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Size-dependent patterns of reproductive investment in the North American invasive plant species Triadica sebifera (L.) Small (Euphorbiaceae)

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Size-dependent patterns of reproductive investment in the North American invasive plant species *Triadica sebifera* (L.) Small (Euphorbiaceae)

A Thesis

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
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Master of Science
in
Biological Sciences

by

Courtney Hymel Babin

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Abstract

Knowledge of sex allocation trade-offs with tree growth in insect-pollinated woody plants is limited, particularly in invasive plants. This study examined patterns of growth and reproductive investment in a North American invasive plant species, *Triadica sebifera*, I hypothesized that the energy limitations of smaller trees may result in the production of more male reproductive structures that are energetically less costly. Diameter at breast height was a significant predictor of seed and catkin mass and regression can describe these relationships across sites. Seed and catkin mass were positively correlated across sites. The relationship between the seed mass:catkin mass ratio and DBH was not significant, nor was seed mass:catkin mass and total investment. Results showed a significant positive relationship between total reproductive investment and tree size across sites. Seed mass:catkin mass ratio and reproduction investment showed substantial variation among individual trees of similar size within sites.

Triadica sebifera; Chinese tallow; life history theory; invasion ecology; reproductive strategy; sex allocation

Introduction

Life history theory seeks to explain organismal growth, reproduction, and survivorship in an evolutionary and ecological context (Stearns, 1992). With respect to polycarpic plants, traits such as dispersal method, seed number and size, and resource allocation to growth and reproduction are important characters that affect life history strategies (Campbell, 2000; Dorken and Pannell, 2008; Freeman et al., 1980; Freeman et al., 1981; Galen, 2000; Obeso, 2002). The trade-offs presented by resource allocation across multiple life history traits have been the focus of numerous studies attempting to explain variation in fecundity, reproductive development, and behavior (e.g., Bell and Koufopanou, 1986; Bosner and Aarssen, 1996; Knops and Koenig, 2012; Reznick, 1985; Silvertown and Dodd, 1999).

One way plants exhibit trade-offs in resources is through sex allocation, in which resources are differentially afforded to male versus female function in response to growth stage and environmental factors (Charnov, 1982; Charnov and Bull, 1977; Freeman et al., 1976; Freeman et al., 1980; Freeman et al., 1981; Galen, 2000; Obeso, 2002; Weiner et al., 2009). A common pattern seen in angiosperms is the high cost of female reproduction relative to the lower cost of male reproduction (Iwasa, 1991; de Jong and Klinkhamer, 2005), and this may influence allocation to reproduction in plants differing in size and energy stores. Most studies of size-dependent patterns of reproductive investment have focused on herbaceous plants (Barret et al., 1999; Bram and Quinn, 2000; Macnair and Cumbes, 1990; Sandmeier and Dajoz, 1997), while a few have explored sex allocation in wind-pollinated woody species (Fox, 1993; Knops and Koenig, 2012; Ne’eman et al., 2011; Santos-del-Blanco et al., 2012). In studies of dioecious plants, males were significantly more abundant in stressed habitats, suggesting the allocation of resources to less costly male function in disturbed habitats may be beneficial compared to expensive female function (Freeman et al., 1976; Obeso, 2002). Conversely, a study by Ne'eman et al. (2011) of an invasive monoecious wind-pollinated conifer, *Pinus halepensis* (Pinaceae), showed that this short-lived woody conifer invested more in female function than male function at an early age; a shift in reproductive function expected in species with short life spans.

Little is known about the effect of life history characters on sex allocation of insect-pollinated woody tree species, particularly in invasive plants. However, sex allocation is of particular interest in invasive plants because they often devote more resources to sexual reproduction (Burns et al., 2012) and reproduce earlier and at smaller sizes than non-invasive species (Rejmanek and Richardson, 1996; Kolar and Lodge, 2001). Identifying patterns of resource allocation within invasive populations can target those individuals that are exceptional in producing propagules, and ultimately help reduce propagule pressure in an invaded ecosystem.

