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Lauren S. Pile
Clemson University

G. Geoff Wang
Clemson University

Jeremy P. Stovall
Stephen F Austin State University, stovalljp@sfasu.edu

Evan Siemann
Rice University

Gregory S. Wheeler
USDA ARS Invasive Plant Research Laboratory

See next page for additional authors

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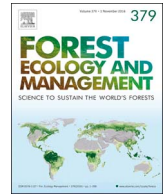
Mechanisms of Chinese tallow (Triadica sebifera) invasion and their management implications – A review

Lauren S. Pile[a,f], G. Geoff Wang[a,*], Jeremy P. Stovall[b], Evan Siemann[c], Gregory S. Wheeler[d], Christopher A. Gabler[e]

[a] Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, United States
[b] Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, Nacogdoches, TX 75962, United States
[c] Department of Ecology and Evolutionary Biology, Rice University, Houston, TX 77005, United States
[d] USDA ARS Invasive Plant Research Laboratory, Ft. Lauderdale, FL 33314, United States
[e] School of Earth, Environmental, and Marine Sciences, University of Texas Rio Grande Valley, Brownsville, TX 78520, United States
[f] High Sierra Ranger District, Sierra National Forest, Prather, CA 93651, United States[1]

ABSTRACT

Ecosystems are under increasing stress from environmental change, including invasion by non-native species that can disrupt ecological processes and functions. Chinese tallow [Triadica sebifera (L.) Small] is a highly invasive tree species in southeastern US forests, prairies, and wetlands, and effectively managing this invasive species is a significant challenge for scientists and land managers. In this review, we synthesize the literature on invasion ecology and management of Chinese tallow. Our review suggests that the invaded range of Chinese tallow is currently limited by dispersal in many areas and by low temperatures and low soil moisture, and by high soil salinity and frequent flooding in others, but these barriers may be overcome by increased dispersal, phenotypic plasticity, and/or rapid evolution. Invasions by Chinese tallow are facilitated by both the invasiveness of the species and the invasibility of the recipient communities. Invasiveness of Chinese tallow has been attributed to fast growth, high fecundity, a persistent seed bank, aggressive resprouting, abiotic stress tolerance, and the ability to transform fire maintained ecosystems. Some of these traits may be enhanced in invasive populations. Anthropogenic and natural disturbances, lack of herbivore pressure, and facilitation by soil microbes enhance the intensity of Chinese tallow invasions. Biological control of Chinese tallow is being developed. Treatments such as herbicides, prescribed fire, and mechanical control can effectively control Chinese tallow at the local scale. A combination of these treatments improves results. However, a proactive management approach would simultaneously achieve invasion control and promote subsequent ecological restoration, especially in the context of legacy effects, secondary invasions, and/or variable ecosystem responses to different control treatments. Future research should clarify the roles of species invasiveness and community invasibility, increase our understanding of the effects of Chinese tallow in invaded communities, and develop viable management regimes that are effective in both controlling or reducing the probability of Chinese tallow invasion and restoring desired native communities.

1. Introduction

Biological invasions are one of the five main causes of declines in global biodiversity and are a fundamental driver of ecosystem degradation resulting in reduced ecosystem services worldwide (MEA, 2005; Pyšek and Richardson, 2010). Elucidating how a species is able to invade, establish, and become dominant in a community is important for advancing invasion ecology and developing guidelines for biological conservation and management action. Whether or not a species is able

to overcome the barriers to invade depends on the biological traits (i.e., invasiveness) that equip the species to be successful in new environments. These traits may include rapid growth, high specific leaf area (SLA), and high levels of reproductive output and dispersal, among others (Rejmanek et al., 2005; Whitney and Gabler, 2008). However, the success of invasive species is also dependent on the communities they invade (i.e., the degree of invasibility) and propagule pressure (i.e., the frequency and abundance of propagules entering the community) (Lonsdale, 1999; Simberloff, 2009). Therefore, a complete

understanding of the success of biological invasion requires knowledge of the roles of invasiveness, invasibility, and propagule pressure.

