Forest Science, 2022, **68**, 17–26
https://doi.org/10.1093/forsci/fxab046
Advance access publication 9 December 2021
Research Article

Forest Management

Response of Chinese Tallow (*Triadica sebifera*) and Coexisting Natives to Competition, Shade, and Flooding

Olaniyi O. Ajala[1,*], Kathryn R. Kidd[1], Brian P. Oswald[1], Yuhui Weng[1], and Jeremy P. Stovall[1]

[1]Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, Nacogdoches, TX 75962, USA (ajalaoo@jacks.sfasu.edu).
*Corresponding author email: ajalaoo@jacks.sfasu.edu

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 (nonflooded and flooded) regimes. In the nonflooded 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 was in competition 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. Our 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 tree species establishment in areas prone to tallow invasion.

Study Implications: Chinese tallow is a highly invasive tree species in the southeastern coastal states and in this study, we examined the growth and survival of tallow in competition with tree species native to the southeastern coastal states, USA. The growth of tallow differed greatly among native species in well-drained environments lacking forest overstory with lower growth metrics when grown with green ash but higher growth metrics when grown with water tupelo and sugarberry. Following density reduction treatments, we recommend management actions that promote the regeneration of native tree species to occupy the open vegetation canopy and suppress reestablishment of tallow.

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

Chinese tallow tree (*Triadica sebifera* [L.] Roxb.), hereafter tallow, is a medium-sized deciduous tree 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 1,231 m/year (Wang et al. 2011a; Suriyamongkol et al. 2016).

Successful control of tallow requires an integrated pest management 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 suggests 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 integrated pest management plan designed specifically for tallow based on its documented physiology was effective in reducing density (Pile et al. 2017). Mastication in the spring decreased

Received: December 16, 2020. **Accepted:** October 7, 2021

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. Although this integrated approach was effective in reducing tallow cover, an open canopy may foster reestablishment. To prevent reestablishment 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 the 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 floodplain forests where the root system is periodically under water. Seedlings survive flooded conditions by developing new secondary roots that 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 North 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 to 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 reestablishment 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, is insect-pollinated, bird-dispersed, and has a 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 University (SFASU), 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 31°37′ N, long 94°39′ W) on the 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, Louisiana, USA, in early January 2018. All seeds were stored at 3°C–5°C 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°C, eight hours, 59% humidity; night: 20°C, 16 hours, 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 S1).

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 31°12′ N, long 95°23′ 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 prior to 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 green house was 28.5°C (maximum temperature) and 21.2 °C (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:

1. Light treatments: (i) high irradiance: containers received ambient light, representing a lack of forest overstory, indicated by H, and (ii) 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.
2. Flooding treatments: (i) nonflooded: containers were watered daily until water flowed out of the bottom of the container representing a well-drained floodplain site, indicated by N; (ii) pulsed-flooded: containers received the nonflooded 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 was replaced with deionized water to avoid salt accumulations (Butterfield et al. 2004).
3. Competition treatments included pair-wise combinations of intraspecific and interspecific competition were replicated four times, as follows: (i) four seedlings of sugarberry per container; (ii) four seedlings of green ash per container; (iii) four seedlings of water tupelo per container; (iv) four seedlings of tallow per container; (v) two seedlings of sugarberry and two of tallow per container; (vi) two seedlings of green ash and two of tallow per container; (vii) Two seedlings of water tupelo and two of tallow per container.