This study investigates sex allocation of the invasive tree, *Triadica sebifera* (L.) Small (Euphorbiaceae), commonly known as Chinese tallow, which is primarily insect-pollinated (Siemann and Rogers, 2003), protogynous (Bruce et al., 1997), and monoecious. Like many invasive species, Chinese tallow reproduces at an early age and has prolific seed production. Trees may begin reproduction in three years (Scheld et al., 1984) and produce more than 100,000 seeds annually, all of which may be viable (Huang et al., 2012; Renne, 2000).

Chinese tallow was introduced to Georgia and South Carolina in the late 18th century as an ornamental and for cultivation due to the high vegetable oil content of the seeds (Chen et al., 2013). In the early 20th century there was a second introduction of Chinese tallow to Louisiana, Texas, and Florida, initiated by the USDA for the soap making industry (Siemann and Rogers, 2001), after which time it escaped from cultivation and invaded native forests of the southeastern United States (Siemann and Rogers, 2001; Chen et al., 2013). Negative impacts of this tree in its introduced range are well documented (Cameron and Spencer, 1989; DeWalt et al., 2011; Meyer, 2011; Siemann and Rogers, 2001, 2003a, and 2003b). Chinese tallow may reach a height of 15 m within 10 years (Godfrey, 1988) and forms dense monospecific stands that effectively exclude native flora (Siemann and Rogers, 2003a). Chinese tallow has relatively low rates of herbivory compared to native species (Siemann and Rogers, 2003b), and it alters soil nutrient dynamics through rapid leaf decomposition (Cameron and Spencer, 1989). Additionally, it has a high tolerance for drought, flooding, and salinity (DeWalt et al., 2011), giving it a competitive advantage over many native species after a disturbance event (Henkel et al., 2016; Howard, 2012; Meyer, 2011).

To understand the impact of an invasive species on biodiversity and devise effective eradication methods, we must first understand the fundamental aspects of reproduction and growth patterns of the study organism. Negative impacts caused by invasive species like Chinese tallow present significant ecological and economic challenges world-wide (Simberloff, 1996). Control efforts applied to invasive species cost the United States billions of dollars (Pimentel et al., 2005; Zhang et al., 2013), and the detrimental effects of invasive species on ecosystem services require improved management strategies that provide adequate control measures across all life stages. The success of Chinese tallow as an invader appears to be directly related to its high seed production (Siemann and Rogers, 2003b). Understanding these factors that influence investment in reproduction can provide insights into potential control strategies.

In this study, I examined size-dependent patterns of reproductive investment in Chinese tallow in its introduced range in the southeastern United States. Although Chinese tallow can produce seeds at an early age, I hypothesized that smaller trees would be more energy limited than large trees, and would invest significantly more in male than in female reproductive structures compared to larger trees. Trade-offs of sex allocation in plants may be identified using the mass of reproductive structures, since mass is a quantifiable measurement of reproductive investment that may be altered based on available resources (Sandmeier and Dajoz, 1997). I predicted that the total mass of male flowers would exceed that of seeds in small trees, and that investment in seeds relative to catkins would increase with increasing diameter at breast height (DBH). To test this, I measured the total mass of seeds and male catkins of varying sized trees and asked if sex-specific reproductive investment was related to tree size.

Methods

Study sites

Three sites in southeastern Louisiana (Fig. 1) with mature Chinese tallow populations were chosen for this study. Sites appeared to vary in species composition, and flooding occurred at one location during the study, in which the inundation of water lasted several months.

