in NH, indicate that these parameters were lowest under intraspecific competition but increased when in competition with green ash, sugarberry, and water tupelo. Among the native species growing with tallow, green ash has the highest stomatal conductance and transpiration rates. Unlike sugarberry and water tupelo, green ash had no reductions in stomatal conductance and transpiration rate when green ash was in competition with tallow. This suggests that when competition with water tupelo and sugarberry, tallow will be better suited to capture and utilize resources in light interception. This is evident by the larger ground diameter, number of leaves, and total biomass of tallow in competition with water tupelo and sugarberry. These findings are consistent with the cited traits of invasiveness which includes rapid growth rates and overall larger sizes at the early life stages when compared to native species (Grotkopp et al. 2002). For tallow specifically, morphological plasticity, high net photosynthesis and the rapid development of fully functional leaves account for the superior performance of tallow seedlings in NH.

Invasive plants do not always perform better than co-occurring native counterparts (Domènech and Vilà 2008). Tallow displayed significantly higher growth metrics when growing with sugarberry and water tupelo. Increased biomass allocation, high net photosynthesis, and development of functional leaves with larger areas were an advantage to tallow in competition with these natives. I observed these advantages only in the absence of shade and flooding.

For bottomland species, tolerance of light and flooding often influences growth and survival. The low survival of sugarberry with flooded conditions in this study suggests the native should not be considered in restructuring unshaded frequently flooded communities invaded by tallow. All three natives might be candidates for restructuring shaded upland communities as the tallow showed modest growth in competition with the selected natives. In the absence of shade and flooding, green ash had the highest growth metrics among the native species, and it may be a strong candidate for restructuring communities invaded by tallow. The higher metrics of green ash relative to the other native species was most likely the result of greater leaf area and no apparent decrease in green ash growth metrics when in competition with tallow except for growth rate. The emerald ash borer (*Agrilus planipennis*), hereafter EAB, is a destructive nonnative ash (*Fraxinus* spp.) tree woodboring pest (Poland and McCullough 2006). The invasive pest has spread to 35 states since its discovery in southeast Michigan in 2002, including Texas, where it was first discovered in Harrison County in Northeast Texas. EAB is to blame for the annihilation of millions of ash trees across much of the country. Because it kills both stressed and healthy ash trees, EAB is a serious threat to urban, suburban, and rural forests (Poland and McCullough 2006).

In conclusion, I have demonstrated that tallow may be less competitive with certain native species. Replacement control through the planting of functionally similar native species may be a potential means of preventing tallow from establishing or re-establishing in areas prone to tallow invasion. Further studies need to be conducted in a floodplain forest where multiple factors (including flooding, shade, herbivory, root competition, disease, and occasional drought) may influence seedling performance and survival.

LITERATURE CITED

Allen, J.A., B.D. Keeland, J.A. Stanturf, A.F. Clewell, and H.E. Kennedy. 2001. A Guide to Bottomland Hardwood Restoration. Forest Service U.S. Department of Agriculture, Southern Research Station. Asheville, NC.

Burns, R.M., and B.H. Honkala. 1990. Silvics of North America. Agriculture handbook: U.S. Dept. of Agriculture, Forest Service.

Butterfield, B.J, W.E Rogers, and E. Siemann. 2004. Growth of Chinese tallow tree (*Sapium sebiferum*) and four native trees under varying water regimes. Texas Journal of Science. 56(4): 335-346.

Domènech, R., and M. Vilà. 2008. Response of the invader *Cortaderia selloana* and two coexisting natives to competition and water stress. Biological Invasions. 10 (6): 903-912.

Enloe, S.F., N.J. Loewenstein, D. Streett, and D.K. Lauer. 2015. Herbicide Treatment and Application Method Influence Root Sprouting in Chinese Tallowtree (*Triadica sebifera*). Invasive Plant Science and Management. 8(02): 160-168.

Funk, J.L., E.E. Cleland, K.N. Suding, and E.S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution. 23(12): 695-703.

Gabler, C.A, and E. Siemann. 2013. Rapid ontogenetic niche expansions in invasive Chinese tallow tree permit establishment in unfavorable but variable environments and can be exploited to streamline restoration. Journal of Applied Ecology. 50(3): 748-756.

Gao, R., Z. Su, Y. Yin, L. Sun, and S. Li. 2016. Germplasm, chemical constituents, biological activities, utilization, and control of Chinese tallow (*Triadica sebifera* (L.) Small). Biological Invasions. 18:809-829.

Grotkopp, E., M. Rejmánek, and T.L. Rost. 2002. Toward a Causal Explanation of Plant Invasiveness: Seedling Growth and Life-History Strategies of 29 Pine (*Pinus*) Species. The American Naturalist. 159(4):396-419.

Guo, X., W. Guo, Y. Luo, X. Tan, N. Du, and R. Wang. 2013. Morphological and biomass characteristic acclimation of trident maple (*Acer buergerianum* Miq.) in response to light and water stress. Acta Physiologiae Plantarum. 35(4):1149-1159.

Hook, D.D., and C.L. Brown. 1973. Root Adaptations and Relative Flood Tolerance of Five Hardwood Species. Forest Science. 19(3):225-229.

Hosner, J.F. 1959. Survival, root, and shoot growth of six bottomland tree species following flooding. Journal of Forestry. 59:927 – 928.

Hosner, J.F., and S.G. Boyce. 1962. Tolerance to water saturated soil of various bottomland hardwoods. Forest Science. 8(2):180 – 186.

Johnson, R.L. 1990. Water Tupelo (*Nyssa aquatica*). In Silvics of North America: 1. Conifers; 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 474-478. Washington, DC: USDA Forest Service. 877 pages.

Jones, R.H., and K.W. McLeod. 1989. Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. Bulletin of the Torrey Botanical Club. 116(4):371-377.

Jones, R.H., and K.W. McLeod. 1990. Growth and photosynthetic responses to a range of light environments in Chinese tallowtree and Carolina ash seedlings. Forest Science. 36:851-862.

Jones, R.H., and R.R. Sharitz. 1990. Effects of root competition and flooding on growth of Chinese tallow tree seedlings. Canadian Journal of Forest Research. 20(5):573-578.

Kennedy, H.E. 1990. Green Ash (*Fraxinus pennsylvanica*). In Silvics of North America: 1. Conifers; 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 348-354. Washington, DC: USDA Forest Service. 877 pages.

Krajicek, J.E., and R.D. Williams. 1990. Hackberry (*Celtis occidentalis* In Silvics of North America: 1. Conifers; 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 262-265. Washington, DC: USDA Forest Service. 877 pages.

Langeland, K.A., and S.F. Enloe. 2002. Natural Area Weeds: Chinese Tallow (*Sapium sebiferum* L.). Agronomy Department, UF/IFAS Extension (UF/IFAS Extension).

Lázaro-Lobo, A., R.D. Lucardi, C. Ramirez-Reyes, and G.N. Ervin. 2021. Region-wide assessment of fine-scale associations between invasive plants and forest regeneration. Forest Ecology and Management. 483:

Li, M., E. Lu., G. Qiang, Q. Zan, P. Wei, L. Jiang, H. Xu, and T. Zhong. 2012. Evaluation of the controlling methods and strategies for *Mikania micrantha* H.B.K. Acta Ecologica Sinica. 32: 3240-3251.

Li, W., J. Luo, X. Tian, W.S. Chow, Z. Sun, T. Zhang, S. Peng, and C. Peng. 2015. A new strategy for controlling invasive weeds: selecting valuable native plants to defeat them. Scientific Reports. 5, 11004; doi: 10.1038/srep11004.

Lin, J., P.A. Harcombe, M.R. Fulton, and R.W. Hall. 2004. Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas. Oecologia. 139(3): 399-407.

McCormick, C.M. 2005. Chinese tallow management plan for Florida. Florida Exotic Pest Plant Council, Chinese Tallow Task Force.

Oswalt, S.N. 2010. Chinese tallow (*Triadica sebifera* (L.) Small) population expansion in Louisiana, east Texas, and Mississippi. United States Department of Agriculture, Forest Service, Southern Research Station. Research Note SRS-20 (Asheville, NC).

Poland, T.M., and D.G. McCullough. 2006. Emerald ash borer: Invasion of the urban forest and the threat to north America's ash resource. Journal of Forestry. 104(3): 118-124.

Pile, L.S., G.G. Wang, T.A. Waldrop, J.L. Walker, W.C. Bridges, Jr., and P.A. Layton. 2017. Managing an Established Tree Invader: Developing Control Methods for Chinese Tallow (*Triadica sebifera*) in Maritime Forests. Journal of Forestry. 115(6):522-529.

Pile, L.S., L. Vickers, M. Stambaugh, C. Norman, and G.G. Wang. 2019. The tortoise and the hare: A race between native tree species and the invasive Chinese tallow. Forest Ecology and Management. 445:110-121.

Siemann, E., and W.E. Rogers. 2003. Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. Journal of Ecology. 91(6):923-931.

Suriyamongkol, T., E. McGrew, L. Culpepper, K. Beck, H.-H. Wang, and W.E. Grant. 2016. Recent Range Expansions by Chinese Tallow (*Triadica sebifera* (L.) Small), the Most Prevalent Invasive Tree in the Forestlands of Eastern Texas. Southeastern Naturalist. 15(sp9):68-75.

Wang, G.B., and F.L. Cao. 2012. Formation and function of aerenchyma in baldcypress (*Taxodium distichum* (L.) Rich.) and Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) under flooding. South African Journal of Botany. 81:71-78.

Wang, H.-H., W.E. Grant, T.M. Swannack, J. Gan, W.E. Rogers, T.E. Koralewski, J.H. Miller, and J.W. Taylor. 2011a. Predicted range expansion of Chinese tallow tree (*Triadica sebifera*) in forestlands of the southern United States. Diversity and Distributions. 17(3):552-565.

Wang, Y., W. Huang, E. Siemann, J.W. Zou, G.S. Wheeler, J. Carrillo, and J.Q. Ding. 2011b. Lower resistance and higher tolerance of invasive host plants: biocontrol agents reach high densities but exert weak control. Ecological Applications. 21:729-738.

Wheeler, G.S. and J. Ding. 2014. Is Chinese tallowtree, *Triadica sebifera*, an appropriate target for biological control in the United States? Invasive Plant Science and Management. 7:345–359.

Wu, J., J. Li, Y. Su, Q. He, J. Wang, Q. Qiu, and J. Ma. 2017. A morphophysiological analysis of the effects of drought and shade on *Catalpa bungei* plantlets. Acta Physiologiae Plantarum. 39 (3):80.

Young, S.L., J.N. Barney, G.B. Kyser, T.S. Jones, and J.M. DiTomaso. 2009. Functionally Similar Species Confer Greater Resistance to Invasion: Implications for Grassland Restoration. Restoration Ecology. 17(6):884-892.

Zheng, H., Y. Wu, J. Ding, D. Binion, W., Fu, and R. Reardon. 2005. Invasive plants established in the United States that are found in Asia and their associated natural enemies. Morgantown, WV, pp. 1–174.

TABLES

Table 3.1: Number of Chinese tallow, water tupelo, green ash, and sugarberry seeds germinating each week in the growth chamber on the Stephen F. Austin State University campus. Percent survival at the end of week eight is in parenthesis.

Week germinated	Number and percent survival			
	Tallow	Tupelo	Green Ash	Sugarberry
1	-	-	-	-
2	-	-	-	-
3	-	-	-	-
4	-	11 (100)	50 (100)	5 (100)
5	5 (100)	28 (100)	30 (100)	5 (100)
6	9 (100)	29 (100)	10 (100)	10 (100)
7	12 (100)	28 (100)	10 (100)	11 (100)
8	15 (100)	29 (100)	8 (100)	25 (100)

Table 3.2: Differences in seedling height, ground diameter and number of leaves at treatment initiation. Values represent means (± SE). Column means for each variable with different letters represent significant differences ($P < 0.05$) among competition treatments according to the Tukey's test (alpha = 0.05).

Competition type	Competition treatment	Height (cm)	Ground diameter (mm)	Number of leaves
Intraspecific	Tallow only	11.52 ± 0.79^{f}	1.91 ± 0.07^{b}	7.00 ± 0.41^{c}
	Green ash only	15.40 ± 0.79^{de}	1.77 ± 0.07^{bc}	11.25 ± 0.42^{ab}
	Water tupelo only	26.84 ± 0.79^{a}	2.38 ± 0.07^{a}	10.51 ± 0.42^{b}
	Sugarberry only	20.63 ± 0.79c	1.28 ± 0.07^{d}	12.03 ± 0.41^{ab}
Interspecific	Tallow with green ash	11.94 ± 1.40^{ef}	1.70 ± 0.09^{bc}	7.09 ± 0.59^{c}
	Tallow with sugarberry	13.03 ± 1.14^{e}	1.78 ± 0.09^{bc}	7.37 ± 0.59^{c}
	Tallow with green ash	11.81 ± 1.12^{ef}	1.70 ± 0.09^{bc}	7.16 ± 0.59^{c}
	Green ash with tallow	17.94 ± 1.13^{dc}	1.89 ± 0.09^{b}	11.38 ± 0.59^{ab}
	Sugarberry with tallow	22.25 ± 1.11^{bc}	1.43 ± 0.09^{cd}	13.47 ± 0.59^{a}
	Water tupelo with tallow	25.41 ± 1.11^{ab}	2.07 ± 0.09^{ab}	10.13 ± 0.59^{b}

Table 3.3: Three-way multivariate analysis of variance to test the effects of species (*S*), light (*L*), flooding (*F*), and their interactions on morphological and physiological parameters.

Leaf traits	*F* and its significance						
	S	*L*	*F*	*S* × *L*	*S* × *F*	*L* × *F*	*S* × *L* × *F*
Growth							
Height (cm)	32.76**	354.08**	10.42**	3.83**	3.20**	28.23**	2.82**
Diameter (mm)	11.24**	835.34**	4.40*	3.91**	3.02**	41.04**	4.42**
Leaf counts	26.65**	217.97^{ns}	0.08**	17.33**	2.23*	1.49^{ns}	2.37*
Stem growth rate	24.12**	493.02**	1.99^{ns}	3.89**	3.16**	9.54**	4.94**
Biomass							
Leaf biomass (g)	4.27**	201.02**	15.56**	3.41**	2.43*	15.92**	2.70**
Stem biomass (g)	6.22**	279.61**	9.89**	4.83**	1.86^{ns}	17.69**	2.26*
Root biomass (g)	4.06**	279.72**	6.62*	2.86**	2.11*	10.25**	2.83**
Total biomass (g)	3.18**	329.49**	10.41**	1.92*	2.24*	15.49**	2.92**
Leaf mass fraction	5.58**	409.08**	0.37^{ns}	3.65**	2.56**	6.23*	2.60*
Stem mass fraction	14.47**	116.66**	0.10^{ns}	8.89**	1.79^{ns}	0.03^{ns}	2.61*
Root mass fraction	9.29**	335.86**	0.30^{ns}	5.86**	2.28*	2.69^{ns}	2.82**
RSR (g g^{-1})	7.70**	245.39**	0.58^{ns}	5.49**	2.14*	2.10^{ns}	2.77**
LAR (cm^{2} g^{-1})	1.82^{ns}	123.29**	16.96**	4.95**	3.22**	9.72**	3.28**
Leaf morphology							
Leaf length (cm)	12.09**	4.76*	15.01**	4.86**	3.62**	38.15**	3.17**
Leaf width (cm)	17.15**	121.60**	7.43**	6.11**	1.42^{ns}	15.81**	2.63*
Leaf area (cm^{2})	8.49**	112.00**	10.36**	6.07**	2.16*	23.45**	3.77**
SLA (m^{2} kg^{-1})	2.16*	38.85**	10.30**	4.06**	3.07**	3.82^{ns}	2.40*
LMA (g m^{-2})	0.92^{ns}	57.59**	5.19*	1.66^{ns}	1.39^{ns}	0.45^{ns}	0.98^{ns}
Gas exchange							
P_n (µ mol m^{-2} s^{-1})	2.81**	249.69**	59.95**	5.87**	1.82^{ns}	56.07**	1.98^{ns}
G_s (m mol m^{-2} s^{-1})	7.29**	10.18**	25.04**	5.25**	1.72^{ns}	58.27**	0.28^{ns}
C_i (µ mol mol^{-1})	9.38**	269.12**	0.72^{ns}	4.87**	7.29**	1.98^{ns}	1.80^{ns}
T_r (µ mol m^{-2} s^{-1})	12.12**	8.44**	14.91**	7.23**	3.24**	41.37**	1.13^{ns}
WUE	5.92**	197.46**	8.27**	4.94**	2.27*	4.72*	1.15^{ns}

F test: *, ** and ns indicate $P \leq 0.05$, $P \leq 0.01$ and $P > 0.05$, respectively. P_n means net photosynthetic rate, G_s means stomatal conductance, C_i means intercellular carbon dioxide, T_r means transpiration rate and WUE (µ mol CO_2/m mol H_2O) means water-use efficiency.

Table 3.4: Seedling survivorship across the different species combinations, competition types, flooding treatments, and light treatments at the end of the 134-day experiment (n = 16).

Flooding	Light	Competition	Competition	Survivorship (%)
Flooded	High irradiance	Interspecific	Tallow with green ash	62.5
			Tallow with sugarberry	87.5
			Tallow with green ash	87.5
			Green ash with tallow	100
			Sugarberry with tallow	0
			Water tupelo with tallow	100
		Intraspecific	Tallow only	81.3
			Green ash only	100
			Sugarberry only	0
			Water tupelo only	100
	Low irradiance	Interspecific	Tallow with green ash	100
			Tallow with sugarberry	87.5
			Tallow with green ash	100
			Green ash with tallow	87.5
			Sugarberry with tallow	100
			Water tupelo with tallow	100
		Intraspecific	Tallow only	100
			Green ash only	93.8
			Sugarberry only	100
			Water tupelo only	100
Non-flooded	High irradiance	Interspecific	Tallow with green ash	100
			Tallow with sugarberry	100
			Tallow with green ash	100
			Green ash with tallow	100
			Sugarberry with tallow	100
			Water tupelo with tallow	100
		Intraspecific	Tallow only	100
			Green ash only	100
			Sugarberry only	75
			Water tupelo only	100
	Low irradiance	Interspecific	Tallow with green ash	100
			Tallow with sugarberry	100
			Tallow with green ash	100
			Green ash with tallow	100
			Sugarberry with tallow	100
			Water tupelo with tallow	100
		Intraspecific	Tallow only	87.5
			Green ash only	100
			Sugarberry only	100
			Water tupelo only	100

Table 3.5: Abbreviations used in this chapter and their full meaning.

Abbreviation	Full meaning of abbreviation
PPFD	Photosynthetic photon flux density
F	Flooded
N	Non-flooded
H	High irradiance
L	Low irradiance
FH	Flooded and high irradiance
FL	Flooded and low irradiance
NH	Non-flooded and high irradiance
NL	Non-flooded and low irradiance
SBSB	Sugarberry growing under intraspecific competition with sugarberry
GAGA	Green ash growing under intraspecific competition with green ash
WTWT	Water tupelo growing under intraspecific competition with water tupelo
CTCT	Chinese tallow growing under intraspecific competition with Chinese tallow
SBCT	Sugarberry growing with Chinese tallow under interspecific competition
CTSB	Chinese tallow growing under interspecific competition with sugarberry
GACT	Green ash growing under interspecific competition with Chinese tallow
CTGA	Chinese tallow growing under interspecific competition with green ash
WTCT	Water tupelo growing under interspecific competition with Chinese tallow
CTWT	Chinese tallow growing under interspecific competition with water tupelo
RSR	Root shoot ratio
SLA	Specific leaf area
LMF	Leaf mass fraction
SMF	Stem mass fraction
RMF	Root mass fraction
P_n	Net photosynthetic rate
G_s	Stomatal conductance
C_i	Intercellular carbon dioxide
T_r	Transpiration rate
WUE	Water-use efficiency

FIGURES

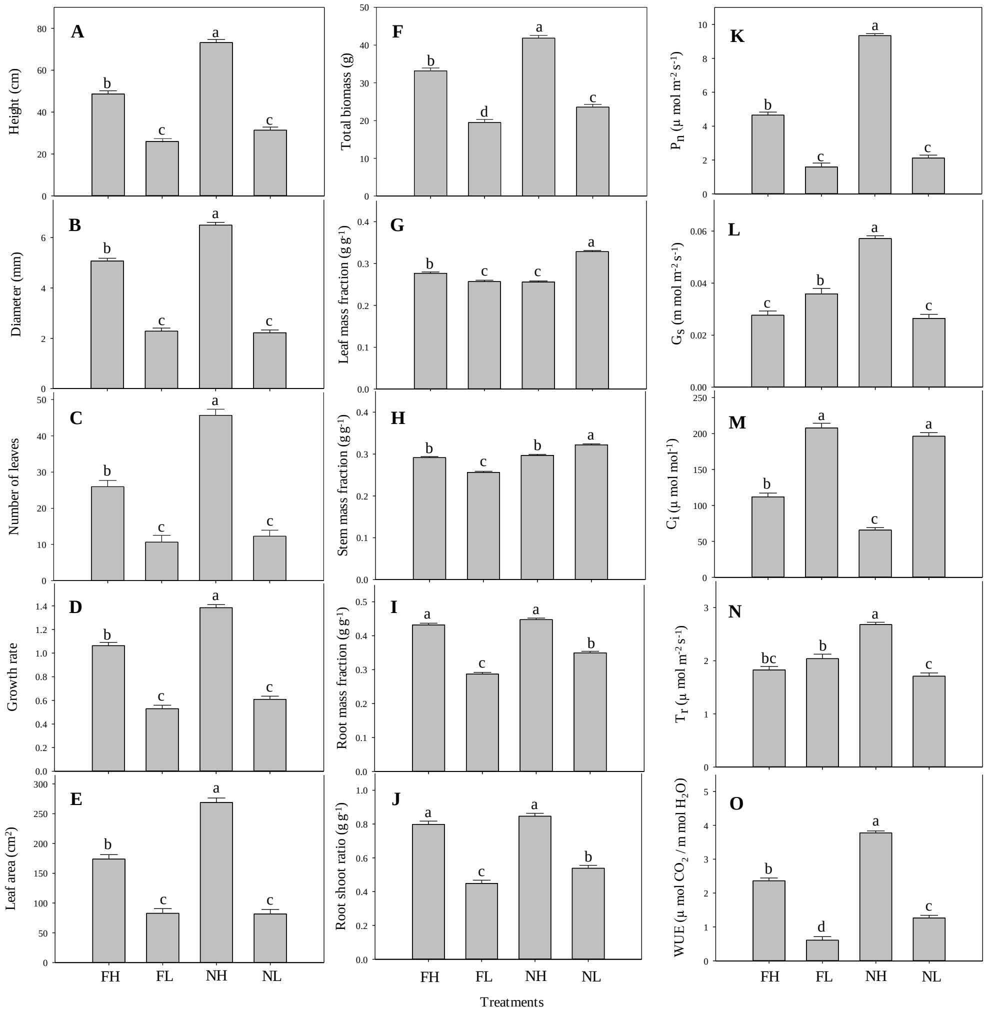

Figure 3.1: Comparisons of the seedling's traits among the different flooding and light treatments at the end of the experiment. The traits include (**A**) height, (**B**) ground diameter, (**C**) number of leaves, (**D**) growth rate, (**E**) leaf area, (**F**) total biomass, (**G**) leaf mass fraction, (**H**) stem mass fraction, (**I**) root mass fraction, (**J**) root shoot ratio, (**K**) net photosynthetic rate (P_n), (**L**) stomatal conductance (G_s), (**M**) intercellular carbon dioxide (C_i), (**M**) transpiration rate (T_r), and (**O**) water use efficiency (*WUE*). The data are shown as the mean ± SE, and different letters above columns indicate significant differences ($P < 0.05$) between flooding and light treatments according to the Tukey's test. FH means flooded and high irradiance treatment, FL means flooded and low irradiance treatment, NH means non-flooded and high irradiance treatment, and NL means non-flooded and low irradiance treatment.