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), 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. 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 point in time measurements 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 10 a.m. and 2 p.m. 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, Nebraska). Measurements were made with the following chamber conditions: 800 µmol m^{-2} s^{-1} photosynthetic photon flux density (under no shade; Li et al. 2015), 350 µmol m^{-2} s^{-1} Photosynthetic photon flux density (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 nine 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. Seedling height, ground line diameters, and leaf counts were recorded at 15 day intervals from the date that the treatments commenced on June 22, 2018. 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 ten 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 (ratio of root dry mass to leaf and stem dry mass, g g^{-1}) and specific leaf area (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). Because 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, we conducted an ANOVA for each variable followed by a 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. We set the significance level at 5% a priori for all statistical tests. We considered any P value ≤ 0.05 as evidence of significant difference. The following model was used to analyze the effects:

$$y_{\mathrm{ijkl}} = \mu + S_{\mathrm{i}} + L_{\mathrm{j}} + F_{\mathrm{k}} + S_{\mathrm{i}} * L_{\mathrm{j}} + S_{\mathrm{i}} * F_{\mathrm{k}} + L_{\mathrm{j}} * F_{\mathrm{k}} + S_{\mathrm{i}} * L_{\mathrm{j}} * F_{\mathrm{k}} + \varepsilon_{\mathrm{ijkl}}$$

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, $S_{\mathrm{i}}*L_{\mathrm{j}}$, $\mathrm{Si}*F_{\mathrm{k}}$, $L_{\mathrm{j}}*F_{\mathrm{k}}$, and $S_{\mathrm{i}}*L_{\mathrm{j}}*F_{\mathrm{k}}$ 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. $\varepsilon_{\mathrm{ijkl}}$ was random error, which is NID $(0, \sigma^2)$, 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 1, MANOVA, $F = 0.98$, $P > 0.05$) and the physiological variables that were not significantly affected by the interaction (Table 1).

Seedling Survivorship

Out of the 448 seedlings planted, 407 survived to the end of the 134-day experiment (Table 2). Survival was highest in NL, where 98% (110 alive from the 112 planted) of the seedlings survived until the end of the experiment, and 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, we observed 100% survival in all species combinations except for tallow (in interspecific competition with sugarberry) and green ash (Table 2). Sugarberry survival was lowest in FH, with no seedlings surviving to the end of the experiment (Table 2). In NH, seedling survival was at a 100% in all species combinations except for sugarberry in intraspecific competition (Table 2). Seedling survivorship in NL was 100% in all species combination apart from tallow in intraspecific competition (Table 2).

Growth and Morphological Response

The morphological traits examined decreased with low irradiance and increased with high irradiance (Figure 1). Growth rate of the seedlings was highest in NH. In this treatment, stems were tallest with the highest leaf count

Table 1. 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 at ground height (mm)	11.24**	835.34**	4.40*	3.91**	3.02**	41.04**	4.42**
Leaf counts	26.65**	217.97$^{\text{ns}}$	0.08**	17.33**	2.23*	1.49$^{\text{ns}}$	2.37*
Stem growth rate	24.12**	493.02**	1.99$^{\text{ns}}$	3.89**	3.16**	9.54**	4.94**
Biomass and partitioning							
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$^{\text{ns}}$	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$^{\text{ns}}$	3.65**	2.56**	6.23*	2.60*
Stem mass fraction	14.47**	116.66**	0.10$^{\text{ns}}$	8.89**	1.79$^{\text{ns}}$	0.03$^{\text{ns}}$	2.61*
Root mass fraction	9.29**	335.86**	0.30$^{\text{ns}}$	5.86**	2.28*	2.69$^{\text{ns}}$	2.82**
Root: shoot ratio (g g^{-1})	7.70**	245.39**	0.58$^{\text{ns}}$	5.49**	2.14*	2.10$^{\text{ns}}$	2.77**
Leaf area ratio ($\text{cm}^2\ \text{g}^{-1}$)	1.82$^{\text{ns}}$	123.29**	16.96**	4.95**	3.22**	9.72**	3.28**
Leaf morphology and structure							
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$^{\text{ns}}$	15.81**	2.63*
Leaf area (cm^2)	8.49**	112.00**	10.36**	6.07**	2.16*	23.45**	3.77**
Specific leaf area ($\text{m}^2\ \text{kg}^{-1}$)	2.16*	38.85**	10.30**	4.06**	3.07**	3.82$^{\text{ns}}$	2.40*
Leaf dry mass per area (g m^{-2})	0.92$^{\text{ns}}$	57.59**	5.19*	1.66$^{\text{ns}}$	1.39$^{\text{ns}}$	0.45$^{\text{ns}}$	0.98$^{\text{ns}}$
Gas exchange							
P_n (μ mol $\text{m}^{-2}\ \text{s}^{-1}$)	2.81**	249.69**	59.95**	5.87**	1.82$^{\text{ns}}$	56.07**	1.98$^{\text{ns}}$
G_s (m mol $\text{m}^{-2}\ \text{s}^{-1}$)	7.29**	10.18**	25.04**	5.25**	1.72$^{\text{ns}}$	58.27**	0.28$^{\text{ns}}$
C_i (μ mol mol^{-1})	9.38**	269.12**	0.72$^{\text{ns}}$	4.87**	7.29**	1.98$^{\text{ns}}$	1.80$^{\text{ns}}$
T_r (μ mol $\text{m}^{-2}\ \text{s}^{-1}$)	12.12**	8.44**	14.91**	7.23**	3.24**	41.37**	1.13$^{\text{ns}}$
WUE (μ mol CO_2/m mol H_2O)	5.92**	197.46**	8.27**	4.94**	2.27*	4.72*	1.15$^{\text{ns}}$