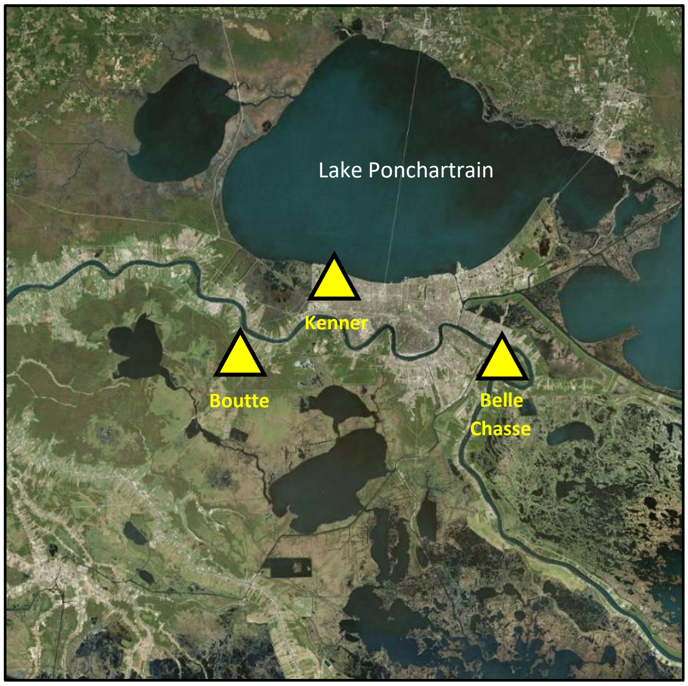

Figure 1: Aerial view of study sites in southeast Louisiana.
(Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community)

The first sampling site was a 5-hectare plot of unmanaged forest in poorly drained soil located in Kenner, Louisiana (Fig. 2). This area was inundated after Hurricane Katrina in 2005 and likely lost a number of salt intolerant native species. It has since become dominated by Chinese tallow with only a few *Quercus* individuals. The understory lacked species diversity as well, containing mostly *Rubus fruticosus* and *Juncus effusus*. The soil is categorized as Kenner muck, drained, which is herbaceous organic material over fluid clayey alluvium (USDA Web Soil Survey, 2016). The site is at sea level with a depth to the water table of approximately 0.3 to 1.2 m (USDA Web Soil Survey, 2016).

Figure 2: Aerial view of Kenner, Louisiana study site.
(Source: USDA Natural Resources Conservation Service, Web Soil Survey, National Cooperative Soil Survey)

The Woodlands Conservancy in Belle Chasse, Louisiana was the second sampling site in this study (Fig. 3). The research area was located within 104 hectares at an elevation of -6 to 0 m (USDA Web Soil Survey, 2016). This is a species-rich location with native canopy trees such as *Quercus virginiana*, *Acer rubrum*, *Magnolia grandiflora*, and *Taxodium distichum*, and an understory containing several species of *Rubus*, *Toxicodendron*, *Iris*, and *Sabal*. The soil at the Woodlands Conservancy is Westwego clay, 0 to 0.5 percent slopes, which is a semifluid clayey alluvium over herbaceous organic material (USDA Web Soil Survey, 2016). The depth to the water table is approximately 0.5 to 0.7 m (USDA Web Soil Survey, 2016).

Figure 3: Aerial view of the Woodlands Conservancy study site in Belle Chasse, Louisiana.
(Source: USDA Natural Resources Conservation Service, Web Soil Survey, National Cooperative Soil Survey)

The third sampling site was located in Boutte, Louisiana on 66 hectares of private property adjacent to prime farmland (Fig. 4). This area is 1 to 4 m above sea level with soil composed of Cancienne silty clay loam, frequently flooded (USDA Web Soil Survey, 2016). The depth to the water table is approximately 0.5 to 1.2 m (USDA Web Soil Survey, 2016). This study site is relatively undisturbed and species rich in flora and fauna. The overstory is composed of several species of *Quercus, Acer, Taxodium, Platanus,* and *Liquidambar*. The understory contains species of *Typha, Cirsium, Rubus, Toxicodendron, Sabal,* and numerous *Pteridophytes*.

Figure 4: Aerial view of Boutte, Louisiana study site.
(Source: USDA Natural Resources Conservation Service, Web Soil Survey, National Cooperative Soil Survey)

Construction and placement of seed and catkin traps

Seed and male catkin traps were constructed from 2.54 cm PVC pipe and mesh window screen (Fig. 5). A 50.8 cm x 50.8 cm PVC square was wrapped with mesh and placed atop 76.2 cm tall PVC legs. Traps were placed with restricted random measures based on the size and direction of the canopy, with one or two traps per tree placed randomly within the canopy cover.

Figure 5: Seed/catkin collection traps.

Data collection

Twelve Chinese tallow trees of varying size classes that bore evidence of previous seed production were selected within each field study site. Each tree was tagged and the GPS coordinates were logged. Measurements of tree height, diameter at breast height (DBH), crown spread, and trap-to-trunk distance were recorded for the 36 trees. The elliptical area of each tree canopy was calculated from the crown spread.