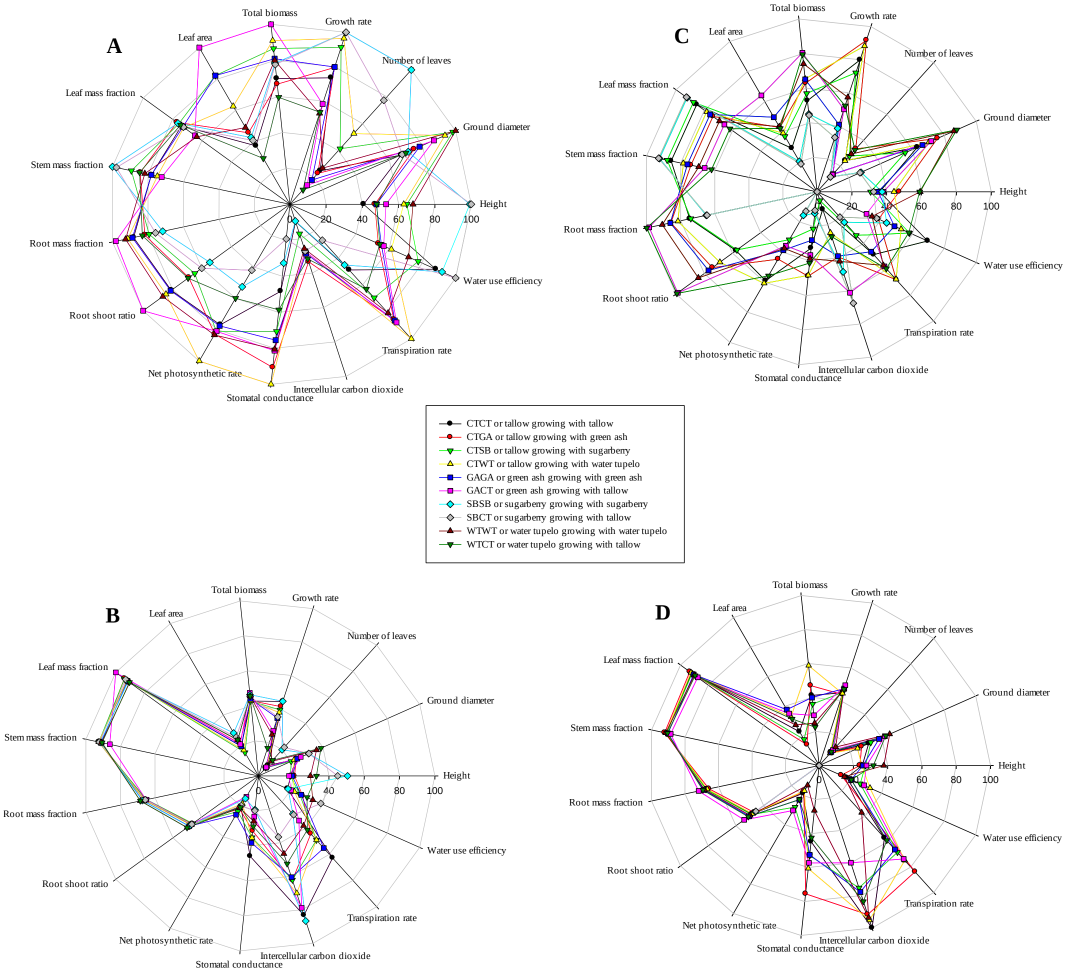

Figure 3.2: Radar plots showing the morphological, biomass, and gas exchange traits of seedlings under the different light and flooding treatments [(**A**) NH – non-flooded and high irradiance, (**B**) NL – non-flooded and low irradiance, (**C**) FH - flooded and high irradiance, and (**D**) FL – flooded and low irradiance]. Variables were scaled to a percent scale by setting the maximum value for each variable equal to 100%.

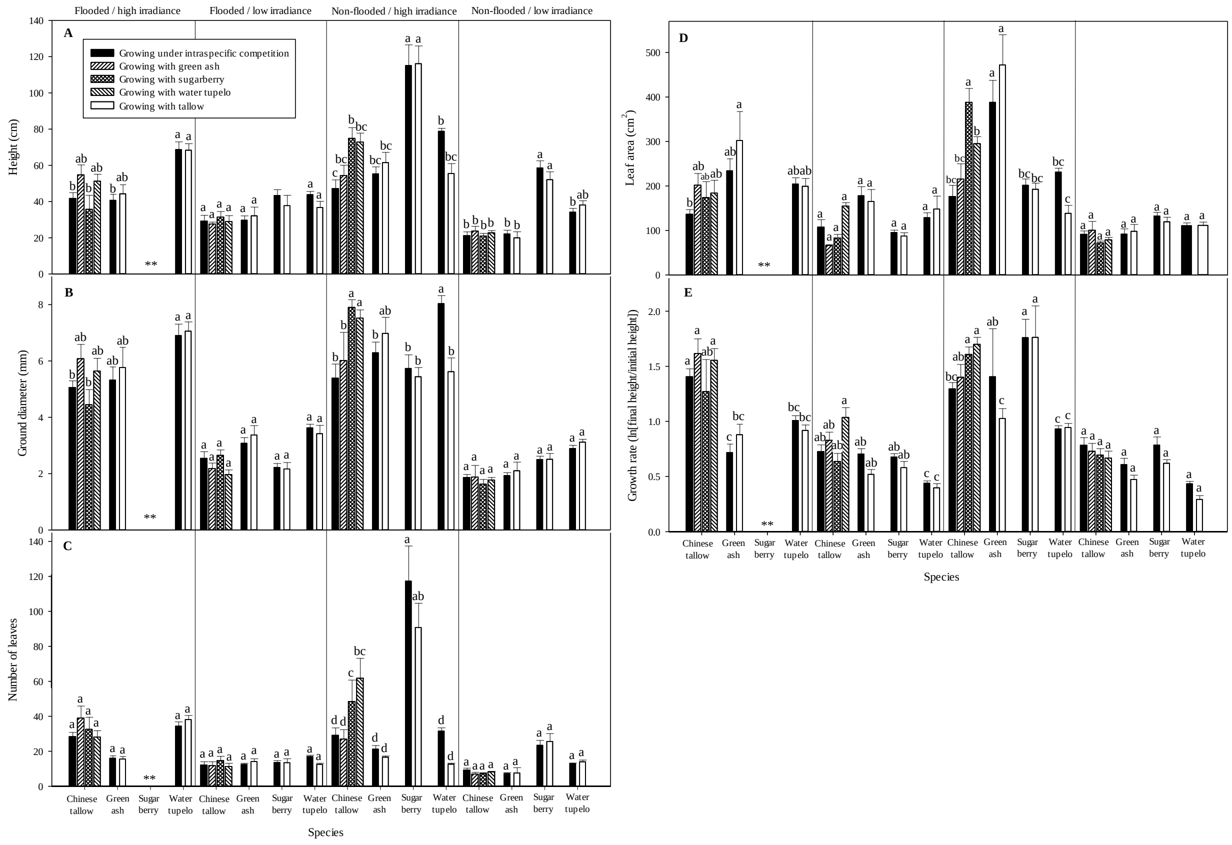

Figure 3.3: Comparisons of morphological traits [(**A**) height, (**B**) ground diameter, (**C**) number of leaves, (**D**) leaf area, and (**E**) growth rate] of species under different light and flooding treatments at the end of the experiment (mean ± SE). Different letters above columns indicate significant differences ($P < 0.05$) according to Tukey's test for multiple comparison. Lowercase letters represents post-hoc contrasts among species within each light and flooding treatment. ** represents 100% mortality.

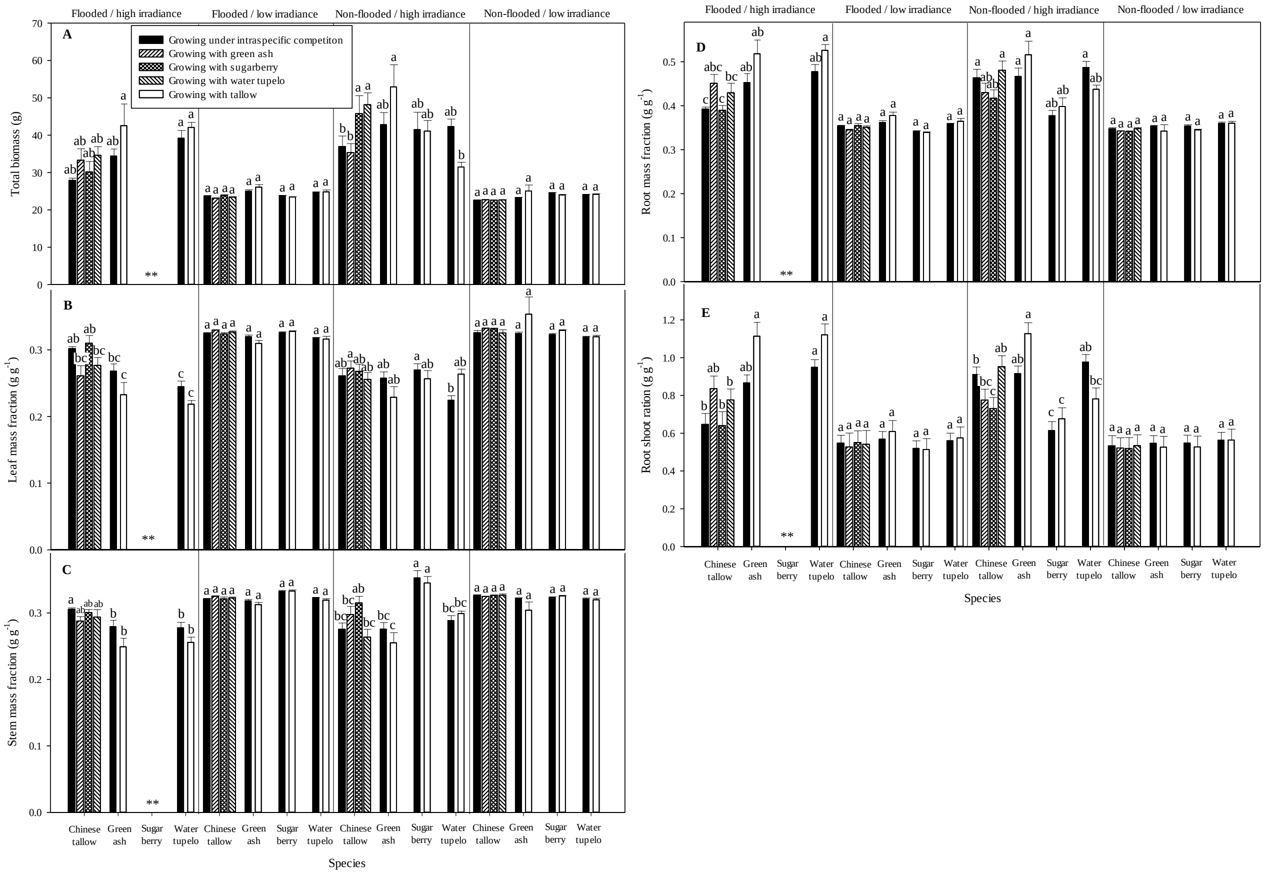

Figure 3.4: Comparisons of biomass traits [(**A**) total biomass, (**B**) leaf mass fraction, (**C**) stem mass fraction, (**D**) root mass fraction, and (**E**) root shoot ratio] of species under different light and flooding treatments at the end of the experiment (mean ± SE). Different letters above columns indicate significant differences ($P < 0.05$) according to Tukey's test for multiple comparison. Lowercase letters represents post-hoc contrasts among species within each light and flooding

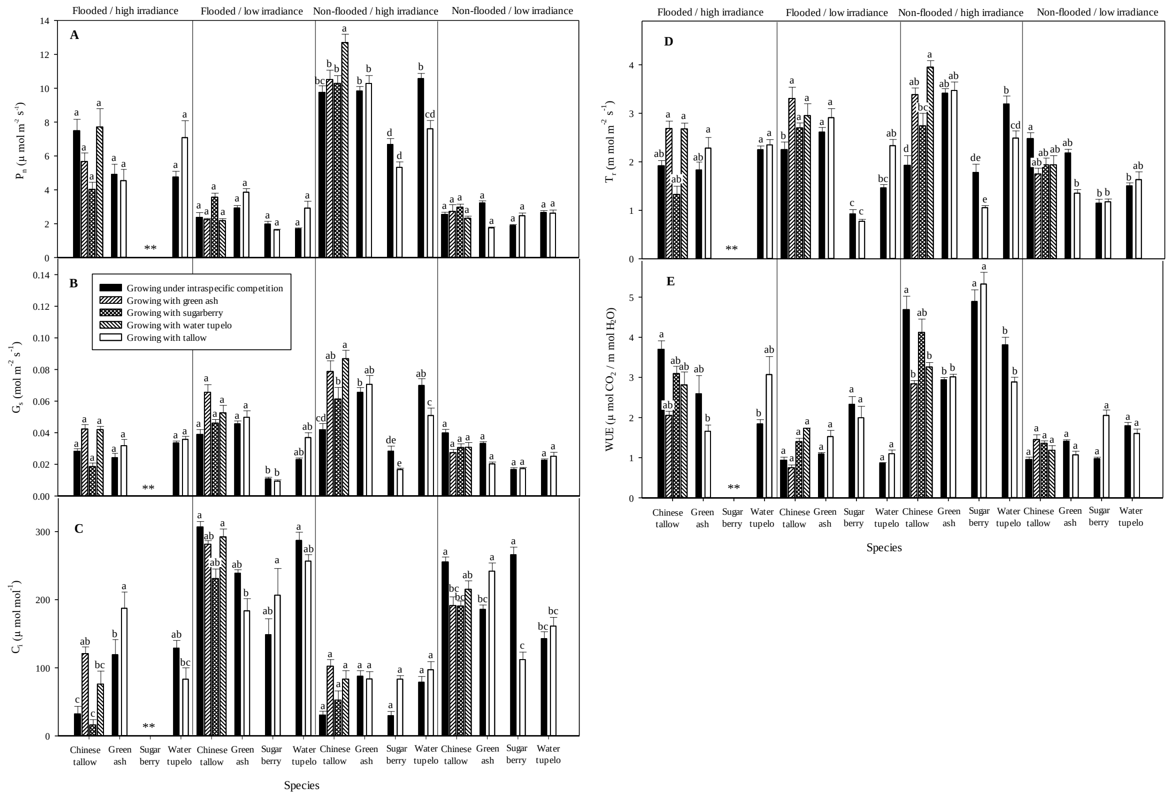

Figure 3.5: Comparisons of gas exchange traits [(**A**) net photosynthetic rate (P_n), (**B**) stomatal conductance (G_s), (**C**) intercellular carbon dioxide (C_i), (**D**) transpiration rate (T_r), and (**E**) water use efficiency (*WUE*) of species under different light and flooding treatments at the end of the experiment (mean ± SE). Different letters above columns indicate significant differences ($P < 0.05$) according to Tukey's test for multiple comparison. Lowercase letters represents post-hoc contrasts among species within each light and flooding treatment. ** represents 100% mortality.

CHAPTER 4

EVALUATING THE GROWTH AND COMPETITIVE ABILITY OF CHINESE TALLOW (TRIADICA SEBIFERA) AND COEXISTING NATIVE SPECIES

ABSTRACT

Two greenhouse experiments were designed to determine the interactive effect of light, flooding, and community types on the growth, dominance, and competitive ability of Chinese tallow (*Triadica sebifera* [L.] Roxb.) and four tree species native to the southeastern United States: water tupelo (*Nyssa aquatica* L.), sugarberry (*Celtis laevigata* Willd.), baldcypress (*Taxodium distichum* [L.] Rich), and green ash (*Fraxinus pennsylvanica* Marshall). The first experiment used a factorial design that received three treatments: community type (native, invasive, and mixed), light (low irradiance and high irradiance), and flood (non-flooded and flooded) regimes. Communities of only native species responded positively in flooded/high irradiance and non-flooded and high irradiance treatments with high total biomass and growth rates, respectively. The mixed community depressed the growth rate of tallow in the flooded and low irradiance treatment, however, leaf area and leaf biomass of tallow increased in the mixed community in the non-flooded/high irradiance treatment. This study demonstrated that establishing a native community may be a feasible and sustainable option to suppress the growth of tallow. The second experiment used a factorial design that received one competition treatment (interspecific and no competition) regime. The results of the second experiment showed that, with the exception of water tupelo, tallow had no significant impact on the biomass of the native species studied.

INTRODUCTION

Invasive species are a serious threat to ecosystem function worldwide, and understanding the mechanisms which give invasive species an advantage over native species is crucial to their management. The success of invasive species is often habitat-dependent because no one species can maximize its ability to grow, reproduce, and compete across all environments (Funk and Vitousek 2007). One hypothesis that accounts for the differences among environments is the fluctuating resource hypothesis, which proposes that invasion is facilitated by an increase in resource availability (Davis et al. 2000). This hypothesis assumes that any factor(s) that increase the availability of limiting resources (e.g., light, nutrients, and water) and displaces native plant communities will increase the susceptibility of a community to invasion (Davis et al. 2000; Funk and Vitousek 2007).

To succeed in communities, invasive species develop strategies that increase resource availability (for example, positive feedback through rapid leaf decomposition cycles; Conway et al. 2002; Siemann and Rogers 2003), promote continued disturbance that increases resource availability (altering fuel loads and fire regimes; Bruce et al. 1995; Grace 1998), enhance resource acquisition, or efficiently use resources (Funk and Vitousek 2007). Compared to their existing native counterparts, invasive species differ quantitatively in functional traits (Funk and Vitousek 2007). Invasive species are usually early successional or faster-growing species that tend to be taller, wider, and have larger leaves (Williamson and Fitter 1996). These characteristics are viewed as the biological predictors of successful invaders (Williamson and Fitter 1996).

Establishing native plant communities following the removal of invasive species is a critical component of ecological restoration (Funk and Vitousek 2007). The best practice for establishing a community would be to design a native community that maximizes the trait similarity between native and invasive species (Funk and Vitousek 2007; Funk et al. 2008). Some studies have proposed multi-trait similarity using early emerging, fast-growing native species that quickly develop highly productive communities to restructure the community invaded by invasive species (Yannelli et al. 2020). The recruitment of the invasive weed *Ipomoea cairica* (L.) Sweet (Convolvulaceae) was prevented when two valuable native species, kudzu vine (*Pueraria lobata* (Willd.) Ohwi.) and Chinese feverine (*Paederia scandens* (Lour.) Merril.), were used to restructure the community (Li et al. 2015). However, the efficacy of planting native hardwood species to control non-native invasive trees is not clear.

Chinese tallow (*Triadica sebifera* [L.] Roxb.), hereafter tallow, is the most aggressive non-native tree species in the southeastern United States due to an unusual combination of fast growth and tolerance to multiple environmental stressors (Butterfield et al. 2004; Gan et al. 2009). First-year seedlings exhibit characteristics of both shade-intolerant and tolerant species with a high tolerance of flooding and low redox potentials (Jones and McLeod 1989; Jones and Sharitz 1990). In deep shade and full sunlight, tallow demonstrates its ability to rapidly grow as it readily outperforms native. In shade and full sunlight, tallow was observed to grow larger with higher net photosynthetic rates than American sycamore (*Platanus occidentalis* L.) and cherrybark oak (*Quercus pagoda* Raf.; Jones and McLeod 1989). Compared to these native species, tallow supported more perennial tissue per unit of leaf dry mass (Jones and McLeod 1989). Under different light conditions, tallow outperformed Carolina ash (*Fraxinus caroliniana* Mill.), with larger dry mass, leaf area, and stem height recorded for the invasive. High net photosynthesis, dry mass partitioning, leaf area ratio, and rapid growth contribute to the success of tallow as an invader. Although its seed fails to germinate in flooded soils, tallow is often found on periodically flooded soils (Gabler and Siemann 2013; Pile et al. 2017). Newly germinated seedlings achieve flood tolerance within a few months and their flood tolerance is comparable to water tupelo (*Nyssa aquatica* L.) which can be identified as a wetland specialist (Jones and Sharitz 1990). Ecological traits which contribute to its success in flooded soils include high shade and flood tolerance, resistance to herbivory, and moderate tolerance to root competition (Jones and Sharitz 1990). Morphological traits which contribute to its success include hypertrophied lenticels, production of thicker feeder roots, and development of adventitious roots (Jones and Sharitz 1990; Pile et al. 2017).