F test: *, **, and ns indicate $P \leq 0.05$, $P \leq 0.01$, and $P > 0.05$, respectively. P_n, net photosynthetic rate; G_s, stomatal conductance; C_i, intercellular carbon dioxide; T_r, transpiration rate; WUE, water-use efficiency.

Table 2. 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 treatment	Light treatment	Competition type	Competition treatment	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	81.25
			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	93.75
			Sugarberry only	100
			Water tupelo only	100
Nonflooded	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

and leaf area (Figures 1A–E). Seedling biomass also increased in this treatment, with seedlings producing the largest biomass in NH and the lowest in FL (Figure 1F). LMF was highest in NL, intermediate in FH, and lowest in FL and NH (Figure 1G). SMF was also highest in NL, intermediate in the high irradiance treatments, and lowest in FL (Figure 1H). The highest RMF value was observed in high irradiance, whereas the lowest was in FL (Figure 1I). Root shoot ratio decreased with decreasing light, with the lowest values in FL (Figure 1J).

Gas Exchange Response

The results of 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 1K and O). There was a significant difference in WUE in FL and NL (Figure 1O). G_s was highest in NH, intermediate in FL, and lowest in FH and NL (Figure 1L). C_i increased with decreasing irradiance and was lowest in the FH and NH, with a significant difference between both treatments (Figure 1M). T_r was highest in NH, with