The apetalous female flowers of Chinese tallow contain a three-lobed ovary and three styles, producing capsular fruits which split open to release three wax-coated seeds. Fruits generally ripen from September through October but may remain on a tree through early spring. Immature green capsules were identified on selected study trees in September 2015. Seeds and capsules were collected weekly at all sites from November 2015 through July 2016.

Inflorescences are spicate with reduced pistillate flowers located at the base, leading to numerous clusters of staminate flowers, or male catkins. Flowers typically mature beginning in April and terminate by July, thus catkins were collected during those months in 2016. Of the 36 tagged Chinese tallow study trees, five were lost at the Kenner site after the commencement of seed collection, three due to unintentional felling and two due to possible death from brackish water intrusion. Consequently, male catkins were collected from the 31 remaining trees across all three study sites. After both seed and catkin collection was completed, one tree was felled at the Belle Chasse site which allowed measurement of overstory density from 30 trees with a spherical densitometer.

For each tree, seed fall/m^2 and catkin fall/m^2 were calculated using the total of samples collected per tree divided by trap area. The number of seeds and catkins produced by each tree was calculated from seed fall/m^2 and catkin fall/m^2 multiplied by the crown area (m^2) for each tree. Estimates of total seed mass per tree were obtained using the mean mass of 10 seeds randomly selected per tree, multiplied by the estimated total number of seeds. Estimates of total catkin mass per tree were obtained by calculating the mean mass of a random sample of 16 catkins collected from each tree, multiplied by the estimated total number of catkins produced. Since catkin mass varied with length, I used the relationship between catkin length and mass to calculate a mean mass for the 16 catkins from each tree. A random sample of 101 mature male catkins were cut from trees from the three study sites to obtain the relationship between catkin length and dry mass. Catkins were dried overnight at 100 degrees C and placed in a Secador Desiccator for 90 minutes where they were allowed to come to room temperature, after which dry length and mass were recorded for each catkin.

Data analysis

All statistical analyses were performed using SYSTAT v 13 (SYSTAT Software Inc., Richmond, CA). Exploratory analyses using ordinary least squares regressions were conducted to determine which allometric parameters provided the best fitted model to explain seed and male catkin variables using independent variables of DBH, tree height, and overstory density. One tree at the Belle Chasse study site was identified as an outlier for all regressions and was removed from all analyses. I used ANCOVA to determine how seed and catkin production varied with tree size across sites, followed by regression to derive equations for the relationships among reproductive parameters and tree characteristics. The relationship between seed mass and catkin mass was explored using Pearson product-moment correlation.

Results

Predictors of seed and catkin mass

Regression analysis showed that DBH was a significant predictor of seed mass ($r^2 = 0.58$; $P < 0.001$) and catkin mass ($r^2 = 0.281$; $P = 0.003$) (Table 1). Tree height also showed a significant relationship with seed mass ($r^2 = 0.136$; $P = 0.029$), but this relationship was much weaker than that between seed mass and DBH. The relationship between catkin mass and tree height was not significant ($r^2 = 0.008$; $P = 0.639$). Overstory density was not a significant predictor of either seed mass or catkin mass (Table 1). Multiple regression using both DBH and height did not significantly improve predictive power for seed mass (DBH regression $r^2 = 0.58$, multiple regression $r^2 = 0.59$), therefore I used DBH as the sole predictor of reproductive investment in all subsequent analyses.

Table 1: Predictor variables for seed and catkin mass.

Measurement	**Seed Mass (r^2)**	**Catkin Mass (r^2)**
DBH	0.580 ($P < 0.001$)	0.281 ($P = 0.003$)
Height	0.136 ($P = 0.029$)	0.008 ($P = 0.639$)
Overstory Density	0.006 ($P = 0.687$)	0.005 ($P = 0.700$)

Female reproductive investment and tree size

Seed mass was significantly related to DBH across all sites ($F_{1,29} = 44.82$, $P < 0.001$). The three sites did not differ significantly in seed production (site effect: $F_{2,29} = 0.30$, $P = 0.745$), and there was no significant interaction between the site and DBH effects ($F_{2,29} = 0.496$,

$P = 0.614$). The regression of seed mass on DBH was given by Mass = 0.295 (DBH) – 3.32 (Fig. 6).