In the field, water tupelo, sugarberry (*Celtis laevigata* Willd.), baldcypress (*Taxodium distichum* (L.) Rich), and green ash (*Fraxinus pennsylvanica* Marshall) frequently coexist with tallow and may have similar functional traits. These native species are adapted to the light and flooding regimes where tallow often persists. Water tupelo is a large, long-lived native tree that grows in swamps and floodplains where its root system is periodically underwater (Hook and Brown 1973; Johnson 1990). Sugarberry is a medium-sized, short-lived native tree that is adapted to a wide range of soil and moisture conditions (Krajicek and Williams 1990). Green ash seedlings have rooting adaptations that enable them to withstand flooding regimes that would kill other species (Kennedy 1990). Baldcypress is a slow-growing, very long-lived deciduous conifer that grows on sites characterized by frequent and prolonged flooding (Wilhite and Toliver 1990).

Aside from these characteristics, these four native species have traits that suggest they can occupy available niches in a community and make limiting resources (e.g., light, nutrients, and water) unavailable for tallow. Water tupelo typically grows in low sloughs and deep swamps along coastal rivers where its shallow root system is periodically submerged in water. Seedlings survive flooded conditions across the growing season, provided their tops are above water. Unshaded environments with saturated soil in moving, aerated and shallow water provide near optimum conditions for growth and development in water tupelo (Johnson 1990). Sugarberry, a fast-growing tree, is widely distributed in broad flats and sloughs of floodplain forests but absent in the deep swamps. Like tallow, sugarberry has the potential to grow in wetter sites, and become established in the understory. Both are insect-pollinated and bird-dispersed. Green ash is the most widely distributed and adaptable member of the *Fraxinus* genus in the United States, showing significant variation in growth rate and morphology (Abrams et al. 1989). Green ash can tolerate seasonal inundation for only 40% of its season. Compared to other bottomland hardwood species, green ash can survive intense weed competition and overcrowding. Baldcypress is the most flood-tolerant of the selected species, but it can also endure partial shading. This deciduous conifer grows across a wide climatic range and is one of the few conifers that resprouts. Drainage is important in determining site suitability for baldcypress, as this deciduous conifer grows on sites characterized by intermittent, frequent, or prolonged flooding (Wilhite and Toliver 1990).

Water tupelo, sugarberry, baldcypress, and green ash were selected to grow in competition with tallow in two greenhouse experiments. These experiments were designed to examine the growth and dominance of tallow (in terms of plant biomass) in competition with functionally similar native species as well as the growth and dominance of native species (in terms of plant biomass) in competition with tallow. The objective of this study was to determine the growth, dominance, and competitive ability of tallow in competition with four native hardwood species under a range of flooding and light-availability conditions.

In the first experiment, tallow was grown in intraspecific and interspecific competition with four native hardwood species. Native species were grown in competition with other native species as well as with tallow. The hypotheses for the first experiment were:

i. Seedlings will have increased growth metrics in high irradiance treatments
ii. Communities consisting solely of tallow will outperform communities consisting solely of native species and communities where tallow is grown with native species
iii. Interspecific competition will reduce tallow's growth and dominance more than intraspecific competition across the different light and flooding treatment combinations.

The second greenhouse experiment used the relative interaction index (RII; Armas et al. 2004) to assess the competitive ability of tallow and the selected native species by considering competitive interactions of native taxa growing with tallow (effect of natives as competitors) and competitive interactions of tallow growing with native taxa (effect of competition on natives). RII is expressed as:

$$RII = \frac{B_w - B_o}{B_w + B_o} \tag{1}$$

where B_w is the observed mass of the target plant when growing with another plant and B_o is the mean mass achieved by the target plant growing in the absence of inter- or intra-specific competition (Armas et al. 2004). This index has several advantages compared to other competition indices such as the relative competition intensity or the relative neighbor effect. The RII has values ranging from –1 to +1 and it is symmetrical around zero. A negative value indicates competition (i.e., the target plant is outcompeted by another plant), and a positive value indicates facilitation (i.e., the growth of the target plant is facilitated by another plant). The hypothesis is that if tallow has a higher competitive ability than the four native species, the following results should be:

i. In terms of tallow’s impact, the RII value from native species interaction with tallow would be more negative than the RII value from native species interaction with other natives. This would imply that the negative effect of tallow is greater for one native on another.

ii. With regard to native’s resistance, the RII value from tallow’s interaction with native species would be less negative than the RII value from native species interaction with other natives. This would indicate that the negative effect of one native species on another is larger than their effect on tallow.

METHODS

Community-based experiment

Seed germination and study site

This study was carried out in a greenhouse at Stephen F. Austin State University in Nacogdoches, Texas (lat. 31º37′N, long. 94º38′W). In December 2019, seeds of tallow were hand collected from three different trees (lat. 29º55′N, long. 95º14′W) on the Greens Bayou Wetland Mitigation Bank, in Houston, Texas, USA. Trees were randomly selected within the forest overstory and within 3 m of each other. In January 2020, seeds of native species were procured from Louisiana Forest Seed Company, LeCompte, Louisiana, USA. Seeds were stored at 3 – 5 ℃ and subsequently stratified early February 2020. Water tupelo seeds were soaked in tap water at 3°C for 63 hours to ensure a high initial moisture content before drying on paper towels at 22°C for 24 hours (Bonner and Kennedy 1973). The pericarp of green ash seeds was removed, and the seeds were stratified for 88 days at 4 °C in plastic bags (Marshall 1981). Baldcypress seeds were soaked in water at 4 °C for 90 days (Bonner et al. 2008). Tallow seeds were soaked in water for 34 days at 2 °C (Bonner et al. 2008). Following stratification, seeds were sown (20 – 25 mm deep) on 3 – 5 March 2020, into containers measuring 10.5 × 15 × 11 cm filled with Miracle-Gro® Potting Mix (ScottsMiracle-Gro, Marysville, OH). Seeds were germinated in a growth chamber (day: 30 ℃, 8 hr., 59% humidity; night: 20 ℃, 16 hr. light, 63% humidity; humidity was ambient and was not controlled).

Experimental design

In April 2020, three weeks after sowing, bare-root seedlings were transplanted and randomly placed into containers (30.5 × 30.5 × 29.2 cm) filled with Miracle-Gro® Garden soil. The soil was not sterilized before use and no fertilizers were added for the duration of this experiment (April 2020 to July 2021: 463 days). Each container represented a plant community mesocosm with tallow and the native species planted either separately or together. The average daily temperature during the experimental period (April 2020 to July 2021) in the greenhouse was 22.5 ℃ and an evaporative cooler was used to maintain greenhouse temperatures. There were three different community types (native, invasive, or mixed) each with 10 seedlings in each container:

i. The native community consisted of two water tupelo seedlings, two green ash seedlings, two baldcypress seedlings, two sugarberry seedlings, and two randomly selected native seedlings from one of those four species.
ii. The invasive community consisted of 10 tallow seedlings.
iii. The mixed community consisted of two water tupelo, two green ash, two baldcypress, two sugarberry, and two tallow seedlings.

Seedlings were randomly selected and placed with even spacing. Seedlings were given one week to acclimate to the greenhouse before treatments commenced on April 17, 2020. The study design involved the following randomly assigned treatments and levels per treatment:

i. Light treatments: (1) high irradiance: containers were not shaded with a black polypropylene shade cloth, and the irradiance was not reduced, indicating a lack of forest overstory, indicated by *H*, and (2) low irradiance: containers were placed under a black polypropylene shade cloth that reduced irradiance simulating a shaded forest understory, indicated by *L*. Shade cloth was mounted on a frame measuring 303 × 123 × 110 cm.

ii. Flooding treatments: (1) non-flooded: containers were watered daily until water flowed out of the bottom of the pots representing a well-drained floodplain site, indicated by *N*, and (2) flooded: containers were permanently submerged in a plastic tub (27.9 × 42.2 × 60.3 cm) filled with water (1-3 cm above soil surface), representing a frequently flooded floodplain site, indicated by *F* (Butterfield et al. 2004).

iii. Community treatments: (1) native community: consisted of ten seedlings of the selected native species, (2) invasive community: consisted of ten seedlings of tallow, and (3) mixed community: consisted of a mixture of two tallow seedlings and eight seedlings of the selected of native species.

Containers were placed in a full factorial design (n = 48, 3 communities × 2 flooding × 2 light × 4 replicates), with four light and flooding treatments: flooded and high irradiance (*FH*), flooded and low irradiance (*FL*), non-flooded and high irradiance (*NH*), and non-flooded and low irradiance (*NL*). Twelve containers were included in each light and flooding treatment. Containers were randomly placed, but evenly in one section of the greenhouse to prevent overlap and container–container shading.

Growth measurements

Initial stem height, basal diameters, and leaf count were recorded for each plant at treatment initiation to account for ontogenetic effects (Table 4.1). At the end of the experiment, the final seedling height, ground line diameters, and leaf counts were measured. Ground line diameter was measured with a digital caliper. Leaf length, width, and area were measured using a portable leaf area meter on 5 fresh leaves sampled from each seedling before harvest (LI-3000A, Li-COR Biosciences, Lincoln, Nebraska, USA) in October 2020. In October 2020, the leaves of all seedlings were harvested and dried at 60 ℃ for 96 hours to constant mass to calculate leaf biomass. In July 2021, all seedlings were harvested and dried at 60 ℃ for 96 hours to constant mass to calculate total biomass. Based on seedling biomass and leaf area measurement, the root: shoot ratio (RSR, ratio of root dry mass to leaf and stem dry mass, g g^{-1}) and specific leaf area (SLA; leaf area per unit leaf mass, cm^2 g^{-1}) were calculated.

Statistical analysis

All analyses were performed using SAS 9.4 (SAS Institute, Cary, North Carolina, USA). The effects of species, light, flooding, and community types on the response variables were analyzed using a four-way Analysis of Variance (ANOVA) followed by a pairwise comparison with the Tukey's test (using PROC GLM). The model assumptions of normality and homoscedasticity were verified using residual plots. Data did not need to be transformed to meet the assumptions of normality and homoscedasticity. The significance level was set at 5% *a priori* for all statistical tests and any P value ≤ 0.05 was considered as evidence of significant difference.

Relative Interaction Index experiment

Seed germination and study site

The second experiment followed the same seed collection, stratification, and germination protocols as the first experiment. In May 2020, five weeks after sowing, seedlings were transplanted into containers (21 cm × 17 cm × 22 cm) filled with Miracle-Gro® Garden soil and placed in the same greenhouse as the first experiment.

Experimental design

This experiment consisted of different competition treatments which included all possible pair-wise combinations of interspecific competition and were replicated three times, as listed in table 4.2. It also included a non-competition treatment that consisted of a single seedling growing alone in a container. The interspecific competition treatments consisted of two seedlings of two different species growing in the same container. Containers were watered daily until water flowed out of the bottom.

Growth measurements

At the end of the experiment, the final seedling height, ground line diameters, and leaf counts were measured. Ground line diameter was measured with a digital caliper. Leaves were collected in October 2020, before they abscised and dried at 60℃ for 96 hours to constant mass to calculate leaf biomass. In November 2020, all seedlings were harvested and dried at 60℃ for 96 hours to constant mass to calculate root, stem, and leaf biomass, and total biomass was a sum of these three. Seedlings were grown for 196 days (May – November 2020).

Table 4.2: Different competition treatments in the relative interaction index experiment which includes all possible pair-wise combinations of interspecific and no competition. Each interspecific treatment consisted of two seedlings of two different species growing in a single container. Each non-competition treatment consisted of a single seedling growing in a container. Each competition treatment was replicated three times.

Species	Competition type	Competition treatment	Notation
Tallow	Interspecific	Tallow with green ash	*T(G)*
		Tallow with baldcypress	*T(B)*
		Tallow with sugarberry	*T(S)*
		Tallow with water tupelo	*T(W)*
	None	Tallow only	*T*
Green ash	Interspecific	Green ash with tallow	*G(T)*
		Green ash with baldcypress	*G(B)*
		Green ash with sugarberry	*G(S)*
		Green ash with water tupelo	*G(W)*
	None	Green ash only	*G*
Baldcypress	Interspecific	Baldcypress with tallow	*B(T)*
		Baldcypress with green ash	*B(G)*
		Baldcypress with sugarberry	*B(S)*
		Baldcypress with water tupelo	*B(W)*
	None	Baldcypress only	*B*
Sugarberry	Interspecific	Sugarberry with tallow	*S(T)*
		Sugarberry with green ash	*S(G)*
		Sugarberry with baldcypress	*S(B)*
		Sugarberry with water tupelo	*S(W)*
	None	Sugarberry only	*S*
Water tupelo	Interspecific	Water tupelo with tallow	*W(T)*
		Water tupelo with green ash	*W(G)*
		Water tupelo with baldcypress	*W(B)*
		Water tupelo with sugarberry	*W(S)*
	None	Water tupelo only	*W*

Statistical analysis

All analyses were performed using the SAS 9.4 (SAS Institute, Cary, North Carolina, USA). The effects of competition treatments on the morphological and biomass traits of seedlings were analyzed using an Analysis of Variance (ANOVA) followed by a pairwise comparison with the Tukey's test (using PROC GLM). To determine whether there was a significant difference between the RII values and zero, a one-sample t-test was used. The model assumptions were verified using residual plots. Where appropriate, data were transformed to meet the assumptions of normality and constant variance. The significance level was set at 5% *a priori* for all statistical tests and any P value ≤ 0.05 was considered as evidence of significant difference.

RESULTS

Community-based experiment

Effects of species, light, flooding, and community

Many indicators showed significant four-way interactions of species, light, flooding, and community effects (Table 4.3), except for growth rate, leaf area ratio, leaf length, leaf width, and specific leaf area which were not significantly affected by the interactions but all had significant community by light by flooding interactions.

Changes in plant growth across community types

While the interactions introduce great complexity in interpreting data, seedlings were generally taller in the high irradiance treatments and shorter in the low irradiance treatments (Figure 4.1A). However, in NL, seedlings in the invasive community were significantly taller than seedlings in the mixed and native communities. In FH, FL, and NH, there was no difference in seedling height among the three communities. The ground diameter was generally largest in FH, intermediate in NH, and smallest in the low irradiance treatments (Figure 4.1B). Seedlings in low irradiance treatments tended to have the smallest leaf count, leaf area, leaf biomass, total biomass, growth rate, and leaf area ratio (Figures 4.1C – 4.1H). Ground diameter, number of leaves, leaf area, and leaf biomass did not differ significantly among the community types and treatments (Figures 4.1B – 4.1E). In FH, seedlings in the native community produced the largest total biomass (Figure 4.1F). In FL, the seedlings in the invasive community had slower growth rates than their counterparts in the mixed community while in NH, seedlings in the native community had the fastest growth rate (Figure 4.1G).

Baldcypress and water tupelo were the tallest seedlings in FH, growing taller than other species in the native and mixed communities (Figure 4.2A). Water tupelo seedlings had the tallest stems among the native species growing in FL, only comparable to tallow in the mixed community (Figure 4.3A). In NH, sugarberry seedlings were the shortest seedlings in the native community (Figure 4.3A). NL represents the only treatment combination where tallow overtopped baldcypress, green ash, and sugarberry (Figure 4.3A). In FH, sugarberry seedlings had the smallest ground diameter in the native community while water tupelo had the largest ground diameter in both communities (Figure 4.3B). Similarly, water tupelo seedlings had the largest ground diameter in FL, only comparable to tallow in the invasive community (Figure 4.3B). In NH, sugarberry seedlings had the smallest ground diameter in the native and mixed communities (Figure 4.3B). In FH, baldcypress produced the highest number of leaves among the species while sugarberry and green ash had the lowest leaf count in the native community (Figure 4.3C). Among the native species in NH, baldcypress produced the highest number of leaves in the native and mixed communities, while sugarberry had the lowest number of leaves in the native community (Figure 4.3C). Despite producing more leaves than tallow and green ash in FH, the leaf area of tallow (in the mixed community) and green ash (in the native community) were greater than that of baldcypress (Figure 4.3C). In the low irradiance treatment, there was no difference in the leaf area (Figure 4.3D). Among the native species in NH, green ash had the largest leaf area only comparable to tallow (Figure 4.3D). In NH, community type impacted the leaf area of tallow as the leaf area of the invasive was smaller in the invasive community but higher in the invasive community (Figure 4.3D).

Among the seedlings growing in the native community, baldcypress and water tupelo produced the highest leaf biomass while sugarberry and green ash produced the least leaf biomass in FH (Figure 4.4A). There was no significant difference in leaf biomass in the low irradiance treatments (Figure 4.4A). In NH, tallow produced greater leaf biomass in the mixed community compared with the invasive community (Figure 4.4A). In FH, baldcypress and water tupelo seedlings produced the largest total biomass while green ash and sugarberry produced the least total biomass in the mixed community (Figure 4.4B). There was no significant difference in seedling total biomass in FL, NH, and NL (Figure 4.4B). In FH, sugarberry had the slowest growth rates among the seedlings in the mixed community (Figure 4.4C). Among the seedlings growing in FL, green ash was the only native species in the mixed community with a higher growth rate than tallow (Figure 4.4C). In FL, the growth rate of tallow was lower in the invasive community but higher in the native community (Figure 4.4C). Baldcypress and sugarberry had the lowest leaf area ratio among the seedlings growing in FH (Figure 4.4D). In FL, water tupelo had the largest leaf area ratio among the seedlings growing in the native community (Figure 4.4D). The leaf area ratio of tallow exceeded that of baldcypress in the high irradiance treatments with no significant differences between the two species in the low irradiance treatments (Figure 4.4D).

Relative Interaction Index Experiment

Changes in seedling growth

When baldcypress, tallow, green ash, sugarberry, and water tupelo were grown alone, there was no significant difference in height compared to when grown under competition (Figure 4.5A). Among the five species, water tupelo was the only seedlings with significant differences in ground diameter (Figure 4.5B). There was no significant difference in the number of leaves among the different species when grown alone and in competition (Figure 4.5C). Green ash was the only species with significant differences in leaf biomass, with greater leaf biomass when grown alone and in competition with water tupelo (Figure 4.5D). The stem and root biomass of water tupelo was impacted by competition as the lowest values were recorded when water tupelo was grown in competition (Figure 4.5E). Similarly, the total biomass of water tupelo was higher when growing alone but lower in competition (Figure 4.5F). The total biomass of green ash was greater when grown with water tupelo but lower when grown with baldcypress (Figure 4.5F).

Relative Interaction Index results

The relative interactive index (RII) describes the interaction between plants which consists of competition and facilitation. The index is symmetrical around zero and has values ranging from –1 to +1, a positive RII indicates a facilitative effect between species and a negative RII indicates competition between species. Although all species interactions had non-zero RII values, only a few were significantly different from zero (Figure 4.6). When water tupelo was grown with baldcypress, green ash, sugarberry, and tallow, the RII value was significantly negative (Figure 4.6). Similarly, when grown with baldcypress and sugarberry, the RII values for green ash and baldcypress (respectively) were significantly different from zero and negative

(Figure 4.6). The RII values of tallow did not differ significantly from zero (Figure 4.6A). This suggests that native competition had no impact on the biomass production of tallow. Similarly, the RII of native species showed no significant difference, indicating that, except for water tupelo, the invader had no impact on biomass production in the native species (Figure 4.6B).

DISCUSSION

Community-Based experiment

This experiment tested the hypothesis that seedlings will have increased growth metrics in high irradiance treatments. With regards to irradiance, this was the case. In the high irradiance treatments, seedlings had faster growth rates, producing taller stems with larger ground diameter, total biomass, and more leaves with a larger area. With regards to flooding and irradiance, seedlings had the highest LAR in FH, which is a determinant of relative growth rate (the increase in plant mass per unit of mass present and per unit of time) in trees and herbaceous species (Feng et al. 2007). This suggests that the seedlings are able to capture and utilize light for growth and fitness in FH. The results are consistent with the silvics of the native species, flood tolerance ranges from intermediate in sugarberry to very tolerant in baldcypress and green ash while shade tolerance ranges from intolerant in baldcypress and water tupelo to very tolerant in sugarberry (Meadows and Stanturf 1997).

The findings did not support the hypothesis that communities made up entirely of tallow would outperform communities made up entirely of native species or communities of tallow and native species mixed. With regards to community types, irradiance, and flooding, the invasive community differed from the native communities with lower growth rates in NH, lower biomass in FH, and taller seedlings in NL. The taller seedlings observed in NL were consistent with the literature on invasive species which classifies most invasive species as shade-tolerant and able to invade successionally advanced communities (Rejmánek and Richardson 1996; Rejmánek et al. 2005; Martin et al. 2008). Tallow is capable of moderate growth in deep shade, it can also outperform native species in high light environments, and does not conform to the traditional classifications of shade-tolerant vs. shade-intolerant (Pile et al. 2017). The fact that the native community produced the most biomass in FH (as opposed to the mixed and invasive communities), suggests that the selected species are better adapted to the flooded and high irradiance environment than tallow. Tallow is classified as flood-tolerant and can achieve considerable flood tolerance within two months (Gabler and Siemann 2013). Compared to more flood-tolerant species, tallow exhibits a greater reduction in the root, shoot, and total biomass in flooded conditions (Conner 1994; Butterfield et al. 2004). Reduction in root biomass has been attributed to root die-off (Conner 1994).