Invasion by non-native, invasive tree species often has profound impacts on recipient communities (Lamarque et al., 2011), leading to changes in species composition and diversity, as well as ecosystem functions, such as primary productivity, biomass distribution, litterfall and decomposition rates, carbon storage, and alterations to hydrology and fire regimes, especially when trees are invading grasslands (Jackson et al., 2002; Yelenik et al., 2004; Pyšek et al., 2012). Until recently, few tree species were featured on lists of the most widespread and damaging invasive species (Richardson and Rejmánek, 2011). Invasive trees differ from other non-native invasive plants in that they are long-lived and large in size. As a result, invasive tree species are able to dominate native vegetation and fundamentally alter community structure, function, and ecological processes (van Wilgen and Richardson, 2014).

The most influential invasive plant species are those that are able to transform the communities they invade (Rejmanek et al., 2005). Chinese tallow (*Triadica sebifera* (L.) Small) is such a species. Chinese tallow is the most pervasive non-native tree species in southern US forests and aggressively displaces native tree species (Gan et al., 2009), due to unusual combination of fast growth and high tolerance to stress (Rogers and Siemann, 2002; Butterfield et al., 2004; Chen et al., 2013; Gabler and Siemann, 2013a; Yang et al., 2014). It has been shown to reduce arthropod diversity either when it displaces grassland or native tree species (Hartley et al., 2004, 2010; Cameron and Spencer, 2010). Leaf deposition has been shown to impact the life cycle of amphibians (Leonard, 2005; Adams and Saenz, 2012). It displaces federally endangered grassland bird species (Herkert et al., 2003; Perkins et al., 2003) by converting coastal tallgrass and wetland communities into woodland thickets (Bruce et al., 1995; Neyland and Meyer, 1997; Wang et al., 2011a), and generally suppresses fire regimes through rapid leaf decomposition and transformation of fuel loads (Cameron and Spencer, 1989; Grace, 1998).

Much of the research on invasive species, and on Chinese tallow in particular, has been focused on studying species invasiveness or community invasibility as separate determinants of invasion success. However, it is necessary to integrate both of these invasion ecology concepts to inform management actions (Richardson and Pyšek, 2006; Pyšek and Richardson, 2010). Therefore, the objective of our review is to provide a synthesis of the current literature on Chinese tallow in relation to its invasiveness, the invasibility of its recipient ecosystems, and scientifically tested management options for its control (Fig. 1). Specifically, we describe the current invaded range of Chinese tallow

and its limiting factors, review the common traits and community or site characteristics that promote the invasion success of Chinese tallow, examine current management practices for controlling Chinese tallow, and discuss future management and research needs.

2. Invasion range and its limiting factors

Chinese tallow was first introduced to the U.S. in Savannah, Georgia in 1772 with seeds provided by Benjamin Franklin (Bell, 1966). Chinese tallow was documented in South Carolina in the late 1700s (Randall and Marinelli, 1996; Meyers, 2011) and was planted across the Gulf Coast by the federal government around 1900 (Potts and Bolley, 1946; Bruce et al., 1997). These later introductions were from a different region of China than the initial one (DeWalt et al., 2011). Chinese tallow was promoted as an agricultural crop for the production of edible oils, industrial oils (including for biodiesel production), biomass, and forage for honey production (Hooper, 1904; Jamieson and McKinney, 1938; Howes, 1949; Scheld and Cowles, 1981; Scheld et al., 1984; Flack and Furlow, 1996).

The Chinese tallow population in the United States has increased dramatically in the past few decades. As of 2008, Chinese tallow occupied 185,000 ha of southern forests, specifically at forest edges, and in openings of the southeastern coastal plain, prairie, and the Mississippi River alluvial floodplain provinces (Oswalt, 2010). Chinese tallow has become the fifth most common tree in Louisiana where it increased by 500% from 1991 to 2005 alone (Oswalt, 2010). In Texas, Chinese tallow increased by 174% in east Texas in the same period (Oswalt, 2010), it has become the most abundant sapling in the floodplain forests of the Big Thicket National Preserve (Harcombe et al., 1999), and it is now the most abundant species in the eight-county area surrounding Houston (Nowak et al., 2005). Although its current range of invasion is centered in the southeastern region, based on its current abiotic tolerances and anticipated changes in climate, Chinese tallow is expected to expand up to 334 km north of its current U.S. range in 115 years (Wang et al., 2011a). Some models predict range expansions as far north as the Ohio River (Pattison and Mack, 2008). Recent work has supported the general trend in northward expansion by Chinese tallow predicted by these previous models, however the mean potential rate of spread of 1940 m/year was faster than those modeled by Wang et al. (2011a) at a rate of 1231 m/year (Suriyamongkol et al., 2016).