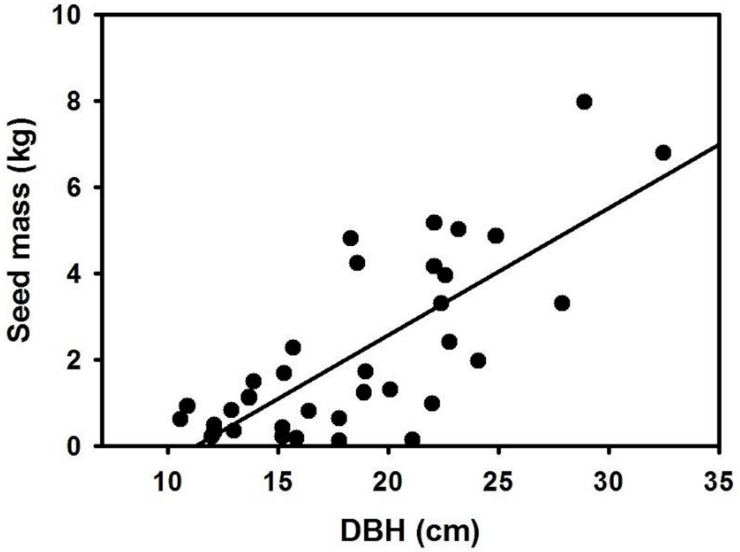

Figure 6: Relationship between seed mass and DBH in *Triadica sebifera* ($N = 35$).
Mass = 0.295 (DBH) – 3.32 ($r^2 = 0.58$; $P < 0.001$).

Catkin mass estimation

I found a significant relationship between catkin dry mass and length ($F_{1,95} = 152.78$, $P < 0.001$). Catkin dry mass was unrelated to site ($F_{2,95} = 1.56$, $P = 0.215$) but there was a significant interaction between site and length ($F_{2,95} = 7.41$, $P < 0.001$). The regression for catkins collected at the Kenner site differed significantly from those collected at the Belle Chasse and Boutte sites (Tukey's HSD test, Kenner vs. Belle Chasse: $P = 0.001$; Kenner vs. Boutte: $P < 0.001$), but Belle Chasse and Boutte did not differ significantly ($P = 0.74$) (Fig. 7). Based on these results, I combined catkins collected at the Belle Chasse and Boutte study sites into a single regression and calculated a separate regression for the Kenner site.

The regression for Belle Chasse and Boutte was given by Mass = 0.042 (length) - 0.076 ($r^2 = 0.742$; $P < 0.001$), which was then used to estimate catkin mass for each tree within these study sites. For the Kenner site, I used the relationship Mass = 0.069 (length) – 0.177 (r^2 = 0.720; $P < 0.001$) to estimate catkin mass for each tree.

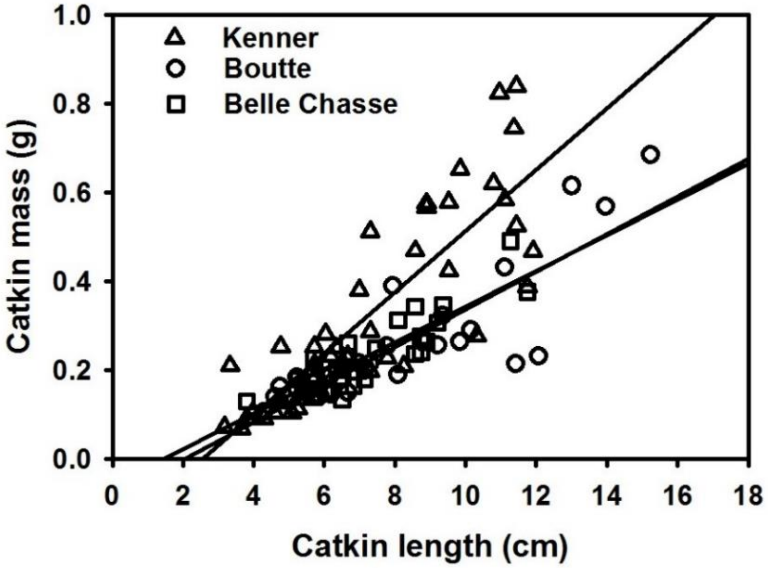

Figure 7: Relationship between catkin mass and length in *Triadica sebifera* at three sites (N = 101).