The results are consistent with the high flood tolerance of baldcypress and water tupelo as both species had the highest growth metrics in FH. In the native community, baldcypress and water tupelo seedlings were the tallest with the largest ground diameter, number of leaves, leaf biomass, and total biomass. When compared to tallow in the mixed community, both species were taller, water tupelo had a larger ground diameter, and baldcypress produced more leaves. Baldcypress and water tupelo tend to thrive in the swamps of floodplain forests where surface water is present year-round (Johnson 1990; Wilhite and Toliver 1990; Conner et al. 1997). Most species will not grow in swamps as they are ill-equipped to handle the stresses characterized by the absence of oxygen in the flooded soils. Morphological adaptations, such as aerenchyma, hypertrophied lenticels, stem hypertrophy, pneumatophores, and adventitious roots that proliferate above the waterline where oxygen is less limiting, allow baldcypress and water tupelo to avoid anoxia (Johnson 1990; Wilhite and Toliver 1990).

The hypothesis that interspecific competition would reduce tallow's growth and dominance more than intraspecific competition was supported in FL but not in NH. When tallow was grown in a mixed community in FL, lower growth rates were observed. In this treatment, tallow was the only species with reduced growth rates across the different community types. Decreased light availability has a negative effect on the growth rate of tallow (Jones and Kenneth 1990; Battaglia et al. 2009; Zou et al. 2009). In addition to growth rate, tallows dry mass (Jones and McLeod 1989), height (Jones and McLeod 1990), basal diameter (Jones and Sharitz 1990), and root mass (Rogers and Siemann 2003) have all been observed to decrease with decreasing light availability. Flooding, also has a negative impact on tallow growth rate (Butterfield et al. 2004). The dominance of tallow could be reduced by establishing an appropriate native community in flooded and shaded environments.

Greater leaf area and higher allocation to leaves may contribute to the success of tallow in NH. Previous studies on tallow report that the roots of nearby plants invading the area containing tallow roots resulted in a significant decrease in tallow leaf area (Jones and Sharitz 1990). The increased leaf area in the present study suggests that in the mixed community, the light interception capacity of tallow is higher than in the invasive community. Irradiance is an important factor that influences the vegetative and reproductive growth in plants and the growth potential and fitness of plants are dependent on their ability to capture and use irradiance (Yu-Long et al. 2009). Competitively advantageous traits (including relative growth rate, lateral spread, greater leaf area, LAR, and leaf nutrient concentration) allow invasive species to acquire and/or make the best use of limiting resources over their native counterparts. Competitively advantageous traits have undoubtedly contributed to the dominance of many invasive species (Gioria and Osborne 2014).

Relative Interaction Experiment

In terms of native species as competitors, I expected that the negative effect of one native species on another would be higher than the effect on the invasive species (Domènech and Vilà 2008; Li et al. 2015). When tallow was the target plant growing in competition with the selected natives, the RII values were not significantly different from zero implying that the natives neither competed with nor facilitated the tallow's growth. This suggests that on an individual level and at an early stage of recruitment, none of the selected native species have the potential to displace or resist competition posed by tallow. Another study that compared the growth response of tallow in competition with native species discovered that when grown with green ash, tallow had lower growth metrics in the early recruitment stages (Ajala et al. 2022). The lower growth metrics observed were in comparison to tallow's growth in comparison to other native species (including water tupelo and sugarberry). My findings did not support these findings as tallow was not less competitive. Post-invasion differences in tallow have been observed in the southeastern United States, where seedlings from different regions are larger, grow faster, have higher biomass, and are more likely to produce seeds (Siemann and Rogers 2001; Butterfield et al. 2004). The differences between Ajala et al. (2022) and my study could be attributed to the seed source for tallow; while Ajala et al. (2022) collected seeds from the Pineywoods vegetational area, I collected tallow seeds from the Gulf prairies and marshes of Texas.

Considering the effect of competition on natives, I expected tallow to reduce the growth of target native species more than their coexisting native counterparts (Domènech and Vilà 2008; Li et al. 2015). Tallow had a non-significant negative impact on baldcypress, but sugarberry had a significant negative impact on baldcypress. This implies that, during the early stages of recruitment in the understory, sugarberry would suppress baldcypress growth more than tallow would. Tallow also had a non-significant negative impact on green ash, but baldcypress had a significant negative impact on green ash. This implies that the baldcypress would reduce the growth of green ash better than the invader would.

Conclusions

While controlled greenhouse experiments such as this may present useful information, they also have some inherent limitations. This study evaluated the effects of irradiance and flooding at low levels whereas regeneration in natural ecosystems occurs in a multidimensional space characterized by more complex scenarios (Ibáñez and Shupp 2001; Gómez 2004). In addition to irradiance and flooding, herbivory, root competition, disease, and occasional drought are factors that affect the success of regeneration (Lin et al. 2004). It is also important to note that trees are long-lived species and trait expression in seedlings may not reflect in mature individuals later in life. Nevertheless, these results are useful in explaining the success of tallow in competition with native species and the importance of establishing a viable native community when controlling the recruitment of tallow.

Among the invasive species in the southeastern United States, tallow has become the most pervasive tree species since its introduction to the United States (Yang et al. 2021). Tallow's presence in the southeastern coastal region is positively correlated with proximity to water bodies, where it converts coastal tallgrass prairies to woodland thickets and aggressively invades wetlands (Wang et al. 2011; Yang et al. 2021). Tallow is more likely to invade low and flat areas near water bodies and roads (Camarillo et al. 2015), and less likely to invade mature forest stands where artificial regeneration through seedling planting is used. Competition from a viable native community of hardwood species could explain why tallow has less of an impact in forest communities than in prairies and grasslands.

Greater leaf area and higher allocation to leaves may contribute to the success of tallow when growing with native species in mixed communities. Natural and human-mediated disturbances contribute to the loss of native species and the spread tallow (Pile et al. 2017; Yang et al. 2021). The greater leaf area and higher allocation to leaves observed in tallow in mixed communities may facilitate the spread of the invader.

LITERATURE CITED

Abrams, M.D., M.E. Kubiske, and K.C. Steiner. 1989. Drought adaptations and responses in five genotypes of *Fraxinus pennsylvanica* Marsh.: photosynthesis, water relations, and leaf morphology. Tree Physiology. 6:305–315.

Ajala, O.O., K.R. Kidd, B.P. Oswald, Y. Weng, and J.P. Stovall. 2022. Response of Chinese Tallow (*Triadica sebifera*) and Coexisting Natives to Competition, Shade, and Flooding. Forest Science. 68(1):17–26.

Armas, C., R. Ordiales, and F.I. Pugnaire. 2004. Measuring plant interactions: a new comparative index. Ecology. 85(10):2682–2686.

Battaglia, L.L., J.S Denslow, J.R. Inczauskis, and S.G. Baer. 2009. Effects of native vegetation on invasion success of Chinese tallow in a floating marsh ecosystem. Journal of Ecology. 97: 239-246.

Bonner F.T. and H.E. Kennedy Jr. 1973. Storage of water tupelo seeds. Tree Planters' Notes 24(4): 7–8.

Bonner, F.T., and R.P. Karrfalt. 2008. The Woody Plant Seed Manual. Agric. Handbook No. 727. Washington, DC. U.S. Department of Agriculture, Forest Service. 1223 p.

Bruce, K.A., G.N. Cameron, and Harcombe, P.A. 1995. Initiation of a new woodland type on the Texas Coastal Plain by the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.). Bulletin of the Torrey Botanical Society. 122(3): 215-225.

Burns, R.M., and B.H. Honkala. 1990. Silvics of North America. Agriculture handbook: U.S. Dept. of Agriculture, Forest Service.

Butterfield, B.J., W.E. Rogers, and E. Siemann. 2004. Growth of Chinese tallow tree (*Sapium sebiferum*) and four native trees under varying water regimes. Texas Journal of Science. 56(4): 335-346.

Camarillo, S.A., J.P. Stovall, and C.J. Sunda. 2015. The impact of Chinese tallow (*Triadica sebifera*) on stand dynamics in bottomland hardwood forests. Forest Ecology and Management. 344, 10–19.

Conner, W.H. 1994. The effect of salinity and waterlogging on growth and survival of baldcypress and Chinese tallow seedlings. Journal of Coastal Research. 10(4): 1045-1049.

Conner, W.H., K.W. McLeod, and J.K. McCarron. 1997. Flooding and salinity effects on growth and survival of four common forested wetland species. Wetlands Ecology and Management. 5: 99–109

Conway, W.C., L.M. Smith, and J.F. Bergan. 2002. Potential allelopathic interference by the exotic Chinese tallow tree (*Sapium sebiferum*). American Midland Naturalist. 148:43–53.

Davis, M.A., J.P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology. 88:528–534.

Domènech, R. and M. Vilà. 2008. Response of the invader *Cortaderia selloana* and two coexisting natives to competition and water stress. Biological Invasions. 10:903–912.

Feng, Y., J. Wang, and W. Sang. 2017. Biomass allocation, morphology, and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. Acta Oecologica. 31:40–47.

Funk, J.L. and P.M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature. 446:1079–1081.

Funk, J.L., E.E. Cleland, K.N. Suding, and E.S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution. 23(12):695–703.

Gabler, C.A., and E. Siemann. 2013. Rapid ontogenetic niche expansions in invasive Chinese tallow tree permit establishment in unfavorable but variable environments and can be exploited to streamline restoration. Journal of Applied Ecology. 50:748–756.

Gioria, M., and B.A. Osborne. 2014. Resource competition in plant invasions: emerging patterns and research needs. Frontiers in Plant Science. 5(501):1–21.

Gómez, J.M. 2004. Importance of burial and microhabitat on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecology. 172:287–297.

Grace, J.B. 1998. Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion? Endangered Species Update. 15(5):70-76.

Henkel, T.K., J.Q. Chambers, and D. A. Baker. 2017. Delayed tree mortality and Chinese tallow (*Triadica sebifera*) population explosion in a Louisiana bottomland hardwood forest following Hurricane Katrina. Forest Ecology and Management. 378:222-232.

Hook, D.D., and C.L. Brown. 1973. Root Adaptations and Relative Flood Tolerance of Five Hardwood Species. Forest Science. 19(3):225-229.

Ibáñez, I. and E.W. Schupp. 2001. Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival. Oecologia. 129:543–550.

Johnson, R.L. 1990. Water Tupelo (*Nyssa aquatica*). In Silvics of North America: 1. Conifers; 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 474-478. Washington, DC: USDA Forest Service. 877 pages.

Jones, R.H. and K.W. McLeod. 1989. Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. Bulletin of the Torrey Botanical Club**.** 116(4): 371-377.

Jones, R.H. and K.W. McLeod. 1990. Growth and photosynthetic responses to a range of light environments in Chinese tallowtree and Carolina ash seedlings. Forest Science. 36: 851-862.

Jones, R.H., and R.R. Sharitz. 1990. Effects on root competition and flooding on growth of Chinese tallow seedlings. Canadian Journal of Forest Research. 20:573–578.

Kennedy, H.E. 1990. Green Ash (*Fraxinus pennsylvanica*). In Silvics of North America: 1. Conifers; 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 348-354. Washington, DC: USDA Forest Service. 877 pages.

Krajicek, J.E., and R.D. Williams. 1990. Hackberry (*Celtis occidentalis*) In Silvics of North America: 1. Conifers; 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 262-265. Washington, DC: USDA Forest Service. 877 pages.

Li, W., J. Luo, X. Tian, W.S. Chow, Z. Sun, T. Zhang, S. Peng, and C. Peng. 2015. A new strategy for controlling invasive weeds: selecting valuable native plants to defeat them. Scientific Reports. 5, 11004; doi: 10.1038/srep11004.

Lin, J., P.A. Harcombe, M.R. Fulton, and R.W. Hall. 2004. Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas. Oecologia. 139(3): 399-407.

Marshall P.E. 1981. Methods for stimulating green ash seed germination. Tree Planters' Notes 32(3): 9–11.

Martin, P.H., C.D. Canham, and P.L. Marks. 2008. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers in Ecology and the Environment. 7(3):142–149.

Meadows, J.S. and J.A. Stantuft. 1997. Silvicultural systems for southern bottomland hardwood forests. Forest Ecology and Management. 90:127–140.

Pile, L.S., G.G. Wang, J.P. Stovall, E. Siemann, G.S. Wheeler, and C.A. Gabler. 2017. Mechanisms of Chinese tallow (*Triadica sebifera*) invasion and their management implications – A review. Forest Ecology and Management. 404:1-13.

Rejmánek, M. and D.M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77:1655–1661.

Rejmánek, M., D.M. Richardson, and P. Pysek. 2005. Plant invasions and invasibility of plant communities. In: van Der Maarel, E. (Ed.), Vegetation Ecology. Blackwell Publishing, Malden, MA, pp. 332–354.

Rogers, W.E. and E. Siemann. 2003. Effects of simulated herbivory and resources on Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasion of native coastal prairie. American Journal of Botany. 90(2): 243-249.

Siemann, E., and W.E. Rogers. 2001. Genetic differences in growth of an invasive tree species. Ecology Letters. 4:514–518.

Siemann, E. and W.E. Rogers. 2003. Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. Journal of Ecology. 91:923–931.

Wang, H.H., W.E. Grant, T.M. Swannack, J. Gan, W.E. Rogers, T.E., Koralewski, J.H. Miller, and J.W. Taylor. 2011. Predicted range expansion of Chinese tallow tree (*Triadica sebifera*) in forestlands of the southern United States. Diversity and Distributions. 17:552–565.

Wilhite, L.P., and J.R. Toliver. 1990. Baldcypress (*Taxodium distichum* [L.] Rich.). In Silvics of North America: 1. Conifers; 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 1153–1164. Washington, DC: USDA Forest Service. 877 pages.

Williamson, M.H. and A. Fitter. 1996. The characters of successful invaders. Biological conservation. 78:163–170.

Yang, S., Z. Fan, X. Liu, and A.W. Ezell. 2021. Predicting the spread of Chinese tallow (*Triadica sebifera*) in the southeastern United States forestland: Mechanism and risk factors at the regional scale. Forest Science and Management. 482:118892.

Yannelli, F.A., C. MacLaren, and J. Kollmann. 2020. Moving away from limiting similarity during restoration: timing of arrival and native biomass are better proxies of invasion suppression in grassland communities. Frontiers in Ecology and Evolution. 8:238.

Yu-Long, Z., F. Yu-Long, L. Wan-Xue, and L. Zhi-Yong. 2009. Growth, biomass allocation, morphology, and photosynthesis of invasive *Eupatorium adenophorum* and its native congeners grown at four irradiances. Plant Ecology. 203(2):263–271.

Zou, J., W.E. Rogers, and E. Siemann. 2009. Plasticity of *Sapium sebiferum* seedling growth to light and water resources: inter-and intraspecific comparisons. Basic and Applied Ecology. 10: 79-88.

TABLES

Table 4.1: Differences in seedling height, ground diameter and number of leaves at treatment initiation. Values represent means (± SE). Column means for each variable with different letters represent significant differences ($P < 0.05$) among species according to the Tukey's test (alpha = 0.05).

Species	Height (cm)	Ground diameter (mm)	Number of leaves
Baldcypress	14.22 ± 0.56^{b}	1.47 ± 0.05^{b}	8.44 ± 0.28^{a}
Tallow	13.29 ± 0.53^{b}	1.57 ± 0.05^{b}	4.63 ± 0.27^{c}
Green ash	10.15 ± 0.55^{c}	1.01 ± 0.05^{c}	7.43 ± 0.28^{b}
Sugarberry	7.94 ± 0.59^{d}	0.62 ± 0.05^{d}	4.98 ± 0.30^{c}
Water tupelo	24.89 ± 0.58^{a}	2.21 ± 0.05^{a}	8.47 ± 0.29^{a}

Table 4.3: Analysis of variance to test the effects of species (*S*), community (*C*), light (*L*), flooding (*F*), and their interactions on morphological parameters in the community-based experiment.

Leaf traits	*F* and its significance										
	S	*C*	*L*	*F*	*S x L*	*S x F*	*L x F*	*C x F*	*C x L*	*C x L x F*	*S x C x L x F*
Growth											
Height (cm)	44.22^{**}	3.69^{ns}	264.36^{**}	1.82^{ns}	4.99^{**}	4.33^{**}	6.19^{*}	2.33^{*}	0.15^{ns}	26.99^{**}	3.22^{*}
Diameter (mm)	75.34^{**}	13.80^{**}	837.23^{**}	3.94^{*}	15.32^{**}	8.28^{**}	23.18^{**}	0.56^{ns}	0.29^{*}	24.13^{**}	5.29^{**}
Leaf counts	48.49^{**}	11.14^{**}	283.85^{**}	0.37^{ns}	18.23^{**}	1.02^{ns}	7.39^{**}	0.03^{ns}	0.10^{ns}	18.67^{**}	3.11^{*}
Stem growth rate	10.37^{**}	8.13^{**}	197.25^{**}	0.05^{ns}	2.45^{*}	0.69^{ns}	5.52^{*}	1.28^{ns}	0.11^{ns}	27.19^{**}	1.74^{ns}
Biomass											
Leaf biomass (g)	12.83^{**}	16.82^{**}	174.09^{**}	0.25^{ns}	3.13^{*}	0.26^{ns}	5.41^{*}	0.86^{ns}	2.85^{ns}	29.79^{**}	4.96^{**}
Total biomass (g)	23.31^{**}	29.07^{**}	356.98^{**}	104.53^{**}	13.41^{**}	8.61^{**}	28.08^{**}	6.59^{*}	3.04^{ns}	2.76^{ns}	5.49^{**}
LAR (cm^2 g^{-1})	33.17^{**}	2.71^{ns}	243.65^{**}	34.41^{**}	6.56^{**}	1.99^{ns}	56.15^{**}	0.10^{ns}	1.01^{ns}	26.65^{**}	1.88^{ns}
Leaf morphology											
Leaf length (cm)	26.53^{**}	1.42^{ns}	173.39^{**}	22.54^{**}	4.75^{**}	0.56^{ns}	62.26^{**}	0.02^{ns}	0.20^{ns}	13.08^{**}	2.03^{ns}
Leaf width (cm)	34.82^{**}	12.11^{**}	198.73^{**}	1.39^{ns}	4.07^{**}	1.19^{ns}	26.31^{**}	0.13^{ns}	1.07^{ns}	19.30^{**}	1.05^{ns}
Leaf area (cm^2)	50.66^{**}	12.28^{**}	181.22^{**}	18.59^{**}	3.66^{**}	8.71^{**}	33.25^{**}	0.28^{ns}	0.03^{ns}	22.25^{**}	3.56^{**}
SLA (m^2 kg^{-1})	64.22^{**}	9.18^{**}	124.12^{**}	7.31^{**}	2.15^{ns}	7.06^{**}	27.34^{**}	0.13^{ns}	1.18^{ns}	21.79^{**}	2.18^{ns}

F test: *, ** and ns indicate $P \leq 0.05$, $P \leq 0.01$ and $P > 0.05$, respectively. Due to a zero value on its degree of freedom, the following interactions were not analyzed: *S x F*, *S x C x L*, and *S x C x F*.

FIGURES

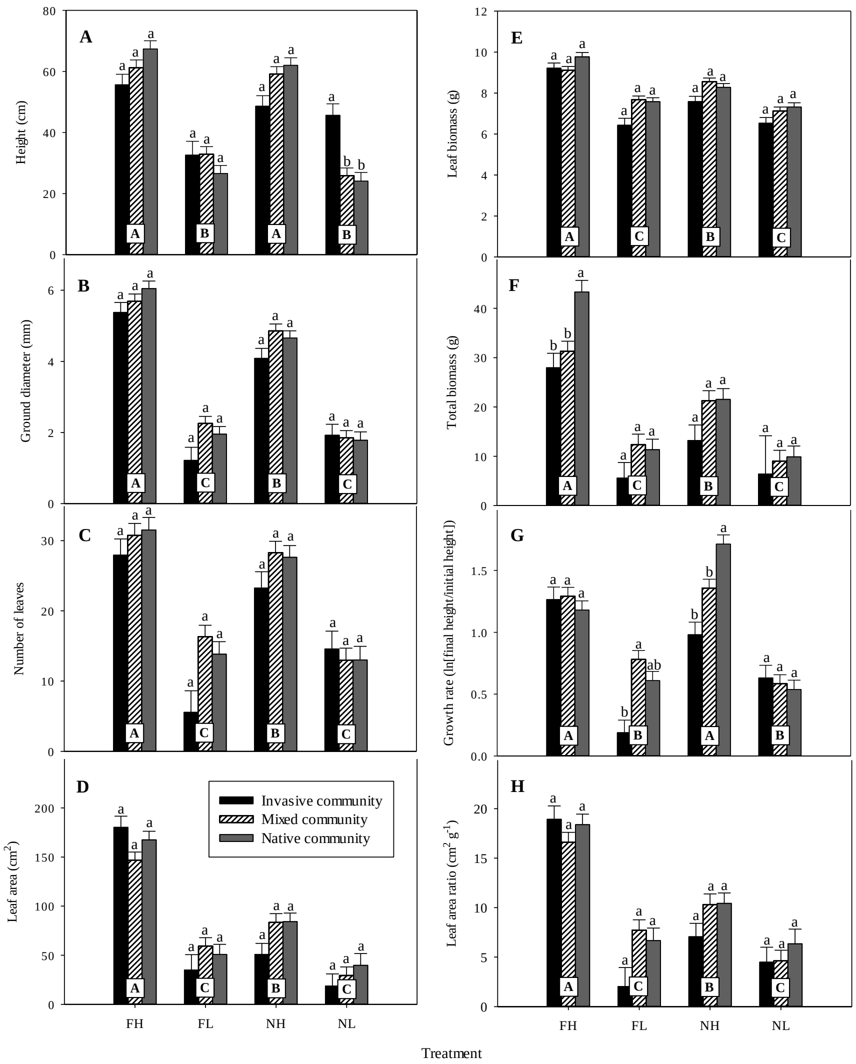

Figure 4.1: Comparisons of the morphological traits of the community types among the different flooding and light treatments at the end of the experiment (mean ± SE). The traits include (**A**) height, (**B**) ground diameter, (**C**) number of leaves, (**D**) leaf area, (**E**) leaf biomass, (**F**) total biomass, (**G**) growth rate, and (**H**) leaf mass ratio. Letters indicate significantly different means ($P < 0.05$) among community types (lowercase) and between treatments (uppercase) according to the Tukey's test for multiple comparison. FH means flooded and high irradiance treatment, FL means flooded and low irradiance treatment, NH means non-flooded and high irradiance treatment, and NL means non-flooded and low irradiance treatment.