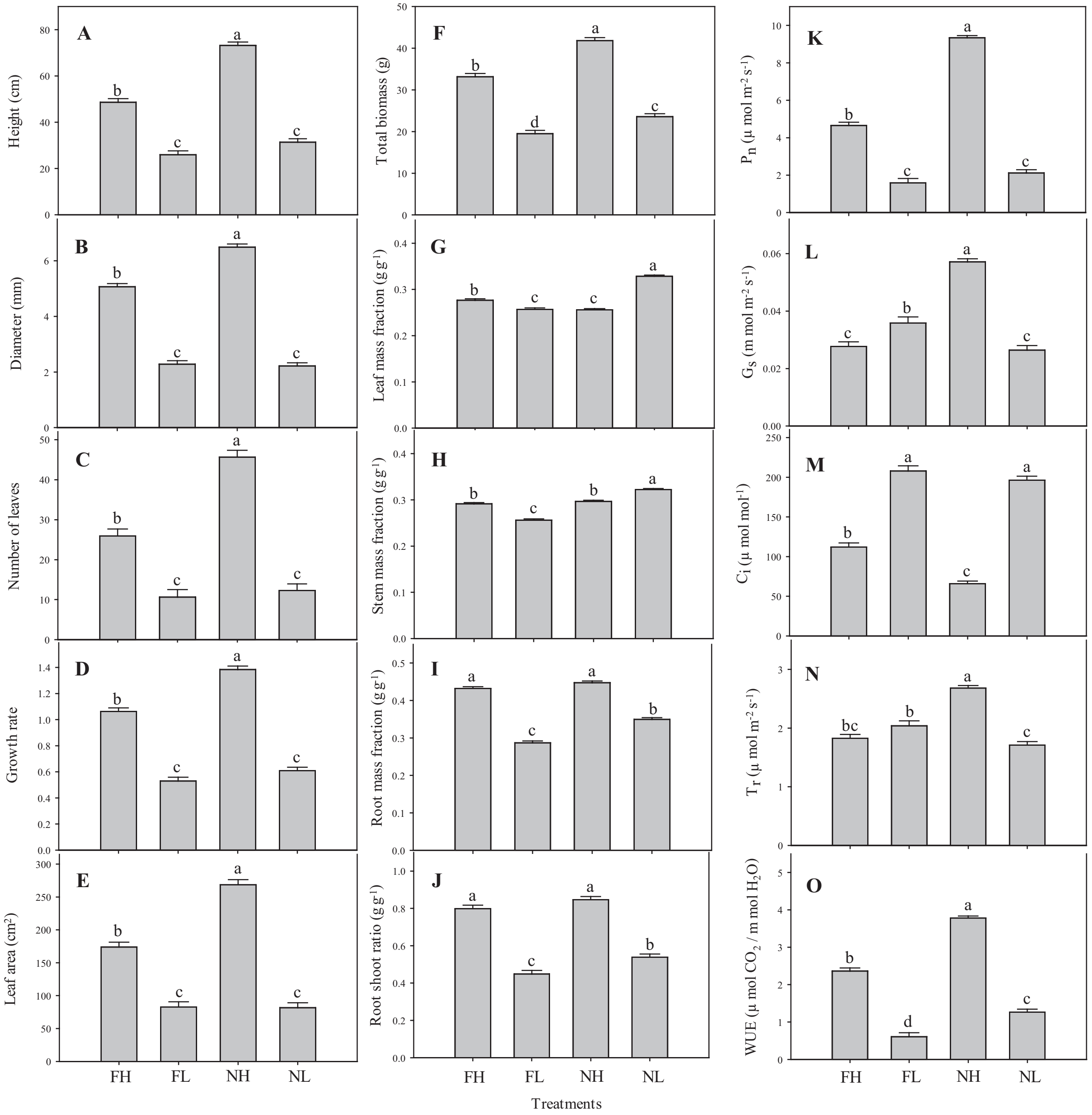

Figure 1. Comparisons of the seedlings traits among the different flooding and light treatments at the end of the experiment. The traits include (A) height, (B) ground diameter, (C) number of leaves, (D) growth rate, (E) leaf area, (F) total biomass, (G) leaf mass fraction, (H) stem mass fraction, (I) root mass fraction, (J) root-shoot ratio, (K) net photosynthetic rate (P_n), (L) stomatal conductance (G_s), (M) intercellular carbon dioxide (C_i), (N) 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, flooded and high irradiance treatment, FL, flooded and low irradiance treatment, NH, nonflooded and high irradiance treatment, NL, nonflooded and low irradiance treatment.

significant difference between FL and NL but no difference between FH, and NL (Figure 1N).

Response to Competition

Morphological variables varied in response to competition across the different treatments (Figure 2; Figure S1). Among the native species growing in intraspecific competition, water tupelo seedlings were tallest in FH, whereas sugarberry was the tallest in NH and NL (Figure 2; Figure S1 A). There was no significant difference in seedling height, ground diameter, number of leaves, and leaf area in FL (Figure 2D; Figures S1 A, S1 B, S1 C, and S1 D). Competition with the native species affected the ground diameter of tallow in NH (Figure 2A; Figure S1 B). 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 S1 B). 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 2A; Figure S1 B). Sugarberry had