Male reproductive investment and tree size

Catkin dry mass was significantly related to DBH across all study sites ($F_{1,24} = 25.05$, $P < 0.001$). Catkin dry mass did not differ significantly across sites ($F_{2,24} = 0.95$, $P = 0.40$), and the interaction between site and DBH was also not significant ($F_{2,24} = 3.05$, $P = 0.66$). The regression for catkin mass was given by Mass = 0.216 (DBH) – 1.72 (Fig. 8).

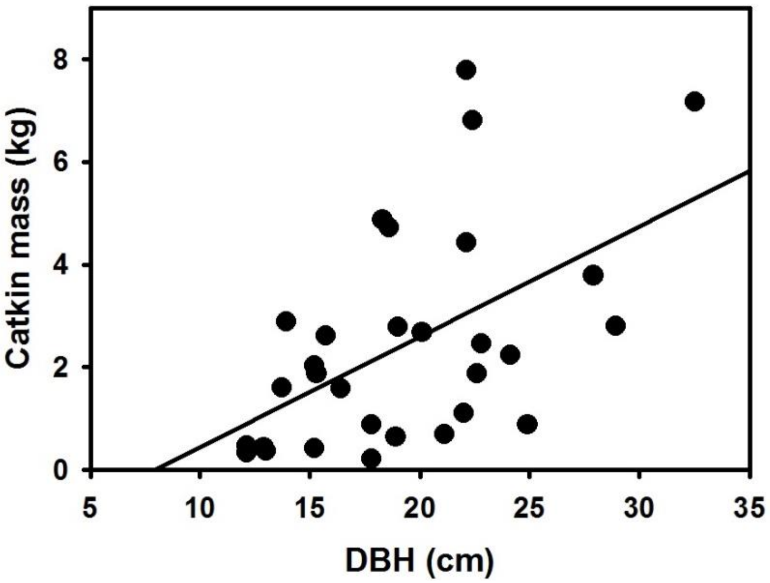

Figure 8: Relationship between catkin dry mass and DBH in *Triadica sebifera* (N = 30). Mass = 0.216 (DBH) – 1.72 (r^2 = 0.28; P = 0.003).

Reproductive investment and tree size

Catkin mass and seed mass produced by individual trees were significantly and positively correlated (Pearson Product-Moment Correlation; r = 0.679, Chi-square = 16.9; df = 1; $P <$ 0.001) (Fig. 9). As a result, total reproductive investment (seed mass + catkin mass) was also significantly related to DBH (Least-Squares regression; r^2 = 0.48; t = 5.13; $P < 0.001$) (Fig. 10). I investigated the relationship between seed mass:catkin dry mass ratio and DBH to determine whether smaller trees invested more in male than female reproductive structures. I also asked whether seed mass:catkin mass ratio was related to total reproductive investment. The regression of seed mass:catkin mass ratio on DBH was not statistically significant ($F_{1,28}$ = 2.95; P = 0.097). The regression of seed mass:catkin dry mass and total reproductive investment across all study sites was also insignificant (r^2 = 0.023; P = 0.425).

Individual trees of similar size showed substantial variation in seed mass:catkin mass ratio as well as total reproductive investment within study sites. For example, trees with a DBH between 20 – 24.99 cm varied in seed mass:catkin mass ratio from 0.21 – 5.56 (Table 2). Within the same size class, individual trees varied in total investment from 0.83 – 11.95.