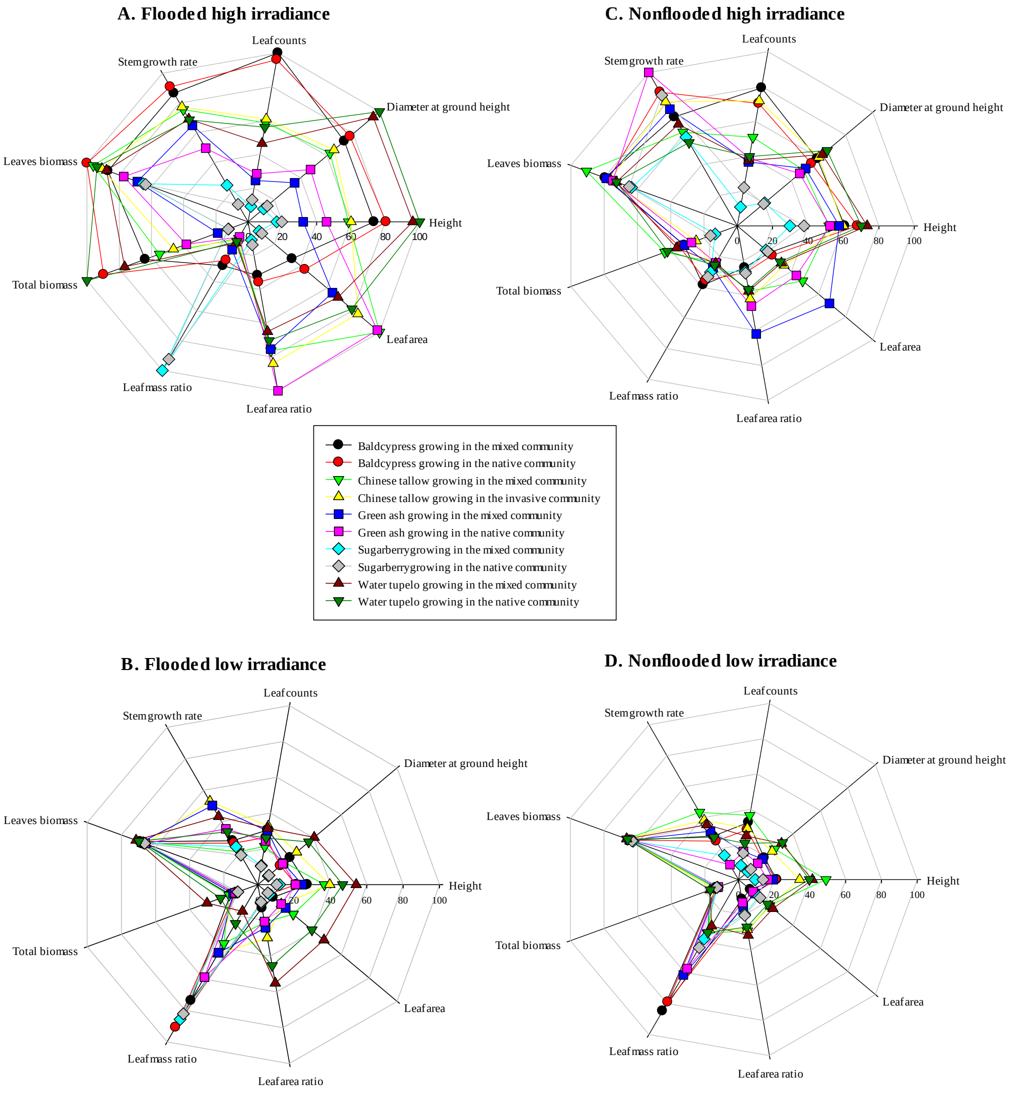

Figure 4.2: Radar plots showing the morphological and biomass traits of seedlings in the community-based experiment. The different light and flooding treatments include: (**A**) FH, flooded and high irradiance, (**B**) FL, flooded and low irradiance, (**C**) NH, non-flooded and high irradiance, and (**D**) NL, non-flooded and low irradiance. Variables were scaled to a percent scale by setting the maximum value for each variable equal to 100%.

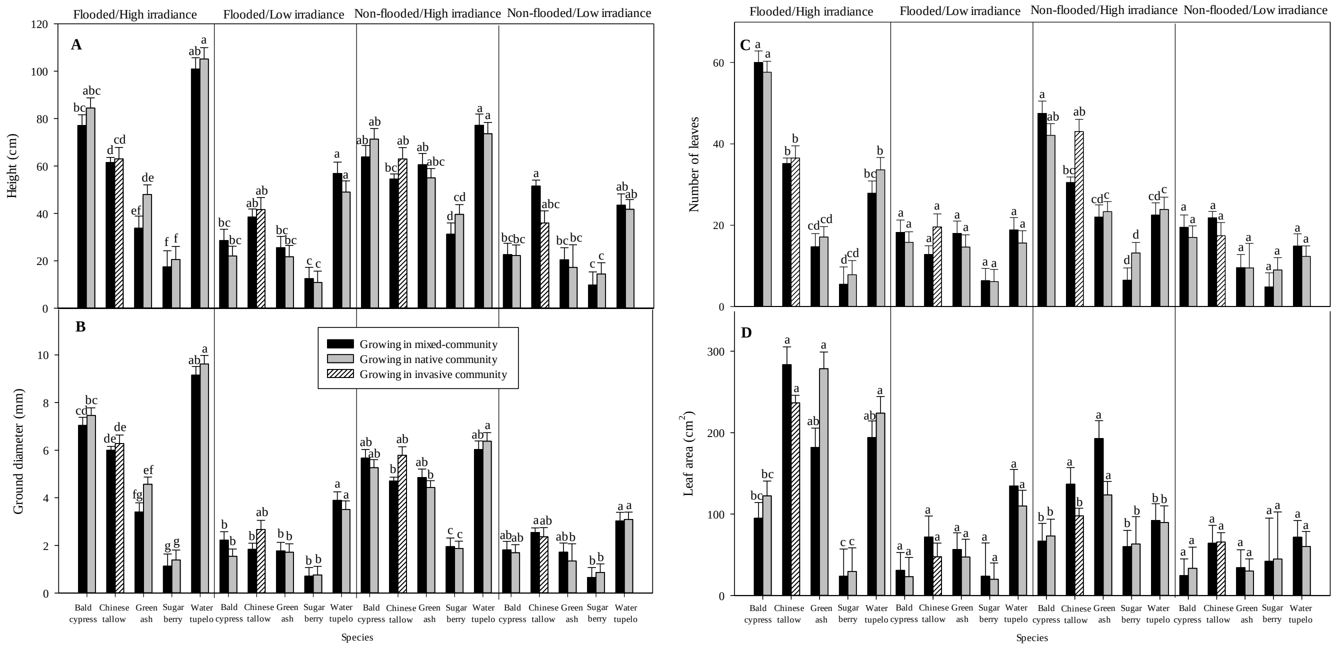

Figure 4.3: Comparisons of morphological traits in the community-based experiment. The traits include (**A**) height, (**B**) ground diameter, (**C**) number of leaves, and (**D**) leaf area. The data are shown as the mean ± SE, and different letters above columns indicate significant differences (*P* < 0.05) according to Tukey's test for multiple comparison. Lowercase letters represent post-hoc contrasts among species within each light, flooding, and community treatment.

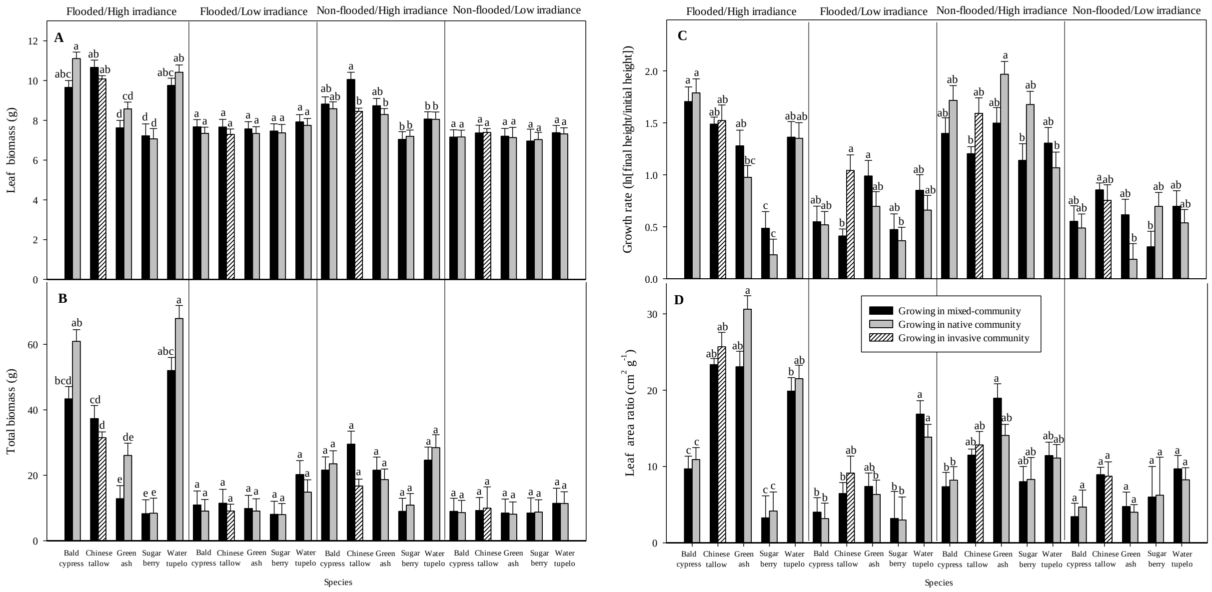

Figure 4.4: Comparisons of morphological traits in the community-based experiment. The traits include (**A**) leaf biomass, (**B**) total biomass, (**C**) growth rate, and (**D**) leaf area ratio. The data are shown as the mean ± SE, and different letters above columns indicate significant differences ($P < 0.05$) according to Tukey's test for multiple comparison. Lowercase letters represent post-hoc contrasts among species within each light, flooding, and community treatment.

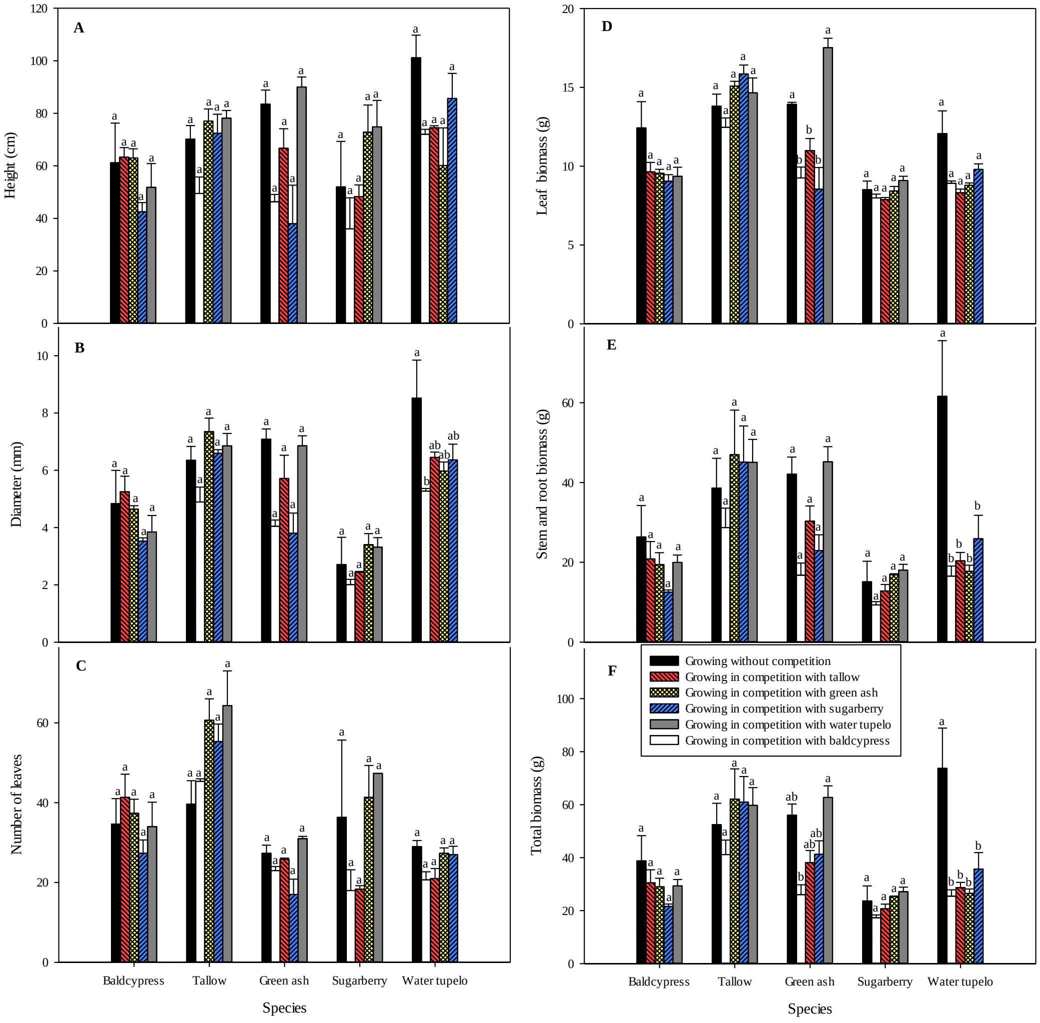

Figure 4.5: Comparisons of the seedling's traits in the relative interaction index experiment. Seedlings were grown alone and under interspecific competition (with tallow, green ash sugarberry, water tupelo, and baldcypress. Seedling traits include (**A**) height, (**B**) diameter, (**C**) number of leaves, (**D**) leaf biomass, (**E**) stem and root biomass, and (**F**) total biomass. The data are shown as the mean (± SE) and the different letters above columns indicate significant differences ($P < 0.05$) within species according to the Tukey's test.

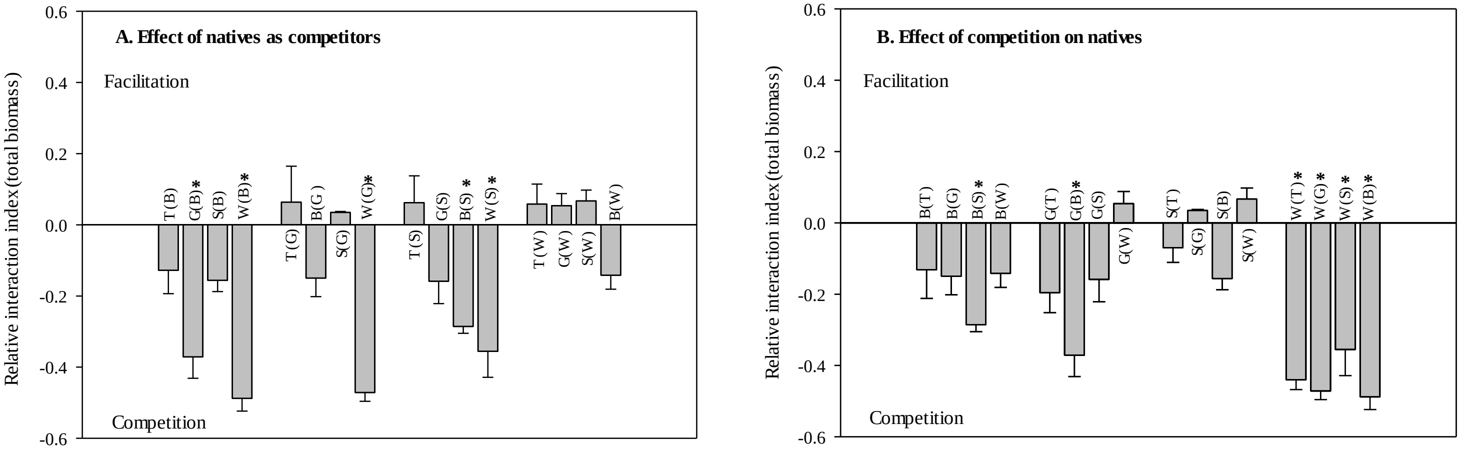

Figure 4.6: A comparison of the relative interaction index (RII) for quantifying native species competition and the invader's impact. Panel **A** shows the effect of natives as competitors and panel **B** shows the effect of competition on natives. For species identification: T means tallow, G means green ash, B means baldcypress, S means sugarberry, and W means water tupelo. For competition treatments: T(B) means the target plant was tallow growing with baldcypress under interspecific competition. The data are shown as the mean (± SE) and * indicates that the RII value for each species combination is significantly different (*P*<0.05) from zero according to a one-sample t-test.

CHAPTER 5

SEEDLING SURVIVAL AND GROWTH OF FOUR FOREST TREE SPECIES: THE ROLE OF RESOURCE GRADIENTS IN BOTTOMLAND HARDWOOD FORESTS

ABSTRACT

Bottomland hardwood (BLHW) forests provide numerous valuable services including wildlife habitat, carbon storage, timber products, and water quality enhancement, and also represent one of the most rapidly diminishing wetland ecosystems in the United States due to land conversion, construction of surface water impediments, and unsustainable timber harvesting activities. The successful restoration of BLHW forests is often difficult and influenced by multiple factors including flooding, shade, herbivory, root competition, disease, and occasional drought. In February 2019, loblolly pine (*Pinus taeda* L.), water oak (*Quercus nigra* L.), water tupelo (*Nyssa aquatica* L.), and baldcypress (*Taxodium distichum* [L.] Rich.) were planted in a BLHW forest in Harris County, TX to compare survival and growth. Three years after planting, survival ranged from 0.01 % (in water oak) to 39.60 % (in baldcypress). Damage by feral hogs (*Sus scrofa*) in form of uprooted stems with consumed rootstocks caused significant mortality. Although baldcypress and water tupelo had higher tree heights than loblolly pine in 2021, only loblolly pine and water tupelo had a significant increase in tree heights between 2019 and 2021. The leaf area index and the proportion of clay and silt in the soil were both significantly but weakly correlated with tree height. Tree survival was correlated with pH, litter layer mass, and the direct and indirect site factors, but only weakly. Baldcypress is recommended for planting as the species had the highest survival rates suggesting it is better adapted to the microenvironmental conditions in the study site.

INTRODUCTION

Floodplain ecosystems are a widely recognized feature of the southern United States landscapes due to the numerous ecosystem services, including wildlife habitat, carbon storage, timber production, and water quality enhancement (King et al. 2009). In the southeastern U.S., floodplain ecosystems consist predominantly of bottomland hardwood forests (BLHW) and other associated wetlands, rivers and streams, and agricultural/urban areas (King et al. 2009). Bottomland hardwood forests are one of the most rapidly diminishing wetland ecosystems in the United States (Taylor et al. 1990); about two-thirds (4.8 million hectares) have been lost due to land conversion to agriculture or the construction of surface water impoundments, and most of what is left are being altered by improper timber harvesting activities (Williams et al. 2002).

Bottomland hardwood forests are hydrologically diverse ecosystems that support a wide variety of woody and herbaceous plants, terrestrial and aquatic animals, and microorganisms (Taylor et al. 1990; Jacques 2017). BLHW forests with unaltered hydroperiods are considered among the healthiest ecosystems due to the aboveground net primary productivity in excess of 1000 g m^{-2} yr^{-1} (Taylor et al. 1990). This natural high productivity provides a variety of natural products harvested by humans including timber, fish, and wildlife (Taylor et al. 1990). The value of southeastern BLHW hardwoods has been estimated from \$3 billion to \$8 billion and they are amongst the most productive habitats for game species (Taylor et al. 1990). BLHWs also act as filters and sinks that allow for the consistent release of carbon and processing of nutrients such as phosphorus, calcium, magnesium, sodium, and potassium (Taylor et al. 1990; Jacques 2017). This results in increased amounts of organic carbon materials in areas downstream and in watersheds that contain BLHW forests (Taylor et al. 1990). Restorations of hardwood communities are underway as the functions and values of intact bottomland hardwood forests are becoming increasingly appreciated (Hodges 1997; Allen et al. 2001). Tree species selection is a demanding task and one of the most important stages in the restoration process due to the large number of species available and their varying needs for establishment, survival, and growth (Allen et al. 2001; Kroschel et al. 2016). An incorrect selection can result in a total planting failure, an inadequately stocked and underproductive forest, or a forest of little value to wildlife (Allen et al. 2001). Although predicting the likelihood of success in restoration projects is difficult because success is influenced by many factors (Lin et al. 2004), a successful approach to restoration is based on the realization that hydrology is the most important factor influencing the local distribution of BHLW species and must be explicitly considered in all projects (Allen et al. 2001). It is unlikely that a project will be successful unless the proper hydrologic regime for the site conditions and tree species chosen for planting is in place (Allen et al. 2001).

The most essential element of the restoration process in BLHW is correctly matching species and sites, because the most desirable species will only survive and grow on a narrow range of sites and conditions (Hodges 1997; Self 2004). Paying more attention to the sites and matching species to the site conditions can increase the likelihood of the process. Specifically, topographical features, elevation, soil characteristics, the presence of pans, pH, and disturbances are all factors that influence this process. Matching the right species to the right location will produce a forest stand that can grow and thrive for a long time.

BLHW forests have been effectively restored using several regeneration methods including direct seeding, planting seedlings, planting cuttings, and transplanting saplings (Allen et al. 2001). Planting tree seedlings is the typical and well-established means of reforestation, owing to the higher rates of seedling establishment and faster initial development of trees than direct seeding (Johnson 1979; Allen and Kennedy 1989; Kennedy 1994; Allen et al. 2001). Because oaks are valued for timber and wildlife habitat, planting bareroot oak seedlings is an old, well-established method of reforestation in these forests (Twedt and Portwood 1997; Williams et al. 2002). Bareroot seedlings can be expected to survive and grow well if planted during the dormant season (December to mid-March), the site is not too dry, and soil conditions are otherwise favorable (Allen et al. 2001).