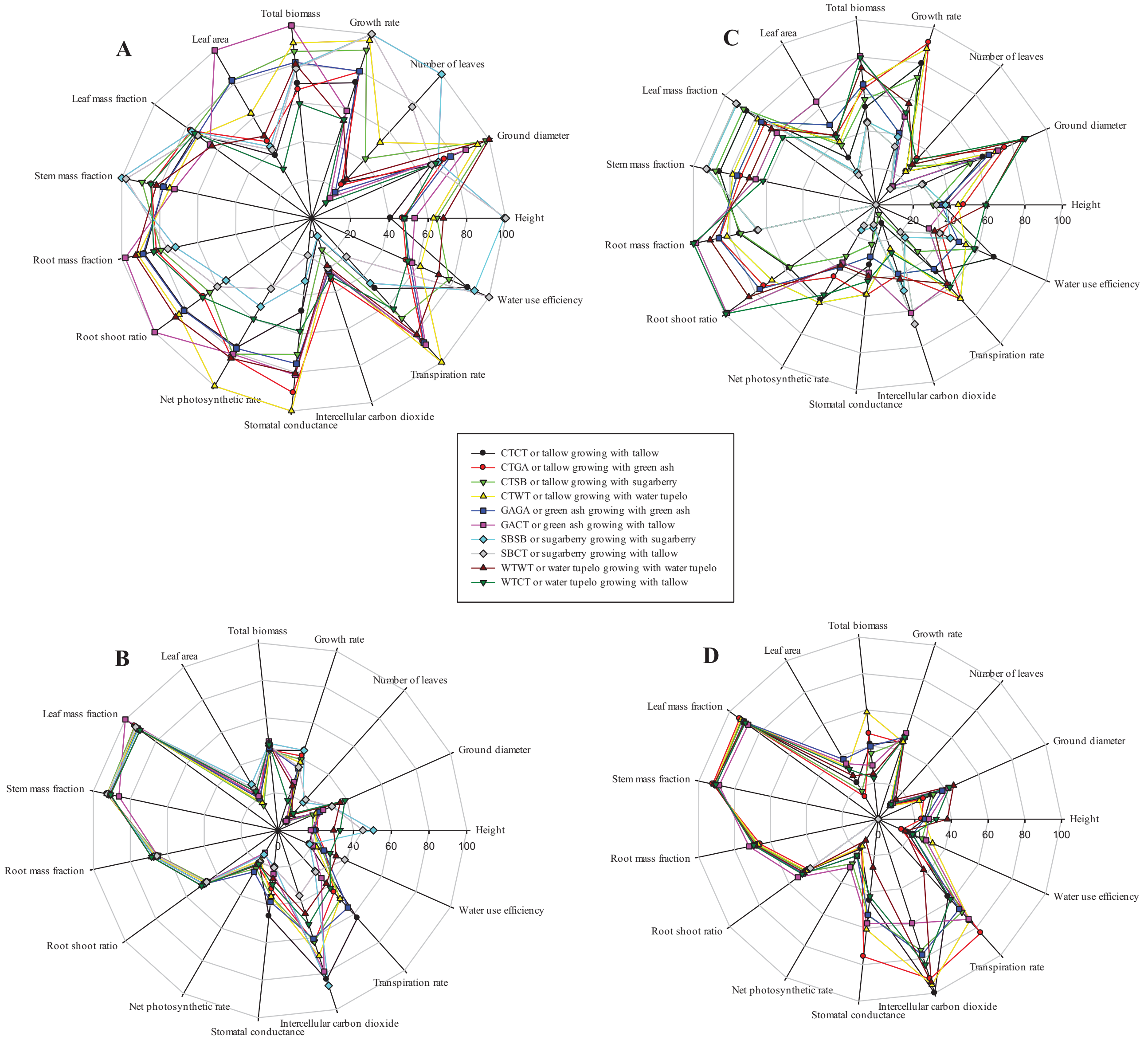

Figure 2. Radar plots showing the morphological, biomass, and gas exchange traits of seedlings under the different light and flooding treatments: (A) NH, nonflooded high irradiance, (B) NL, nonflooded low irradiance, (C) FH, flooded high irradiance, and (D) FL, flooded low irradiance. Variables were scaled to a percent scale by setting the maximum value for each variable equal to 100%.