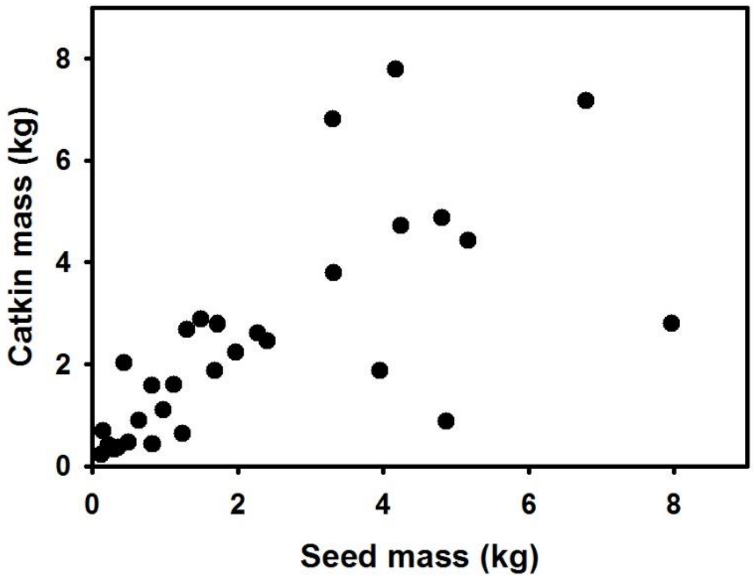

Figure 9: Scatterplot of catkin dry mass and seed mass in *Triadica sebifera*.

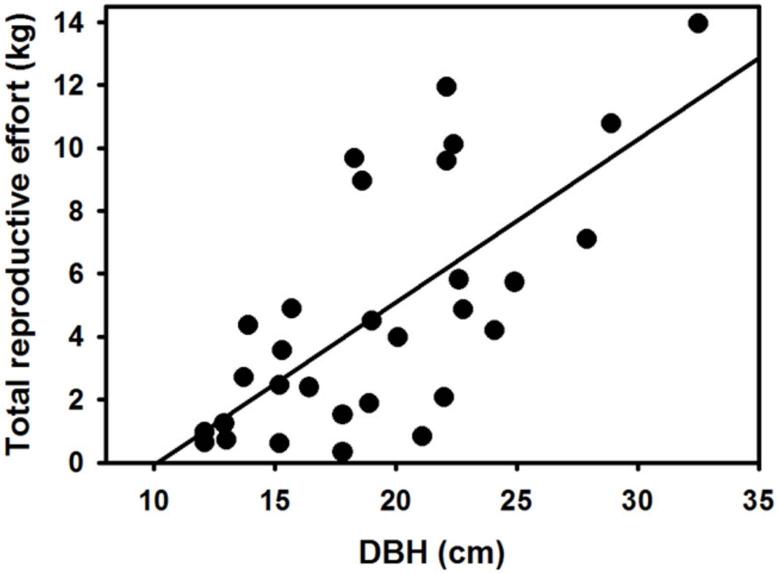

Figure 10: Relationship between total reproductive investment and DBH. Mass = 0.52 (DBH) – 5.25.

Table 2: Mean values of estimated reproductive characteristics among *Triadica sebifera* size classes and estimated range of values among individual trees.

DBH (cm)	*N*	Mean ± SD	Range
< 15			
Total seed mass (kg)	9	0.70 ± 0.42	0.21 – 1.49
Total catkin dry mass (kg)	6	1.01 ± 1.04	0.33 – 2.89
Seed mass:catkin dry mass	6	1.01 ± 0.48	0.51 – 1.89
Total investment (kg)	6	1.78 ± 1.48	0.64 – 4.37
15 – 19.99			
Total seed mass (kg)	12	1.53 ± 1.56	0.12 – 4.80
Total catkin dry mass (kg)	11	2.06 ± 1.60	0.22 – 4.88
Seed mass:catkin dry mass	11	0.80 ± 0.45	0.21 – 1.95
Total investment (kg)	11	3.71 ± 3.13	0.34 – 9.68
20 – 24.99			
Total seed mass (kg)	11	3.02 ± 1.77	0.14 – 5.16
Total catkin dry mass (kg)	10	3.09 ± 2.47	0.69 – 7.78
Seed mass:catkin dry mass	10	1.33 ± 1.58	0.21 – 5.56
Total investment (kg)	10	5.91 ± 3.59	0.83 – 11.95
>25			
Total seed mass (kg)	3	6.02 ± 2.42	3.31 – 7.97
Total catkin dry mass (kg)	3	4.59 ± 2.29	2.80 – 7.17
Seed mass:catkin dry mass	3	1.55 ± 1.12	0.87 – 2.84
Total investment (kg)	3	10.61 ± 3.43	7.10 – 13.95