The objective of this study was to investigate how microenvironmental site conditions affect the establishment and survival of one-year-old bare-root planting stock (1-0) in a BLHW forest in Harris County, TX. This study was a 3–year field experiment designed to examine the growth and survival of an evergreen (*Pinus taeda* L.) and three deciduous species (*Quercus nigra* L., *Nyssa aquatica* L., and *Taxodium distichum* L.) across the Green Bayou Wetland Mitigation Bank (GBWMB) in Harris County, TX. With increasing interest in the ecological restoration of BLHW forests, it is critical to understand early growth and survival patterns to inform species selection and match the right species to the right location. This study aims to expand on existing best management practices related to establishing seedlings in BLHW forests by addressing this hypothesis. Data collected should allow managers to focus on high-success restoration treatments in BLHW forests, rather than planting seedlings that will not survive due to inappropriate soil drainage or excessive overstory shading.

METHODS

Study site

The Green Bayou Wetlands Mitigation Bank is located along the floodplains of the Garners and Greens Bayou in Harris County, TX, U.S.A. (29.93°N, −95.22°W). The GBWMB is 389 ha of mostly open ponds, marshes, grassland prairies, and wetlands (Figure 5.1). The Garners and Green Bayou form the western boundary while the Texas 8 Beltway forms the northern boundary. The elevation is less than 45 m above sea level with several minor topographic variations. The area is characterized by hot, humid summers, and moderate winters with a mean annual temperature of 22 ℃. The growing season is approximately 250 days, and the average annual rainfall is 1264 mm (National Oceanic and Atmospheric Administration).

Planting

In 2014, 36 plots were installed on a systematic basis across all forested acres on the GBWMB to assess the native and invasive species present on the site (Brian Blades, unpublished data). The plots were inventoried them using overstory (0.02 ha), sapling (0.002 ha), and seedling (0.0001 ha) plots. Based on inventory results and available species at the nursery, the following species were selected and planted at the same level of abundance across the property: loblolly pine, water oak, water tupelo, and baldcypress.

In January 2019, one-year-old bare-root planting stock (1-0) of the selected species were obtained from ArborGen seedlings, South Carolina, USA. The following month, 20 plots of 220 × 220 cm were installed, where 64 seedlings (16 seedlings per species) were planted on a 60 by 60 cm spacing (Figure 5.2). Light availability, yearly saturation, and soil conditions were used to stratify locations on the GBWMB. Plot locations were then grouped and chosen at random within these strata, to cover the widest possible range of light, flooding, and soil conditions on GBWMB, from open spaces (>90% full sunlight) to shady microhabitats (<10% full sunlight) under the canopy of tree and shrub species (Figure 5.1).

Characterization of the abiotic environment

The aboveground (light availability) and belowground (soil textural and chemical characteristics) environments were characterized for each plot. Canopy cover, direct light, and indirect light transmitted through the canopy were estimated using hemispherical canopy photography (Evans and Coombe 1959; Rich 1990). Photographs were taken in the center of each plot, using a SIGMA SD15 digital camera with a 4.5 mm 1:2.8 fisheye lens (SIGMA Japan) mounted on a tripod at 1.3 m above the ground and leveled so the center of the lens was focused on the zenith with a marker to magnetic north. Photographs were taken of each plot between June and July 2020, and the second set in August 2021. All photographs were taken pre-dawn, post-dusk, or on overcast days when cloud cover prevents direct sunlight from creating errors in interpretation. We analyzed the images and determined thresholds for pixel classification using SideLook version 1.1 (Nobis and Hunziker 2005). SideLook is a free and accessible software program used to analyze vegetation structure from digital images. Each pixel in the image was classified as either sky or canopy based on established thresholds, and we then estimated the Direct and Indirect Site Factors (DSF and ISF) using the Hemiview canopy analysis software (Delta T, Cambridge, United Kingdom). DSF and ISF are defined as the proportion of direct and diffuse radiation, respectively, transmitted through the canopy under clear sky conditions at the study site.

Three soil samples were collected from random locations within each plot before planting seedlings with a shovel or auger at a depth of 0 to 20 cm to analyze the textural and chemical soil properties. Soil samples were analyzed in the Soil, Plant, and Water Analysis Laboratory at Stephen F. Austin State University for the standard physio-chemical properties. Two soil properties determined included pH (with a pH meter) and percentages of sand, clay, and silt (Bouyoucos hydrometer method; Bouyoucos 1962).

At each plot, all above-ground components of the vegetation were collected from four (25 × 25 cm) randomly selected quadrants, including litter and the living materials of herbs and tree seedlings. The planted seedlings were not included in the above-ground components. Each component was stored in a plastic bag and transported to the laboratory where they were dried at 60 °C for 96 hours to constant mass and weighed to calculate litter layer mass. Litter layer mass (g) was then converted to litter layer mass per square meter for each plot (g/m^2).

Seedling monitoring

Each seedling within a plot was tagged and monitored periodically until August 2021. We tracked seedling survival and height once a month through December 2019 and quarterly through August 2021. Seedling status was recorded by visual inspection: seedlings were deemed dead if there was a lack of aboveground green tissue or leaves, and/or the seedling could not be located. Missing stems and stems pulled from the ground with their rootstock consumed were assumed to have been eaten by feral hogs (*Sus scrofa*; Mayer et al. 2000). Across the southeastern United States, hogs systematically go from one seedling to the next, pulling seedlings out of the ground, chewing up and consuming the plant's rootstock and lower portion of the stem (Mayer et al. 2000; Jacques 2017; Oliver et al. 2019; Bradley and Lockaby 2021). From these data, four response variables were calculated: (a) the first-year survival (i.e., after one growing season), calculated as the proportion of the seedlings alive at the end of the first summer (October 2019), (b) the cumulative final survival (i.e., after three years), calculated as the proportion of the seedlings alive in August 2021, (c) the first-year height (i.e., after one growing season), and (d) cumulative final height (i.e., after three years).

Statistical analysis

The following linear model was used to examine tree height and survival:

$$y_{\mathrm{ijkl}} = \alpha + \beta \times Yr + \mathcal{E}_{\mathrm{ijkl}}$$

where, y_{ijkl} was the tree height of the k^{th} year (m = 1, 3, where 1 and 3 represent the values at the end of the first- and third-years following establishment, respectively) of the l^{th} tree of the i^{th} species, growing at the j^{th} plot. The term α was the model intercept, was β the slope associated with Yr, and $\mathcal{E}_{\mathrm{ijkl}}$ was random error, which is NID (0, σ^2), where σ^2 is the error variance. These were further incorporated into the linear model:

$$\alpha = \alpha_0 + S_{\mathrm{i}}$$

$$\beta = \beta_0 + S_{\mathrm{i}}$$

S_{i} was the i^{th} species effect. All factors were treated as fixed. $\mathcal{E}_{\mathrm{ijkl}}$ was random error, which is NID (0, σ^2), where σ^2 is the error variance. Thus, linear model was rewritten as:

$$y_{\mathrm{ijkl}} = (\alpha_0 + S_{\mathrm{j}}) + (\beta_0 + S_{\mathrm{j}}) \times Yr + \mathcal{E}_{\mathrm{ijkl}}$$

A Pearson correlation was used to determine the effects of the abiotic variables on tree height (first year and cumulative) and survival (first year and cumulative). These data were analyzed performed using PROC MIXED, PROC REG, or PROC CORR in the SAS software version 9.4 (SAS Institute, Cary, North Carolina, USA). Due to the operational nature of the experiment, an alpha value of 0.10 was used to determine the significance.

RESULTS

Establishment heights and survival

Two months after establishment, baldcypress seedlings (59.09 ± 0.69 cm) were significantly taller than water oak (46.67 ± 0.71 cm), which were taller than water tupelo (43.15 ± 0.70 cm), and taller than loblolly pine (23.43 ± 0.70 cm). Seedlings were tallest in plot 4 (61.83 ± 1.68 cm), with that of baldcypress (77.77 ± 3.18 cm) and water tupelo (73.11 ± 3.20 cm) greater than those of water oak (56.40 ± 3.90 cm) and loblolly pine (40.03 ± 3.18 cm). The lowest survival rates were recorded during the first year in June, September, and November. Four months after planting (July 2019), survival across all species was 54% (Figure 5.3).

Observed heights and survival

Across all three years, significant species-by-year interactions were observed for survival (Table 5.1). First year baldcypress survival rates were higher than those of water tupelo and loblolly pine, which were higher than those of water oak (Figure 5.4A). Third-year survival of baldcypress (39.6 %) was also significantly higher than that of loblolly pine (6.4 %) and water tupelo (3.9 %), and thus greater than that of water oak (0.1 %; Figure 5.4A).

Tree height generally showed species-by-year interactions (Table 5.1). In 2019, baldcypress heights were significantly taller than those of water tupelo and water oak, which were both taller than loblolly pine (Figure 5.4B). Baldcypress, water oak, and water tupelo mean heights did not differ in 2021, but baldcypress and water tupelo were significantly taller than loblolly pine (Figure 5.4B). Baldcypress and water oak had similar mean heights between 2019 and 2021, indicating a relatively slow growth rate in comparison to the other species (Figure

5.4B). Loblolly pine, on the other hand, more than doubled in mean height between 2019 and 2021, with water tupelo showing significant growth also (Figure 5.4B).

Variation of abiotic factors

Soil texture analysis showed that sand was a major particle across the property, constituting more than 40% of the particles across the plots sampled, with a mean value of 70.6%, and a range of 47.8 – 92.4% (Table 5.2). The soil pH ranged from 4.24 to 7.52 and the litter layer mass per unit area ranged from 130.08 to 1456.78 g/m^2 (Table 5.2).

Edaphic factors

The proportion of silt and sand particles in the soil had a significant correlation with the overall survival and height of the trees (Figure 5.5). Silt was found to be positively related to survival and height, whereas sand was found to be negatively related (Figure 5.5). Clay was the only soil particle with no significant ($p = 0.183$) correlation with survival ($r = 0.036$) but a significant ($p = 0.079$) correlation with height ($r = 0.133$; Figure 5.5). The proportion of sand and clay particles in the soil was found to be significantly correlated with baldcypress first- and third-year height, while silt was found to be correlated with only third-year height (Table 5.3).

Soil pH had a significant ($p = 0.008$) and positive ($r = 0.073$) correlation with survival but not with overall tree height (Figure 5.6). Only baldcypress and loblolly pine were significantly correlated with soil pH among the selected species (Table 5.3). While height of baldcypress had a significant and negatively correlated with soil pH, loblolly pine had a significant and positive correlation (Table 5.3).

Litter layer mass had a significant (p = 0.001) but negative (r = – 0.143) correlation with tree survival (Figure 5.7). This correlation was only significant and negatively correlated in the first-year height of loblolly pine and water tupelo (Table 5.3).

Light environment

While indirect site factors were significantly correlated to survival and height, direct site factors were significantly correlated to survival (Figure 5.8). In the first and third years, indirect site factors were significantly and positively correlated with the height of all species (Table 5.3). Direct site factors were only significant and negatively correlated with the first-year height of baldcypress (Table 5.3). Leaf area index had a significant (p = 0.004) and negative (r = – 0.004) correlation with tree height (Figure 5.9). Among the four species, leaf area index was significantly correlated with the height of all species but loblolly pine (Table 5.3).

DISCUSSION

Baldcypress outperformed the selected species in terms of survival, but loblolly outperformed the selected species in terms of stem growth rate. Baldcypress performance could be attributed to the species' ability to tolerate a wider range of environmental conditions (Williston et al. 1980; Neufeld 1983; Souther and Shaffer 2000), as well as a wide geographic range (Wilhite and Toliver 1990). The performance of the loblolly pine can be attributed to its inherent ability to grow and survive on wet sites (Baker and Langdon 1990; McCrady and Jokela 1998).

The greater survival rates of baldcypress in this study builds on existing evidence that baldcypress can grow in different hydrologic regimes and tolerate a wide range of light levels (Dickson et al. 1972; Neufeld 1983; Young et al. 1995; Keim et al. 2012). Baldcypress is a dominant canopy tree species of the deep-water swamps and bottomland forests of the southeastern United States (Young et al. 1995). It grows in hydrological regimes ranging from anaerobic soil conditions (representing sites subjected to frequent and extended periods of flooding) to saturated-aerated soil conditions (Neufeld 1983; Young et al. 1995). In anaerobic conditions, baldcypress exhibits greater radial growth by maintaining its actively growing root systems with unrestricted nutrient uptake, root growth, and top growth (Young et al. 1995). Anaerobic conditions provide increased soil moisture, decreased competition, and an influx of nutrients to wetland species following higher stream flows (Young et al. 1995). The natural hydrologic regimes of wetlands in the United States have been modified due to urbanization and the construction of levees, roads, and reservoirs (Young et al. 1995; Mahaffey and Evans 2016). These modifications alter the frequency, depth, and duration of floods, providing increased soil moisture, decreased competition, and an influx of nutrients to wetland species (Young et al. 1995; Mahaffey and Evans 2016). Given the ability of baldcypress to survive and grow in different hydrologic regimes, the species may respond positively to alterations of natural hydrologic regimes in wetlands.

Between the time of establishment and the time of the final measurements, all species experienced significant decreases in survival. This is most likely due to a lack vegetation weed control after initial establishment (Williams et al. 2002). Vegetation control provides a variety of benefits that restore or improve soil properties and productivity (Neaves et al. 2017). These include increased rooting zone soil temperature and aeration, improved soil drainage, increased nutrient availability, and reduced abundance of neighboring vegetation to improve light availability and reduce the risk of physical damage (Spittlehouse and Childs 1990; Boateng et al. 2009). Despite the benefits of vegetation weed, it can reduce the survival of planted seedlings and make seedlings more vulnerable to herbivory (Jacques et al. 2017; Oliver et al. 2019).

The above-average precipitation that Harris County received between 2019 and 2021 (2019 = 1403 mm, 2020 = 1413 mm, 2021 = 1392 mm; historical mean rainfall in Harris County = 1264 mm) may have affected survival. In this study, stems of loblolly pine, water oak, and water tupelo were pulled out of the ground and the rootstock was consumed in many plots, suggesting they were predated by hogs. Depredation by feral hogs has been reported as the leading cause of failure in intensive planting operations in Texas, Alabama, Florida, Louisiana, and Mississippi (Mayer et al. 2000; Jacques et al. 2017). Feral hogs change forest composition by eating seeds, killing seedlings, and affecting soil structure (Mahaffey and Evans 2016). Despite the damage caused by hogs, their effects can be mitigated with silvicultural and management activities (Siemann et al. 2009; Jacques et al. 2017).

The importance of abiotic factors across the study site suggests that they may have influenced species growth as well. The relative proportion of sand, silt, and clay particles in soil texture was significant and correlated with seedling height and survival. The higher sand component correlated with seedling growth and causes water to percolate faster, making water less available to seedling roots (Hooker et al. 2021). Because sand particles are relatively large, so are the pores between them. The large pores in sandy soils reduce the soil's water-holding capacity, causing it to drain quickly, allowing more air into the soil and leaving less moisture for plant roots to absorb (Weil and Brady 2008).

The correlation between the growth metrics and below-canopy light environment suggests that they may have a significant impact on species survival and height. The positive correlation with site factors (direct and indirect) suggests that increased direct and diffused solar radiation relative to an open canopy will benefit seedling survival and growth. The inverse relationship between leaf area index and height suggests that canopy closure may impede tree growth after establishment. Low levels of light in the forest understory, combined with other stresses, limit seedling and sapling growth and survival (Jones et al. 1989). My findings support the literature on floodplain forests, where predications of regeneration success and succession are primarily influenced by light availability and competition (Battaglia et al. 2000; Lin et al. 2003).

Conclusions

Predictions of regeneration success in floodplain forests are difficult because many factors influence them, including light, flooding, herbivory, competition, drought, and disease (Lin et al. 2004). Seedling height was significantly correlated with the indirect site factors, leaf area index, and relative proportions of sand and silt, whereas seedling survival was significantly correlated with all abiotic factors except the relative proportion of silt and leaf area index.

Baldcypress had the highest survival rates across the study site reflecting the wider ecological amplitude and suggesting that this native is better adapted to the microenvironmental conditions influencing seedling growth and survival. The increase in baldcypress trees suggest the species could have increases in year one instead of later. Although baldcypress grew taller, loblolly pine and water tupelo were the only species with significant increases in height between establishment and final measurements, indicating that these species grow at a faster rate. I would recommend continuous measurements be taken to determine changes in growth and survival.

LITERATURE CITED

Allen, J.A., and H.E. Kennedy, Jr. 1989. Bottomland hardwood reforestation in the Lower Mississippi Valley. U.S. Department of Interior, Fish and Wildlife Service, National Wetlands Research Center, Slidell, Louisiana, and U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, Stoneville, Mississippi.

Allen, J.A., B.D. Keeland, J.A. Stanturf, A.F. Clewell, and H.E. Kennedy, Jr. 2001. A guide to bottomland hardwood restoration: U.S. Geological Survey, Biological Resources Division Information and Technology Report USGS/BRD/ITR-2000-0011. U.S. Department of Agriculture, Forest Service, Southern Research Station, General Technical Report SRS-40:132.

Baker, J.B., and O.G. Langdon 1990. Loblolly pine (*Pinus taeda* L.) In Silvics of North America: 1. Conifers. Edited by R.M. Burns and B.H. Honkala, 1018–1051. Washington, DC: USDA Forest Service. 1383 pages.

Battaglia, L.L., S.A. Fore, and R.R. Shantz. 2000. Seedling emergence, survival, and size in relation to light and water availability in two bottomland hardwood species. Journal of Ecology. 88:1041–1050.

Boateng, J.B., J.L. Heineman, L. Bedford, G.J. Harper, and A.F.L. Nemec. 2009. Long-term effects of site preparation and post-planting vegetation control on *Picea glauca* survival, growth, and predicted yield in boreal British Columbia. Scandinavian Journal of Forest Research. 24:111–129.

Bouyoucos, G.J. 1962. Hydrometer Method Improved for Making Particle Size Analyses of Soils. Agronomy Journal. 54(5):464–465.

Bradley, E.A., and G. Lockaby. 2021. Invasive wild pigs: a significant disturbance in coastal forests. Forests. 12,1042.

Dickson, R.E., T.C. Broyer, and C.M. Johnson. 1972. Nutrient uptake by tupelo gum and bald cypress from saturated or unsaturated soil. Plant and Soil. 37: 297–308.

Evans, G., and D. Coombe. 1959. Hemispherical and woodland canopy photography and the light climate. Journal of Ecology. 47:103–113.

Hodges, J.D. 1997. Development and ecology of bottomland hardwood sites. Forest Ecology and Management. 90:117–125.

Hooker, J.M., B.P. Oswald, J.P. Stovall, Y. Weng, H.M. Williams, and J. Grogan. 2021. Third Year Survival, Growth, and Water Relations of West Gulf Coastal Plain Pines in East Texas. Forest Science. 67(3):347–355.

Jacques, R.J. 2017. Herbivory impacts on growth and survival of seedlings in bottomland hardwood forest restoration sites in the post oak savannah and Blackland prairie ecoregions of Texas, USA. Stephen F. Austin State University, Electronic Theses, and Dissertations.

Jones, R.H., R.R. Sharitz, and K.W. McLeod. 1989. Effects of flooding and root competition on growth of shaded bottomland hardwood seedlings. American Midland Naturalist. 121(1):165–175.

Johnson, R.L. 1979. Adequate oak regeneration: A problem without a solution. In Management and Utilization of Oak: Proceedings of the 7th annual hardwood symposium of the Hardwood

Research Council, May 1979. Cashiers and Asheville, North Carolina: Hardwood Research Council, p. 59–65.

Kennedy, H.E. Jr. 1994. Artificial regeneration of bottomland oaks. In Symposium Proceedings of oak regeneration: Serious problems, practical recommendations. September 8–10, 1992, Knoxville, Tennessee. General Technical Report SE–84. Asheville, North Carolina: USDA Forest Service, Southeastern Experimental Station, p. 241–249.

Keim, R.F., C.W. Izdepski, and J.W. Day Jr. 2012. Growth responses of baldcypress to wastewater nutrient additions and changing hydrologic regime. Wetlands. 32: 95–103.

King, S.L., R.R. Sharitz, J.W. Groninger, and L.L. Battaglia. 2009. The ecology, restoration, and management of southeastern floodplain ecosystems: A synthesis. Wetlands. 29 (2):624-634.

Kroschel, W.A., S.L. King, and R.F. Keim. 2016. Tree Regeneration by Seed in Bottomland Hardwood Forests: A Review. Southeastern Naturalist. 15:42–60. https://www.jstor.org/stable/26454783

Lin, J., P.A. Harcombe, M.R. Fulton, and R.W. Hall. 2004. Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas. Oecologia. 139 (3):399-407.

Mahaffey, A., and A. Evans. 2016. Ecological Forestry Practices for Bottomland Hardwood Forests of the Southeastern U.S., Forest Stewards Guild, p. 45.

Mayer, J.J., E.A. Nelson, and L.D. Wike. 2000. Selective depredation of planted hardwood seedlings by wild pigs in a wetland restoration area. Ecological Engineering. 15: S79-S85.

McCrady, R.L., and E.J. Jokela. 1998. Canopy dynamics, light interception, and radiation use efficiency of selected loblolly pine families. Forest Science. 44:64–72.

Neaves, C.M., W.M. Aust, M.C. Bolding, S.C. Barrett, C.C. Trettin, and E. Vance. 2017. Loblolly pine (*Pinus taeda* L.) productivity 23 years after wet site harvesting and site preparation in the lower Atlantic coastal plain. Forest Ecology and Management. 401:207–214.

Neufeld, H.S. 1983. Effects of Light on growth, morphology, and photosynthesis in baldcypress (*Taxodium distichum* (L.) Rich.) and Pondcypress (*T. ascendens* Brongn.) seedlings. Bulletin of the Torrey Botanical Club. 110(1): 43–54.