Currently, propagule dispersal appears to limit the range of Chinese tallow across the central and eastern US, but, eventually, poleward Chinese tallow distribution is expected to be limited by low temperatures (Pattison and Mack, 2008). According to Gan et al. (2009),
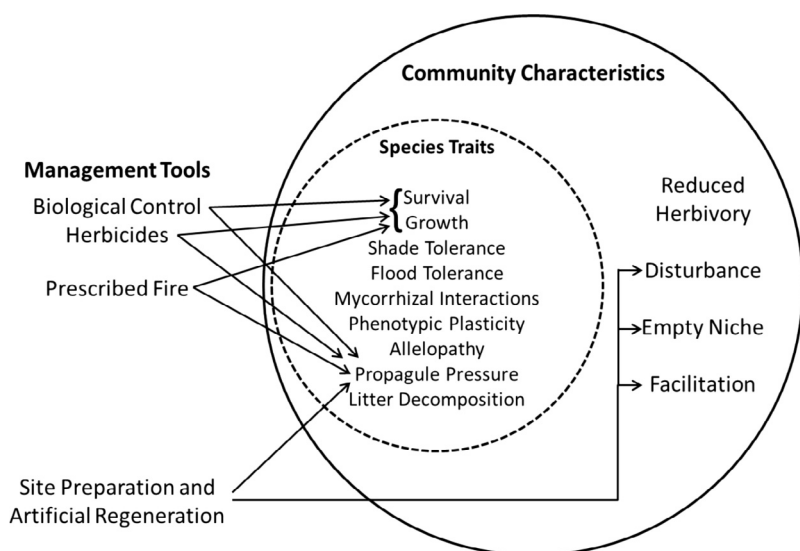

Fig. 1. Schematic of species traits that lead to Chinese tallow invasiveness, community traits that increase Chinese tallow invasibility, and management tools that are employed in attempts to control or eradicate Chinese tallow. Arrows indicate specific species traits impacted by each management tool.

approximately 80% of the existing Chinese tallow invasions of southern US forests occur at elevations lower than 50 m and on slopes less than 2 degrees, with no invasions reported on elevations higher than 165 m or on slopes greater than 18 degrees. Chinese tallow also has not been reported in areas where minimum extreme temperatures in January were lower than −12 °C (Gan et al., 2009). However, differences in cold hardiness have been documented between two genetically distinct populations of Chinese tallow, with greater cold hardiness in North Carolina than South Carolina genotypes, suggesting that range expansion could be influenced by source population not only by climatic conditions (Park et al., 2012). In the Central Valley of California, establishment potential is limited by seedling drought tolerance but riparian habitats in this region are extremely vulnerable to Chinese tallow invasion (Bower et al., 2009).