Discussion

Sex ratios and total investment

I found no evidence that allocation to male vs. female reproductive function varied with size or reproductive effort in my study of Chinese tallow. In woody perennial plants, resources allocated to growth at early stages of development determine thresholds that may maximize future reproduction (Thomas, 2011). Since age at first reproduction for Chinese tallow is early compared to other woody species, I expected to find evidence of a sex-allocation trade-off with tree size, with larger trees investing more in female function (Charnov, 1982). Although studies of other species have shown that sex allocation varies with plant size (Freeman et al., 1976; Solbrig, 1981; McKone, 1990; Obeso, 2002), my results suggest that sex allocation in Chinese tallow may instead be regulated by environmental or genetic factors. Since growth and reproduction are strongly influenced by available resources, it is possible that spatial or temporal variation in light, soil nutrients and water availability may account for the differences in reproductive investment I observed among individual trees.

My results showed no support for light limitation as an explanation for differential investment in male vs. female function, but evidence from other studies suggests a potential role for nutrient and moisture availability. For example, a study by Knops and Koenig (2012) found that variation in aboveground annual net productivity among individual trees of three California oak species was correlated with water availability and soil fertility, indicating an adaptive plastic response to abiotic variation, rather than a life history trade-off, was responsible for a negative correlation between male and female function. Although data on reproductive responses to nutrient availability are lacking, Chinese tallow seedlings from invasive origins have been shown to be P limited (Zhang et al., 2013) and exhibited significantly higher vegetative growth rates in response to increased levels of inorganic N compared to native seedlings (Zou et al., 2006).

Additionally, inter- and intraspecific competition may exacerbate variation in resource availability, ultimately affecting growth and reproductive effort of Chinese tallow. In a study of co-occurring native and invasive irises (Mopper et al., 2016), interspecific competition had no effect on the invasive *I. pseudacorus*, but a significant reduction of biomass was found in the native *I. hexagona*. A study by Gabler and Siemann (2013) showed the length of time Chinese tallow experienced favorable moisture conditions before exposure to water-related stress and competition impacted final size, biomass, and abundance, but fertilization had weak effects. The spatiotemporal availability of resources may affect patterns of reproduction in Chinese tallow, but long-term studies of individual trees will be needed to identify sources of variation among similar-sized trees.

Size-dependent patterns of male and female reproduction

While both seed mass and catkin mass were related to DBH, the relationship between seed mass and DBH was stronger than that of catkin mass and DBH. I speculate that Chinese tallow may prioritize seed production over catkin production, which may explain the tendency of small trees to produce seeds and to contribute to its success as an invader. It is possible that the trees in this study may exhibit a proportional investment for female reproductive output and increased growth mediated by available resources within the study sites. For example, a study of holm oaks revealed that nutrient addition increased shoot growth and male flower production but had no effect on the quantity of female flowers, suggesting that surplus nutrients may lead to differential allocation to less costly male function (Pulido et al., 2014). Further investigation would be required to establish how soil nutrients affect growth relative to male and female investment in Chinese tallow.

Reproduction and invasion success

The ability of Chinese tallow to reproduce early and often under variable conditions is integral to its successful establishment. In this study, the variation in the seed mass:catkin mass ratio was similar across size classes, indicating that early reproduction is not primarily focused on less costly male structures as would be expected from predictions of life history theory. Smaller trees do produce viable seeds which contribute greatly to the ability of this species to establish and spread in its introduced range. The substantial amount of female investment from the first age of reproduction, coupled with an early onset of reproduction, may be a crucial difference between this invasive species and native plants in its invaded range. Although the factors governing patterns of reproductive investment in Chinese tallow are still unclear, I expect that studies of environmental influences on reproductive allocation patterns will reveal the mechanisms underlying its success as an invader.

Conclusion and future implications

The sources of variation in reproductive investment of Chinese tallow do not appear to arise directly from life history trade-offs. Future research should focus on small-scale spatial and temporal variation of major resources, including water and soil nutrients, to reveal the reasons for differences in reproductive effort among individuals within populations. Establishing relationships between growth, fecundity, and survival would benefit management strategies for effective control of this noxious plant.

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