Nobis, M., and U. Hunziker. 2005. Automatic thresholding for hemispherical canopy photographs based on edge detection. Agricultural and Forest Meteorology. 128:243–250.

Oliver, L.B., J.P. Stovall, C.E. Comer, H.M. Williams, and M.E. Symmank. 2019. Weed control and overstory reduction improve survival and growth of under-planted oak and hickory seedlings. Restoration Ecology. 27(1):70–81.

Rich, P.M., 1990. Characterizing plant canopies with hemispherical photographs. Remote Sensing Reviews. 5:13–29.

Self, B. 2004. Bottomland hardwood management species/site relationships. Extension Service of Mississippi State University, cooperating with U.S. Department of Agriculture. 7 p.

Siemann, E., J.A. Carrillo, C. Gabler, and R. Zipp. 2009. Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. Forest Ecology and Management. 258(5): 546-553.

Souther, R.F. and G.P. Shaffer. 2000. The effects of submergence and light on two age classes of baldcypress (*Taxodium distichum* [L.] Richard) seedlings. Wetlands. 20(4): 697 – 706.

Spittlehouse, D.L. and S.W. Childs. 1990. Evaluating the seedling moisture environment after site preparation. In S.P. Gessel, D.S. Lacate, G.F. Weetman and R.F. Powers (Eds.), Sustained productivity of forest soils. Proceedings of the 7th North American Forest Soils Conference, University of British Columbia, Vancouver, BC pp. 80–94).

Taylor, J.R., M.A. Cardamone, and W.J. Mitsch. 1990. Bottomland hardwood forests: their functions and values. In Coastal Ecology Institute (ed.), Ecological Processes and Cumulative Impacts Illustrated by Bottomland Hardwood Wetland Ecosystems: Taylor & Francis. pp. 728

Twedt, D.J., and J. Portland. 1997. Bottomland hardwood reforestation for neotropical migratory birds: Are we missing the forests for the trees? Wildlife Society Bulletin. 25(3):647–652.

Weil, R.R., and N.C. Brady. 2008. The Nature and Properties of Soils. United Kingdom: Prentice-Hall.

Wilhite, L.P., and J.R. Toliver. 1990. Baldcypress (*Taxodium distichum* [L.] Rich.). In Silvics of North America: 1. Conifers; 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala, 1153–1164. Washington, DC: USDA Forest Service. 877 pages.

Williams, B., D. Johns, H. Williams, and W. Ledbetter. 2002. Converting Pine Plantations to Bottomland Hardwood Wetlands: Lessons Learned from a Unique Restoration Effort at The Nature Conservancy Roy E. Larsen Sandyland Sanctuary in Southeast Texas. Ecological Restoration. 20 (2):88-95.

Williston, H.L., F.W. Shropshire, and W.E. Balmer. 1980. Cypress management: a forgotten opportunity. U.S. Department of Agriculture, Forest Service, Washington, DC, USA. Forestry Report SA-FR 8.

Young, P.J., B.D. Keeland, and R.R. Sharitz. 1995. Growth response of baldcypress [*Taxodium distichum* (L.) Rich.] to an altered hydrologic regime. The American Midland Naturalist 133(2): 206–212.

TABLES

Table 5.1: Results of analyses of covariance on growth of tree height and survival post establishment.

		Height		Survival	
Parameter	Effect	*F* value	*Pr* > *F*	*F* value	*Pr* > *F*
Intercept	Species	143.51	0.001	510.37	0.001
Slope	Year	6.23	0.013	268.37	0.001
	Species*Year	12.10	0.001	21.27	0.001
		Estimate	SE	Estimate	SE
Residual	σ^2	146.40	5.84	0.12	0.01

Table 5.2: Descriptive data including mean, standard error, and range of values for the edaphic and irradiance factors observed on the 20 plots across the Green Bayou Wetland Mitigation Bank. Trees were planted in February 2019; soil measurements were recorded in March 2019 and the other measurements were recorded between June and August 2020.

Abiotic factors	Mean	Standard Error	Maximum value	Minimum value
Sand (%)	70.6	3.0	92.4	47.8
Clay (%)	11.6	1.7	25.3	1.3
Silt (%)	17.8	1.5	28.8	5.6
ISF	0.3	0.1	0.5	0.2
DSF	0.3	0.1	0.5	0.1
LAI	1.5	0.1	2.1	1.0
pH	5.7	0.2	7.5	4.2
Litter layer (g/m^2)	771.7	317.1	1456.8	130.1

Abiotic factors were determined as follows: sand, silt, and clay percentages were determined by the Bouyoucos hydrometer method; light availability (estimated as indirect site factor – ISF, direct site factor – DSF, and leaf area index – LAI) by hemispherical photography; and litter layer mass by sampling four 25 × 25 cm quadrants in each plot.

Table 5.3: Correlation coefficients showing effects of edaphic and irradiance variables on the height of baldcypress, loblolly pine, water oak, and water tupelo at Green Bayou Wetland Mitigation Bank, Harris County, TX, U.S.A. Trees were planted in February 2019.

	Baldcypress		Loblolly pine		Water oak		Water tupelo	
	First-year	Third-year	First-year	Third-year	First-year	Third-year	First-year	Third-year
Abiotic factors	*r*	*r*	*r*	*r*	*r*	*r*	*r*	*r*
Sand	0.133^{**}	-0.214^{**}	-0.018^{ns}	-0.315^{ns}	0.089^{ns}	-	-0.052^{ns}	-0.548^{ns}
Clay	-0.197^{**}	0.113^{**}	0.014^{ns}	0.326^{ns}	-0.073^{ns}	-	0.022^{ns}	-0.210^{ns}
Silt	-0.038^{ns}	0.285^{**}	0.022^{ns}	0.257^{ns}	-0.096^{ns}	-	0.078^{ns}	0.609^{ns}
pH	-0.213^{**}	0.059^{ns}	0.108^{**}	-0.041^{ns}	-0.084^{ns}	-	0.010^{ns}	-0.150^{ns}
ISF	0.039^{ns}	0.239^{**}	-0.133^{**}	0.303^{ns}	0.124^{**}	-	0.204^{**}	0.607^{ns}
DSF	-0.124^{**}	-0.037^{ns}	-0.055^{ns}	0.075^{ns}	0.024^{ns}	-	-0.004^{ns}	0.284^{ns}
LAI	0.013^{ns}	-0.200^{**}	0.056^{ns}	-0.013^{ns}	-0.112^{**}	-	-0.183^{**}	-0.604^{ns}
Litter layer (g/m^2)	-0.006^{ns}	-0.546^{ns}	-0.122^{**}	-0.316^{ns}	-0.045^{ns}	-	-0.113^{**}	-0.575^{ns}

** and ^{ns} indicate $P \leq 0.10$ and $P > 0.10$, respectively. Abiotic factors were determined as follows: sand, silt, clay percentages were estimated by the Bouyoucos hydrometer method; light availability (estimated as indirect site factor – ISF, direct site factor – DSF, and leaf area index – LAI) were estimated by hemispherical photography; and litter layer mass by sampling four 25 × 25 cm quadrants in each plot.

FIGURES

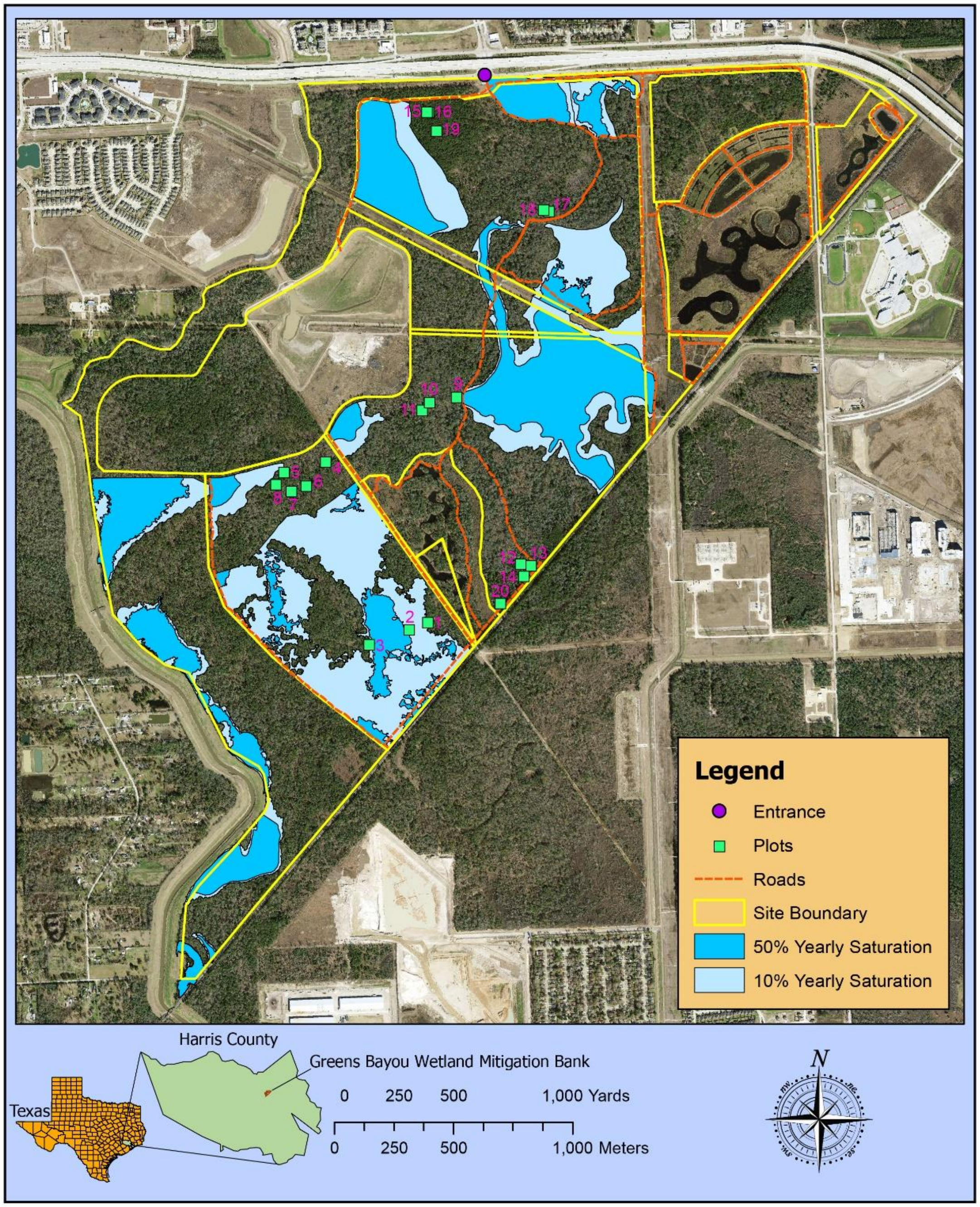

Figure 5.1: Plots located in Greens Bayou Wetland Mitigation Bank (GBWMB). Twenty plots were installed for a field study identifying the main factors contributing to seedling survival and growth at different sections of GBWMB at Harris County, Texas, 2019–2021.

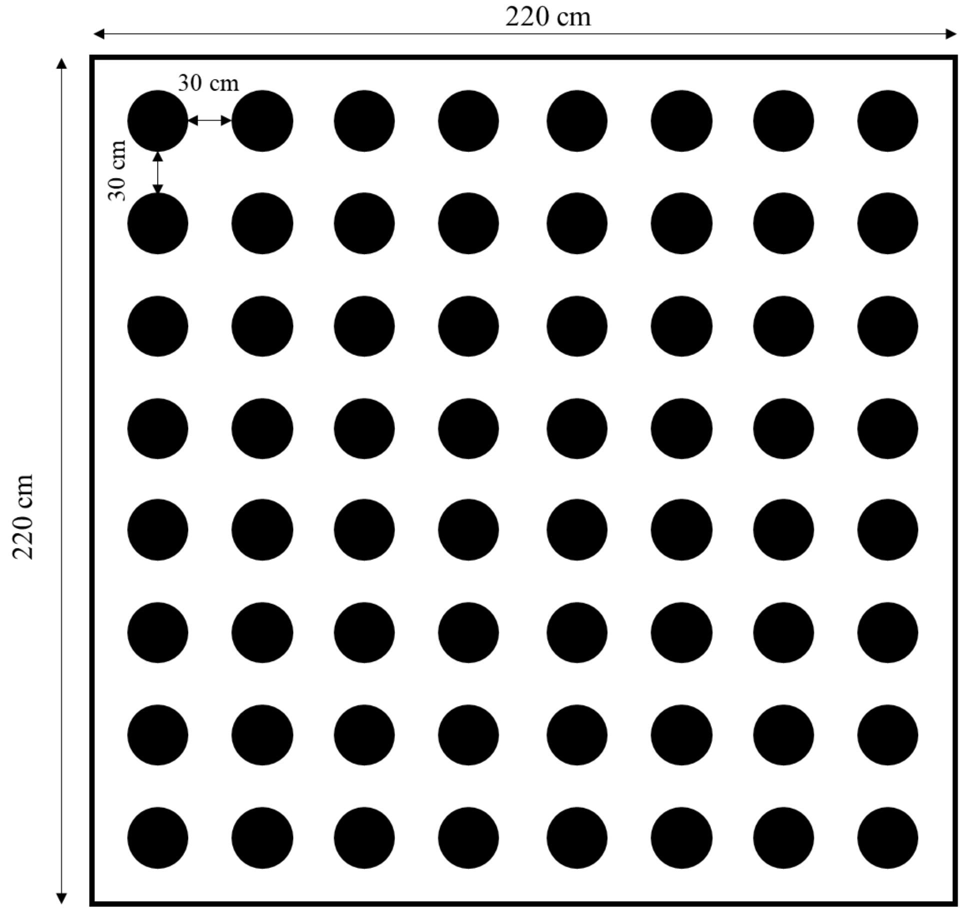

Figure 5.2: Schematic showing what plots look liked at the Green Bayou Wetlands Mitigation Bank in Harris County, TX, U.S.A. Seedlings were planted in February 2019.

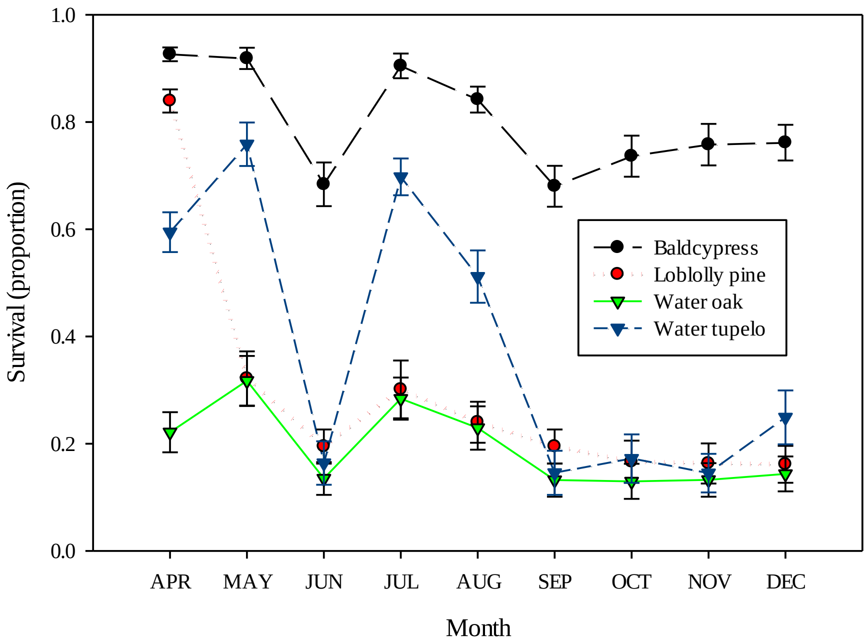

Figure 5.3: Survival proportion during the first year after planting of baldcypress, loblolly pine, water oak, and water tupelo across the Green Bayou Wetlands Mitigation Bank in Harris County, TX, U.S.A. Seedlings were planted in February 2019. The drop and increase in survival was a result of seedlings that resprouted after top-kill or seedlings that were incorrectly called dead and later leafed out.

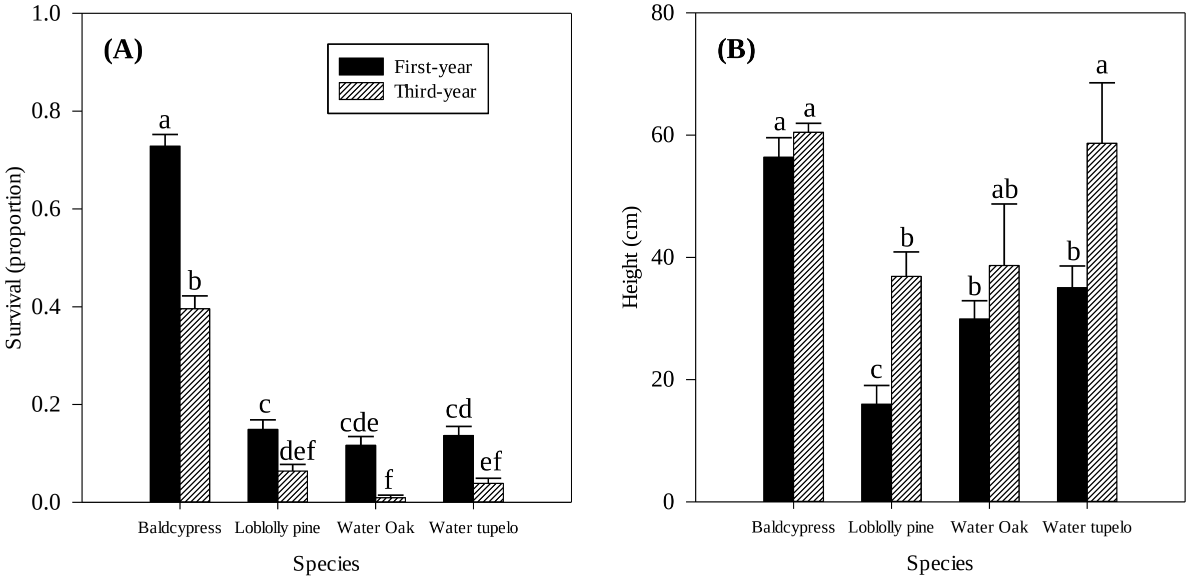

Figure 5.4: Comparison of the mean (**A**) survival and (**B**) height of baldcypress, loblolly pine, water oak, and water tupelo during the first-year (solid bar) and third-year (striped bar) post establishment at Green Bayou Wetlands Mitigaation Bank in Harris County, TX, U.S.A. Seedlings were planted in February 2019. Letters indicate significantly different means ($P < 0.01$) within species in the same year.

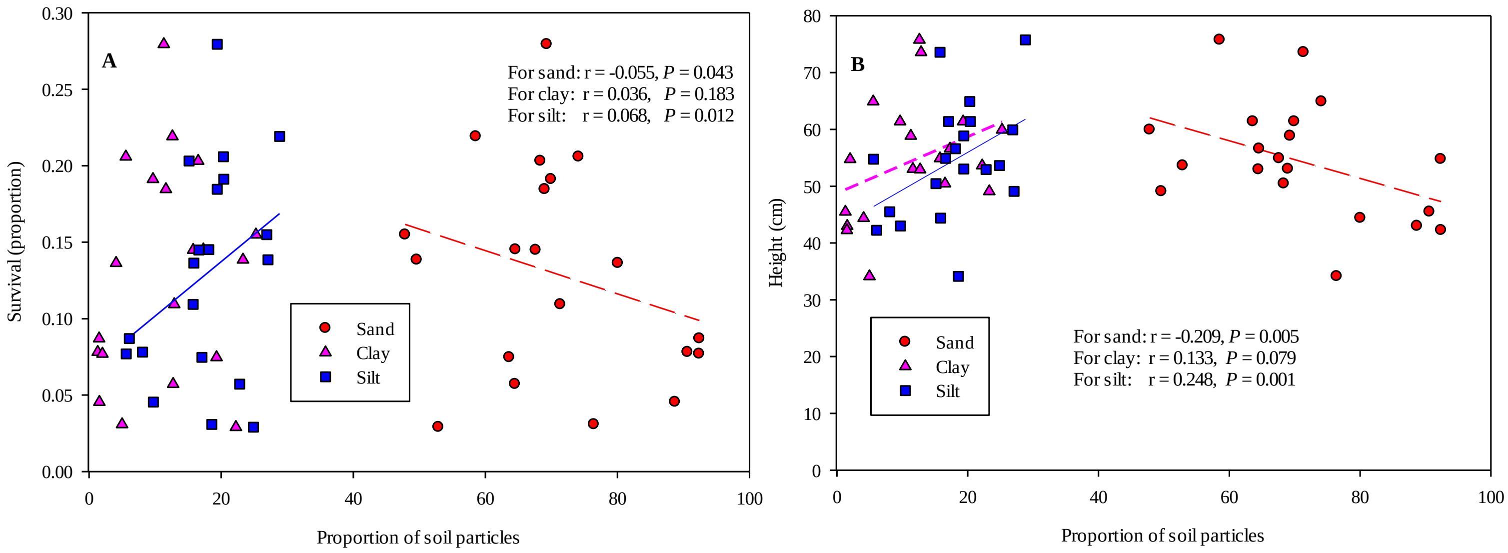

Figure 5.5: The effect of soil particles on third year tree (**A**) survival and (**B**) height at the Green Bayou Wetland Mitigation Bank, Harris County, TX, U.S.A. Trees were planted in February 2019. The proportion of sand, silt, and clay were estimated using the Bouyoucos hydrometer method. Data points represent mean height and survival values from the 20 plots installed. Regression lines are included where the trend is significant ($P < 0.10$).