The availability of resources affects Chinese tallow establishment success and performance at the site level. Its growth rate varies with light levels (Urbatsch, 2000; Rogers and Siemann, 2002; Siemann and Rogers, 2003b), but it has a higher growth rate than co-occurring native trees at all light levels above deep shade (Lin et al., 2004). Additionally, the seedlings of Chinese tallow have a strong competitive advantage over herbaceous plants in low light levels (Siemann and Rogers, 2003a). Invasion may occur at faster rates on sites with higher moisture levels, when compared to drier locations (Hsu, 1928; Lin et al., 1958; Khan et al., 1973; Scheld and Cowles, 1981; Helm et al., 1991; Singh et al., 1993). However, invasion success has been found to be reduced in sites with high flood stress (Gabler and Siemann, unpublished data), in part because germination of Chinese tallow is inhibited in saturated or flooded soils (Gabler and Siemann, 2013a). Chinese tallow can grow well on poorly drained or intermittently flooded soils (Cameron and Spencer, 1989). In contrast, it is limited by extremely arid conditions, although Chinese tallow is considered drought tolerant as an adult, particularly in clayey soils (Bruce, 1993; Barrilleaux and Grace, 2000). However, even among 2-year-old Chinese tallow seedlings, survival was high in southeast Texas during Texas' record drought in 2011 (Gabler and Siemann, unpublished data). Competition for water may limit establishment in dry environments, as shown in greenhouse (Gabler and Siemann, 2013b) and field experiments in upland open-canopy habitats (Pattison and Mack, 2008) and 11 sites across a moisture gradient in southeast Texas (Gabler and Siemann, unpublished data). Chinese tallow is also tolerant of high soil salinity (Conner and Askew, 1993; Conner, 1994; Chen et al., 2013; Yang et al., 2014; Paudel and Battaglia, 2015) and it may benefit from some disturbances (e.g., storm surge that accompanies hurricanes) (Chapman et al., 2008; Conner et al., 2014; Henkel et al., 2016). In addition, Chinese tallow has strong responses to nitrogen availability (Rogers et al., 2000; Siemann and Rogers, 2007) and anthropogenic nitrogen deposition increases invasion success (Siemann and Rogers, 2003a, 2007; Siemann et al., 2007).

Barrilleaux and Grace (2000) examined factors contributing to the distribution of Chinese tallow in the coastal prairie of the southern US (south Texas through southwestern Louisiana), where more invasion occurred in the central and eastern portion of the prairie and less so in the western portion. The differences in soil characteristics within the coastal prairie strongly affected growth rates of Chinese tallow (Barrilleaux and Grace, 2000). Limited growth in western soils was attributed to elevated soil salinity, possibly caused by higher ratios of evapotranspiration to precipitation common in arid regions (Savenije and Pagès, 1992; Ben-Asher, 1994), or a greater coastal influence from salt spray or saltwater inputs (Barrilleaux and Grace, 2000). However, others have shown, as discussed above, that Chinese tallow has a fairly high salinity tolerance (Conner and Askew, 1993; Conner, 1994; Chen et al., 2013; Yang et al., 2014; Paudel and Battaglia, 2015) which points to other factors being critical. Western soils also had higher sand content, lower carbon and nitrogen contents, and higher phosphorous content, in addition to higher sodium and electrical conductivity when compared to eastern soils (Barrilleaux and Grace, 2000). Importantly, rainfall also varies significantly across the coastal prairies of Texas and

Louisiana, with rainfall decreasing from ca. 1600 mm/year in Louisiana to ca. 650 mm/year in south Texas (PRISM, 2013). Greater sand content may also reduce the water holding capacity of western soils. Given Chinese tallow's increased performance in moist soils, water limitation is likely a key factor in limiting its western distribution. This notion is substantiated by experimental manipulations of soil moisture in previously tallow-dominated restoration sites across a soil moisture gradient in southeast Texas by Gabler and Siemann (unpublished data). They found that Chinese tallow establishment and performance were significantly influenced by soil moisture and were lowest in the most arid, westerly sites, but artificially increasing soil moisture permitted Chinese tallow establishment in some arid sites and generally increased its performance in all but the wettest sites.

3. Invasiveness – Species traits

The term *invasiveness* refers to the traits of a given species and the ability of those traits to increase competitive success under a given set of environmental conditions (Richardson et al., 2011). This includes the life history traits and modes of reproduction that define their ability to overcome barriers to invasion. Understanding the traits that make a non-native species invasive is important (a) prior to the initial introduction/invasion stage, in order to evaluate risk associated with movement of a particular species and, more generally, in the development of invasive species risk assessment plans (Whitney and Gabler, 2008), and (b) after a species has become established and invasive in a new range, for managing against those factors that aid in competitiveness and instead managing for the traits that favor native communities. In the case of Chinese tallow, populations in the introduced range may have traits that contribute to invasiveness that differ from populations in the native range. Species traits associated with invasiveness have been reviewed by Rejmánek and Richardson (1996), Whitney and Gabler (2008), and others. Only those traits considered important to Chinese tallow invasiveness are considered here.