the highest leaf count in NH, and tallow produced more leaves in competition with sugarberry and water tupelo in the same treatment (Figure S1 C). There was no significant difference in the number of leaves and leaf area in FH, FL, and NL (Figures S1 C and S1 D). Among the native species, green ash had the highest leaf area in NH (Figure S1 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 S1 D). In FH, interspecific competition did not affect the growth rate of any of the species and tallow had the highest growth rates in intraspecific competition (Figure 2C; Figure S1 E). Among the native species in FL, green ash and sugarberry had the highest growth rates, and water tupelo had the lowest growth rates (Figure 2D; Figure S1 E). Water tupelo seedlings were on the 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 S1 E). Green ash was the only native species to experience reduction in growth rate when in competition with tallow in NH (Figure S1 E).

Total biomass of the selected native species was not affected by competition across the NH treatment (Figure 2A; Figure S2 A). In NH, 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 2A; Figure S2 A). There was no significant difference in seedling total biomass in FL and NL (Figure S2 A). There was also no significant difference in LMF and SMF in NL and FL (Figure 2B and D; Figures S2 B and S2 C). Sugarberry also had the highest SMF among the native species in NH (Figure 2A; Figure S2 B). We also observed no significant differences in RMF in FL, NH, and NL (Figure 2B–D; Figure S2 D). There was no significant difference in root-shoot ratio in NL and FL (Figure 2B and D; Figure S2 E). Among the native species in NH, green ash had the highest root-shoot ratio under interspecific competition with tallow (Figure 2A; Figure S2 E).

With the gas-exchange parameters, there was no significant difference between P_n, G_s, and *WUE* in FH, FL, and NL (Figure 2B–D; Figures S3 A, S3 B, and S3 E). 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 2A; Figure S3 A). Tallow had its lowest G_s value under intraspecific competition in NH, but G_s increased in competition with native species (Figure 2A; Figure S3 B). 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 2A; Figure S3 B). In NL and FH, C_i of green ash was lower under intraspecific competition but higher under interspecific competition with tallow (Figure 2B and C; Figure S3 C). In NL, C_i of sugarberry was lower under interspecific competition (with tallow) and higher intraspecific competition (Figure S3 C). Unlike sugarberry, C_i of green ash was lower in intraspecific competition but higher in interspecific competition (Figure 2A; Figure S3 C). Among the native species in interspecific competition, green ash had the highest C_i in FH (Figure 2C; Figure S3 C). There was no significant difference in C_i in FL and NH (Figure S3 C). Sugarberry had the lowest T_r among native species under intraspecific competition in NH (Figure 2A; Figure S3 D). In NH and FL, T_r of tallow was lowest under intraspecific competition but significantly higher under interspecific competition (Figure 2A and D; Figure S3 D). Among the native species under interspecific competition, water tupelo had the lowest T_r in FL and sugarberry had the lowest T_r in NH (Figure 2D; Figure S3 D). There was no significant difference in WUE in NL and FL (Figure 2A and D; Figure S3 E). Among the native species in NH, sugarberry had the highest WUE in both intraspecific and interspecific competition (Figure 2A; Figure S3 E).

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, we 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 nonflooded and high irradiance treatment (NH) attempted to simulate 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 significant decrease in the growth metrics of the two native species. Although 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 recruitment of invasive vines and perennials (Li et al. 2012, 2015). Similarly, the competitive advantages of invasive tree species could be diminished with fast-growing native tree species (Pile et al. 2019; Lázaro-Lobo et al. 2021). 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). Our 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 nonflooded 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 suggests 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, and ground diameter, tallow seedlings exhibited modest growth in shade conditions, but we observed superior competitive ability of the invasive in full light conditions.