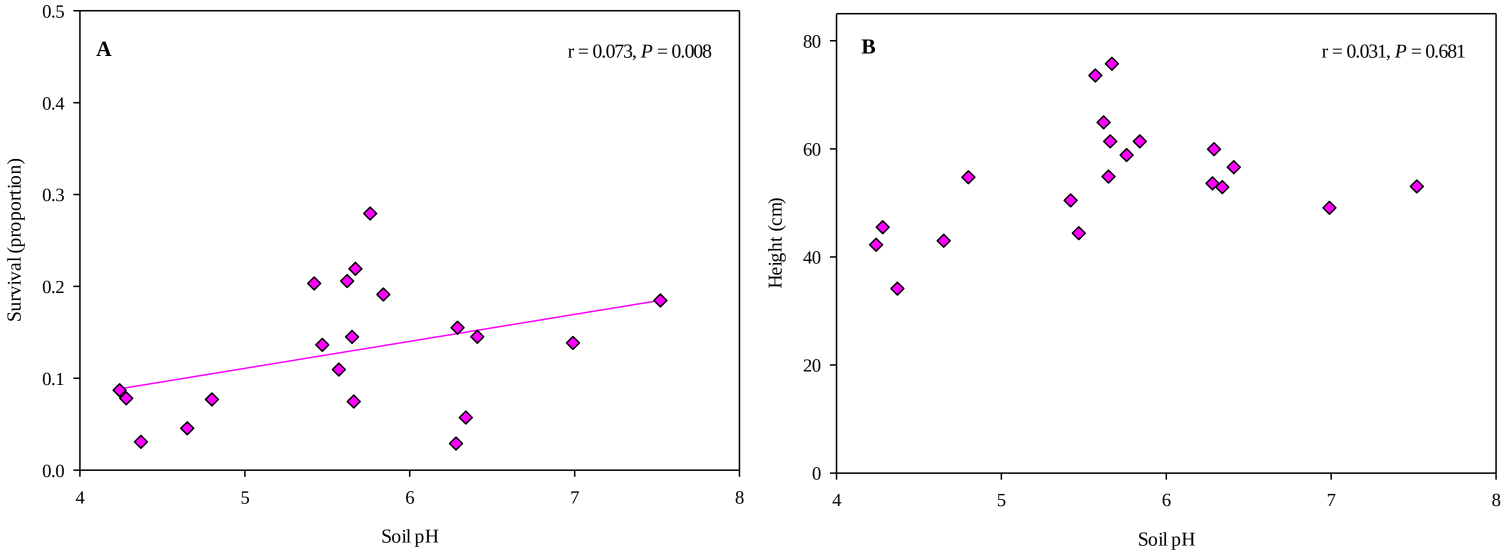

Figure 5.6: The effect of soil pH on third year tree (**A**) survival and (**B**) height at the Green Bayou Wetland Mitigation Bank, Harris County, TX, U.S.A. Trees were planted in February 2019. Soil pH was measured with a pH meter. Data points represent mean height and survival values from the 20 plots installed. Regression lines are included where the trend is significant ($P < 0.10$).

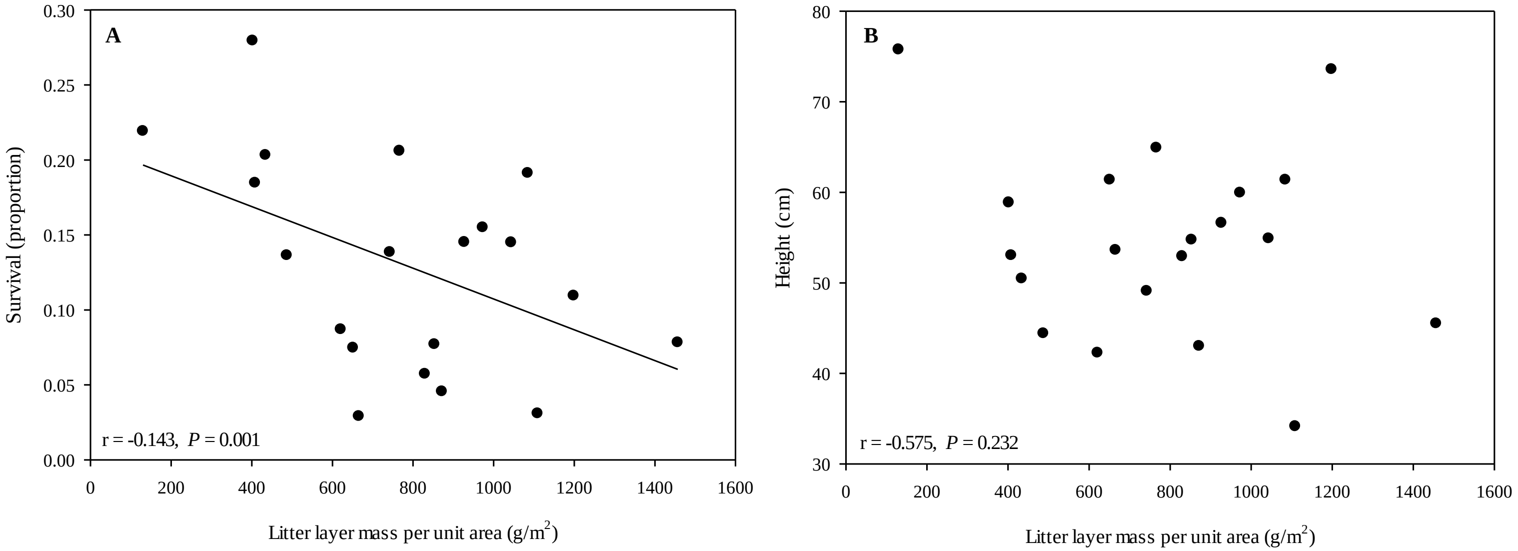

Figure 5.7: The effect of litter layer mass per unit area on third year tree (**A**) survival and (**B**) height at the Green Bayou Wetland Mitigation Bank, Harris County, TX, U.S.A. Trees were planted in February 2019. Litter layer mass was estimated by sampling four (25 × 25 cm) randomly selected quadrants in across the 20 plots. Data points represent mean height and survival values from the 20 plots installed. Regression lines are included where the trend is significant ($P < 0.10$).

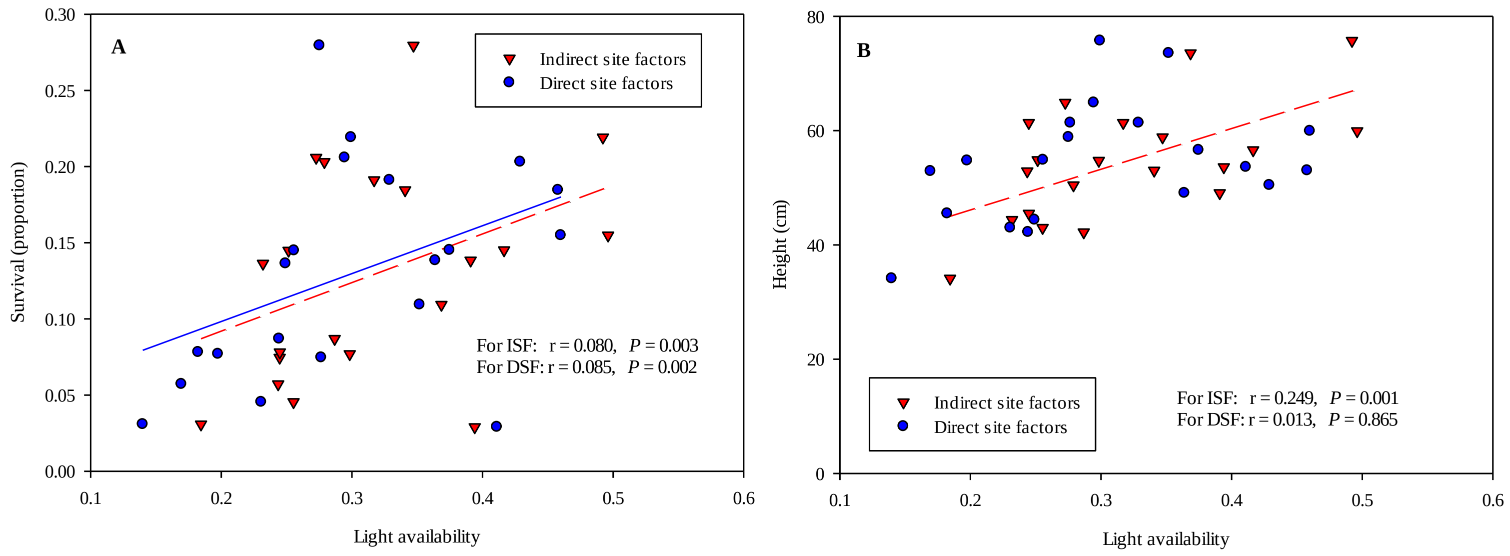

Figure 5.8: The effect of light availability on third year tree (**A**) survival and (**B**) height at the Green Bayou Wetland Mitigation Bank, Harris County, TX, U.S.A. Trees were planted in February 2019. Indirect site factor and direct site factor were estimated using hemispherical canopy photography. Data points represent mean height and survival values from the 20 plots installed. Regression lines are included where the trend is significant ($P < 0.10$).

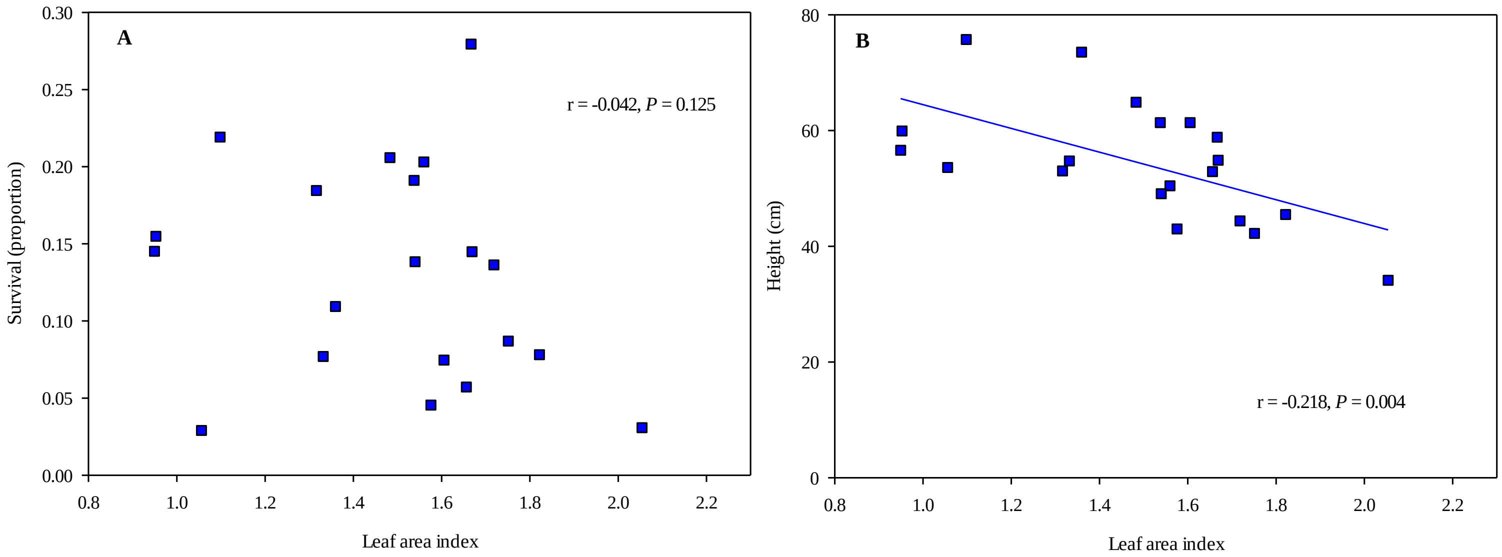

Figure 5.9: The effect of leaf area index on third year tree (**A**) survival and (**B**) height at the Green Bayou Wetland Mitigation Bank, Harris County, TX, U.S.A. Trees were planted in February 2019. Leaf area index was estimated using hemispherical canopy photography. Data points represent mean height and survival values from the 20 plots installed. Regression lines are included where the trend is significant (*P* < 0.10).

CHAPTER 6

CONCLUSIONS

Management of invasive plant species requires an integrated pest management plan that incorporates mechanical control techniques, herbicides, and fire (McCormick 2005). Chemical control, such as herbicide spraying, and mechanical removal, such as cutting target stems, are both used to quickly suppress invasive plants. Biological control introduces safe, effective natural enemies (such as invertebrates, vertebrates, and microbes) to reduce density and attenuate the rate of expansion into new habitats (Van Driesche and Bellows 1996; McCormick 2005). This integrated approach reduces an invader's density and cover, but the native community should be restructured with native species to hamper re-establishment. The studies in this dissertation were designed to improve understanding of the restoration of forested ecosystems invaded by the exotic Chinese tallow (*Triadica sebifera* [L.] Roxb.), hereafter tallow. I reviewed the research on the growth, survival, and competitiveness of tallow and tree species native to the southeastern United States. Based on this synthesis, I was able to identify current knowledge gaps in tallow invasion ecology. I attempted to fill knowledge gaps about the effects of promoting the regeneration of functionally similar native species as a control mechanism for tallow during the stand initiation stage. This was attempted by investigating the growth, survival, performance, and competitiveness of tallow in competition with native hardwood species across a gradient of flooding and light treatments representative of floodplain growth conditions. I also investigated the growth and survival of selected native species across a bottomland hardwood forest.

Investigating the structure and dynamics of plant communities that can resist reestablishment by tallow after its removal can advance knowledge of the traits of native species that confer resistance to invasion and the ecological conditions of communities that favor reduced susceptibility to invasion. According to the principle of limiting similarity, there is a finite limit to the similarity in resource use between coexisting species and thus invasive species will be unlikely to establish if there are native species with similar traits present in the resident community (Funk et al. 2008). In the floodplain forests of the southeastern United States, tallow frequently coexists with water tupelo (*Nyssa aquatica* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and sugarberry (*Celtis laevigata* Willd; Ajala et al. 2022). I investigated the changes in morphological and physiological traits of tallow in competition with these native species, as well as the changes in morphological and physiological traits of each native species, in a greenhouse experiment. While tallow had faster growth rates when young and was more resistant to competition at both stand and landscape scale, this study examined tallows growth, survival, and physiological responses of tallow in competition with native hardwood species under a range of flooding and light-availability conditions representative of natural conditions in floodplain forests. There were four light and flooding treatments: flooded and high irradiance (FH), flooded and low irradiance (FL), nonflooded and high irradiance (NH), and nonflooded and low irradiance (NL). FH represented a frequently flooded floodplain site lacking a forest overstory, FL represented a frequently flooded floodplain site with a shaded overstory, NH represented a well-drained floodplain site lacking a forest overstory, and NL represented a well-drained floodplain site with a shaded overstory. In NH, tallow had lower growth metrics when grown with green ash, with no discernable decrease in green ash growth metrics except for growth rate. Tallow, on the other hand, had higher growth metrics when grown with water tupelo and sugarberry, while the two native species had significant decreases in the growth metrics. The results showed that the growth metrics of the early recruitment stages of tallow in well-drained sites lacking forest overstory will differ greatly among species.

The findings of this study contributed to a better understanding of the role of replacement control as a potential means of preventing the reestablishment of tallow in areas prone to tallow invasion. Native species will have a significant impact on tallow’s growth after the invader has been suppressed by mechanical removal or chemical control if they are matched to the proper growth conditions. Future management decisions should focus on the regeneration of native tree species with similar functional traits, which will initially suppress growth and eventually outcompete tallow.

Invasive ecotypes of tallow are generally more phenotypically plastic than native ecotypes and native species (Siemann and Rogers 2003). However, native communities with functional similarities to tallow might confer increased resistance to invasion through direct competition for resources. For example, mature oaks in east Texas' floodplain forests may be able to competitively exclude tallow (Camarillo et al. 2015), whereas sweetgum and slash pine in South Carolina's marine forests may maintain long-term dominance over the invader (Pile et al. 2019). In a second greenhouse experiment, I investigated the growth and dominance of tallow in three different community types (native, invasive, and mixed) across a range of flooding and light-availability conditions. The native community consisted of interplanting only native species, including water tupelo, sugarberry, green ash, and baldcypress (*Taxodium distichum* [L.] Rich) seedlings. The invasive community consisted of only tallow seedlings while the mixed community included a mixture of native species and the invader. Only native species communities responded positively to flooded/high irradiance and non-flooded/high irradiance treatments with high total biomass and growth rates, respectively. The mixed community reduced tallow growth rate in the flooded/low irradiance treatment but increased tallow leaf area and leaf biomass in the non-flooded/high irradiance treatment. The study demonstrated that establishing a native community may be a feasible and long-term method of suppressing tallow growth and explains why tallow is more likely to invade low and flat areas near water bodies and roads but less likely to invade mature forest stands where artificial regeneration through seedling planting is used.

The relative interaction index (RII; Armas et al. 2004) was used in the third greenhouse experiment to investigate the competitive ability of tallow, green ash, baldcypress, sugarberry, and water tupelo. This was achieved by examining the competitive interactions of native species growing with tallow (effect of natives as competitors) and competitive interactions of tallow growing with native species (effect of competition on natives). Regarding the impact of native competition, my findings suggest that the effects of native species on tallow were not significantly different from zero, implying that they neither competed with nor aided tallow growth. This implies that, at the individual level and an early stage of recruitment, none of the selected native species have the potential to displace or resist tallow competition. Regarding the impact of the invader, tallow had a non-significant negative impact on baldcypress, but sugarberry had a significant negative impact on baldcypress. This implies that sugarberry would suppress baldcypress growth more than tallow would during the early stages of recruitment in the understory. Tallow had a non-significant negative impact on green ash, whereas baldcypress had a significant negative impact. This implies that the baldcypress would suppress the growth of green ash more effectively than the invader. On an individual basis, native species may not significantly impact tallows growth but the presence of a viable native community may suppress the invader's growth.

Although controlled greenhouse experiments provide valuable information, they are frequently limited in scope and may fail to capture the many factors that influence regeneration success and succession in floodplain forests. In natural ecosystems, regeneration occurs in a multidimensional space characterized by complex scenarios in which irradiance, flooding, herbivory, root competition, disease, and the occurrence of drought are all factors influencing regeneration success (Lin et al. 2004).

In a bottomland hardwood forest, I investigated how microenvironmental site conditions affect the establishment and survival of one-year-old bare-root planting stock. Specifically, I examined the growth and survival of an evergreen (*Pinus taeda* L.) and three deciduous species (*Quercus nigra* L., *Nyssa aquatica* L., and *Taxodium distichum* L.) across the Green Bayou Wetland Mitigation Bank in Harris County, TX. Across the property, 20 plots of 220 × 220 cm were installed, where 64 seedlings (16 seedlings per species) were planted on a 60 by 60 cm spacing. The aboveground (light availability) and belowground (soil textural and chemical characteristics) environments were characterized for each plot. Survival ranged from 0.01% (in water oak) to 39.60% (in baldcypress) at the end of the experiment. Feral hogs (*Sus scrofa*) may have caused significant mortality by uprooting stems with consumed rootstocks. Although baldcypress had the highest survival rates after planting, only loblolly pine and water tupelo showed a significant increase in tree heights between establishment and final measurements. Both the leaf area index and the proportion of clay and silt in the soil were significantly but weakly related to tree height. Tree survival was found to be weakly related to pH, litter layer mass, and the direct and indirect site factors.

Overall, the studies conducted in this dissertation improved our understanding of the effects of promoting the regeneration of functionally similar native species as a tallow control mechanism during the stand initiation stage. Furthermore, by conducting greenhouse experiments, I was able to fill some of the current knowledge gaps in tallow invasion ecology. The information provided here may be useful to land managers attempting to restore tallow-infested forested ecosystems.

LITERATURE CITED

Ajala, O.O., K.R. Kidd, B.P. Oswald, Y. Weng, and J.P. Stovall. 2022. Response of Chinese Tallow (*Triadica sebifera*) and Coexisting Natives to Competition, Shade, and Flooding. Forest Science. 68(1):17–26.

Armas, C., R. Ordiales, and F.I. Pugnaire. 2004. Measuring plant interactions: a new comparative index. Ecology. 85(10):2682–2686.

Camarillo, S.A., J.P. Stovall, and C.J. Sunda. 2015. The impact of Chinese tallow (*Triadica sebifera*) on stand dynamics in bottomland hardwood forests. Forest Ecology and Management. 344, 10–19.

Funk, J.L., E.E. Cleland, K.N. Suding, and E.S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution. 23(12):695–703.

Lin, J., P.A. Harcombe, M.R. Fulton, and R.W. Hall. 2004. Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas. Oecologia. 139(3): 399-407.

McCormick, C.M. 2005. Chinese tallow management plan for Florida. Florida Exotic Pest Plant Council, Chinese Tallow Task Force.

Pile, L.S., L. Vickers, M. Stambaugh, C. Norman, and G.G. Wang. 2019. The tortoise and the hare: A race between native tree species and the invasive Chinese tallow. Forest Ecology and Management. 445:110-121.

Siemann, E., and W.E. Rogers. 2003. Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. Oecologia. 135:451–457.

Van Driesche, R.G. and T.S. Bellows, Jr. 1996. Introduction of New Natural Enemies: Principles. In: Biological Control. Springer, Boston, MA. https://doi.org/10.1007/978-1-4613-1157-7_8

VITA

Olaniyi Olaoye Ajala was born on December 18, 1990, in Lagos State, Nigeria to Samuel Omoloye Ajala and Bolanle Catherine Ajala. Olaniyi graduated from Staff School, the University of Lagos in 2002, and International School Lagos (I.S.L) in 2007. He received the degree of Bachelor of Science in Zoology from the University of Lagos, Nigeria in 2011. He spent the next two years serving Nigeria through the National Youth Service Corps (N.Y.S.C), during which he taught agricultural science and biology to high school students. In August 2014, he moved to Mount Pleasant, Michigan where he received his Master of Science in Conservation Biology from Central Michigan University in 2016. Following his master's degree, he moved to Nacogdoches, Texas, to attend Stephen F. Austin State University where he completed a Doctor of Philosophy in Forestry in May 2022.

Permanent address: 408 Ginger Bend Dr. Apt 310
Champaign IL 61822-3572

Forest Science

This dissertation was typed by Olaniyi O Ajala