3.1. Growth

Rapid growth rates and overall larger size, especially at early life stages (when compared to native species or non-invasive introduced congeners), are commonly cited traits of invasiveness (Pyšek and Richardson, 2007; Whitney and Gabler, 2008; Pyšek et al., 2014). Under optimum conditions, Chinese tallow can grow 2.8 m tall in the first two years after germination (Scheld and Cowles, 1981). Growth of new stems produced after coppicing was 3.4–3.7 m at the end of one and more than 5.5 m after two years (Scheld and Cowles, 1981). High stand biomass (16.16 Mg ha^{-1}) and above-ground net primary productivity (ANPP) (8.08 Mg ha^{-1} yr^{-1}) were reported for the first two years following coppicing (Scheld and Cowles, 1981). The 12–15 year old control stands in the same study had a biomass and ANPP of 94.02 Mg ha^{-1} and 6.96 Mg ha^{-1} yr^{-1}, respectively. However, these values are lower than southeastern bottomland hardwood forests and baldcypress [*Taxodium distichum* (L.) Rich.] – water tupelo [*Nyssa aquatica* L.] swamps (17.33 and 15.16 Mg ha^{-1} yr^{-1} respectively) (Conner and Day, 1976). In a comparison by Harcombe et al. (1993), pine plantations exceeded the wood production of Chinese tallow, although Chinese tallow was more productive (3.90 Mg ha^{-1}) than hardwood stands (i.e., chestnut oak, yellow-poplar, oak-hickory, and pine hardwood stands) (Edwards et al., 1989). Under full sunlight, Chinese tallow seedlings outperformed all co-occurring native tree species in the southeastern US. It grew faster than cherrybark oak (*Quercus pagoda* Raf.), and supported more root plus stem mass per unit of leaf mass than American sycamore (*Platanus occidentalis* L.) or cherrybark oak (Jones and McLeod, 1989). When subjected to various resource conditions (nitrogen and light levels), Chinese tallow out performed sugarberry (*Celtis laevigata* Willd.) even though sugarberry is one of the fastest growing native trees in Texas (Harcombe et al., 1999;

Siemann and Rogers, 2003a). However, direct comparisons of growth rates to fast growing, co-occurring, native species in field conditions and over a long time period are limited, especially in forested systems where native tree species are often longer-lived and larger in stature than Chinese tallow [but see Lin et al. (2004)].

3.2. Shade tolerance

Most invasive plant species are classified as *r*-strategists and most invasive tree species are classified as shade intolerant (Rejmánek and Richardson, 1996). However, some invasive tree species are tolerant of shade. Shade tolerance allows these species to invade successfully advanced communities, which makes them an unusual conservation concern and management challenge (Rejmanek et al., 2005). Invasive species such as common buckthorn (*Rhamnus cathartica* L.), privet species (*Ligustrum* spp.), and Japanese stiltgrass [*Microstegium vimineum* (Trin.) A. Camus] are shade tolerant species that are having significant ecological and management impacts in the United States. Remarkably, Chinese tallow is able to outperform native trees in both shade and high light conditions and so does not seem to conform to traditional classifications of shade tolerant vs. shade intolerant species. Chinese tallow seedlings are capable of moderate growth in deep shade (Jones and McLeod, 1990; Lin et al., 2004), are able to regenerate in full shade (Paudel and Battaglia, 2015), and can compensate for herbivore damage even in low light in its native range (Wang et al., 2011b). Lin et al. (2004) found that Chinese tallow saplings had a top quartile growth rate 62% and 120% higher than fast growing, shade intolerant sweetgum (*Liquidambar styraciflua* L.) and water oak (*Quercus nigra* L.), respectively, while simultaneously having lower mortality rates than even shade tolerant species such as red maple (*Acer rubrum* L.) and American hornbeam (*Carpinus caroliniana* Walter), down to 15% light. Manipulative experiments have found similar results, with Chinese tallow outperforming shade tolerant species in low light (Jones and McLeod, 1989) and shade intolerant species in high light (Jones and McLeod, 1989, 1990; Rogers and Siemann, 2002; Siemann and Rogers, 2003a).