Changes in growth metrics relative to competition underpins 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 was in competition with sugarberry and water tupelo than when tallow was in competition with green ash and itself. By contrast, the ground diameter of water tupelo decreased when the native was in competition with tallow as compared with growth in intraspecific competition. Similarly, tallow stems had higher growth rates when in competition with sugarberry and water tupelo than 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 with 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 the ability to spread its crown over a larger area due to the formation of large branches with greater number of leaves, Competition for light with tupelo may have resulted in the 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 use 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 include rapid growth rates and overall larger sizes at the early life stages when compared with 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 cooccurring 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. We observed these advantages only in the absence of shade and flooding.

For bottomland species, tolerance of light and flooding often influences growth and survival (Lin et al. 2004). 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 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.

In conclusion, we have demonstrated that tallow may be less competitive with certain native species. Replacement control through planting of functionally similar native species may be a potential means of preventing tallow from establishing or reestablishing in areas prone to tallow invasion. Further studies should 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.

Supplementary Material

Supplementary material is available at *Forest Science* online.

Acknowledgments

We would like to acknowledge Harris County Soil and Water Conservation District; Harris County Flood Control District; Arthur Temple College of Forestry and Agriculture at Stephen F. Austin State University; National Institute of Food and Agriculture, U.S. Department of Agriculture, McIntire Stennis project (226427) for providing funding for this study.

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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.* USDA Forest Service, Southern Research Station, Asheville, NC.

Burns, R.M., and B.H. Honkala. 1990. *Silvics of North America.* Washington, DC: USDA Forest Service, Agriculture handbook.

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. *Tex. J. Sci.* 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. *Biol. Invas.* 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*). *Invas. Plant Sci. Manage.* 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 Ecol. Evol.* 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. *J. Appl. Ecol.* 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). *Biol. Invas.* 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. *Am. Nat.* 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 Physiol. Plant.* 35(4):1149–1159.

Hook, D.D., and C.L. Brown. 1973. Root adaptations and relative flood tolerance of five hardwood species. *For. Sci.* 19(3):225–229.

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

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

Johnson, R.L. 1990. Water tupelo (*Nyssa aquatica*). P. 474–478 in *Silvics of North America: 1. Conifers; 2. Hardwoods*, Burns, R.M., and B.H. Honkala (eds.). USDA Forest Service, Washington, DC. 877 p.

Jones, R.H., and K.W. McLeod. 1989. Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. *Bull. Torrey Bot. 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. *For. Sci.* 36:851–862.

Jones, R.H., and R.R. Sharitz. 1990. Effects of root competition and flooding on growth of Chinese tallow tree seedlings. *Can. J. For. Res.* 20(5):573–578.

Kennedy, H.E. 1990. Green Ash (*Fraxinus pennsylvanica*). P. 348–354 in *Silvics of North America: 1. Conifers; 2. Hardwoods.* Burns, R.M., and B.H. Honkala (eds.). USDA Forest Service, Washington, DC. 877 p.

Krajicek, J.E., and R.D. Williams. 1990. Hackberry (*Celtis occidentalis*). P. 262–265 in *Silvics of North America: 1. Conifers; 2. Hardwoods.* Burns, R.M., and B.H. Honkala (eds.). USDA Forest Service, Washington, DC. 877 p.

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. *For. Ecol. Manage.* 483:1–9.

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 Ecol. Sin.* 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. *Sci. Rep.* 5:11004.

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.* Gainesville, FL: 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.* USDA Forest Service, Research Note SRS-20, Southern Research Station, Asheville, NC.

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. *J. For.* 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. *For. Ecol. Manage.* 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. *J. Ecol.* 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. *Southeast. Nat.* 15(sp9):68–75.

Wang, G.B., and F.L. Cao. 2012. Formation and function of aerenchyma in bald cypress (*Taxodium distichum* (L.) Rich.) and Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) under flooding. *South Afri. J. Bot.* 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. *Divers. Distrib.* 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. *Ecol. Appl.* 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? *Invas. Plant Sci. Manage.* 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 Physiol. Plant.* 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. *Restor. Ecol.* 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: The U.S. Department of Agriculture (USDA), 1–174 p.