3.3. Flood tolerance

Chinese tallow is often found on moist or periodically flooded areas. It has been proposed that such conditions may facilitate invasion because Chinese tallow is unusually tolerant of flooding and anaerobic soil conditions (Jones and Sharitz, 1990; Conner, 1994; Bruce et al., 1997; Butterfield et al., 2004; Gabler and Siemann, 2013b,a). Chinese tallow was found to have greater resistance to cavitation than co-occurring common persimmon (*Diospyros virginiana* L.) (Pratt and Black, 2006). Although its seeds will not germinate in flooded or saturated soils, once germinated, Chinese tallow seedlings achieve considerable flood tolerance within two months (Gabler and Siemann, 2013a). Its tolerance to flooding in the first year of growth is comparable to water tupelo, a wetland specialist (Jones and Sharitz, 1990). The higher leaf-to-stem mass ratio of Chinese tallow relative to water tupelo indicates that Chinese tallow may be able to survive very wet conditions under dense canopies, where water tupelo may not be able to capture enough light (Jones and Sharitz, 1990; Butterfield et al., 2004). Even when grown in competition with native wetland grasses, newly germinated Chinese tallow seedlings achieved flood tolerance in months (Gabler and Siemann, 2013b). Morphological characteristics that may be indicative of the flood tolerance of Chinese tallow include: hypertrophy of lenticels, development of adventitious roots, and production of thicker feeder roots (Jones and Sharitz, 1990). The presence of hypertrophied lenticels was found to be prolific on Chinese tallow stems, which may indicate a capacity for partial oxygen stress avoidance (Kozlowski, 1984; Conner, 1994).

3.4. Mycorrhizae

Mycorrhizae play a key role in the dynamics of temperate forests by promoting plant performance that influences the outcome of competition (Johnson et al., 1997; van der Heijden and Sanders, 2002). In a study of lignite overburden sites in Texas that are notably deficient in nitrogen, phosphorus, and organic matter, Davies and Call (1990) found that Chinese tallow inoculated with endo- and ecto-mycorrhizae had enhanced growth and development compared to those without inoculation. Nijjer et al. (2004) studied the effect of mycorrhizal inoculum on Chinese tallow and five native tree species: sweetgum, blackgum (*Nyssa sylvatica* Marshall), loblolly pine (*Pinus taeda* L.), white oak, (*Quercus alba* L.), and water oak. They found that Chinese tallow had a significant positive growth response (65% increase) that was markedly different from the neutral to negative responses of the native species with a generalist mychorrhizal inoculation. Not only does Chinese tallow have higher rates of mycorrhizal association than native trees in the USA, it also has higher rates of association in the USA than in China (Yang et al., 2013, 2014, 2015a,b). These results suggest that an unusual relationship may occur between North American mycorrhizal species and Chinese tallow, resulting in increased invasion success of the tree, especially when native trees are unable to benefit from generalist mycorrhizae (Bever, 2002; Klironomos, 2003).

3.5. Phenotypic plasticity

Phenotypic plasticity is suggested to play an important role in the success of invading plants (Rice and Mack, 1991; Richards et al., 2006; Whitney and Gabler, 2008). There are relatively few studies comparing phenotypic plasticity of Chinese tallow to native species. Chinese tallow had greater phenotypic plasticity to light and water conditions than did little bluestem (*Schizachyrium scoparium* Michx. Nash), with Chinese tallow having more robust growth under stressful light conditions (Zou et al., 2009). Other studies suggest that invasive populations of Chinese tallow have greater plasticity than native Chinese tallow populations, which suggests that increased plasticity has evolved in the introduced range (Zou et al., 2009; Chen et al., 2013). The evolution of increased phenotypic plasticity post-introduction in response to shade is also posited as a reason for the observed lag time for Chinese tallow to become invasive (Zou et al., 2009).

3.6. Allelopathy

Allelopathy is the process by which plants release phytochemicals directly into their surrounding environment, inhibiting seed germination and growth of established neighboring species (Rice, 1995). The novel weapons hypothesis states that non-native plant species may have increased competitive abilities because they have biochemicals that are not native to the introduced environment and are especially effective at suppressing native plants (Callaway and Ridenour, 2004). Chinese tallow has been documented to contain a variety of secondary compounds including coumarins (Yang and Kinghorn, 1985), glycosides (Hsu et al., 1994), diterpene-esters (Ohigashi et al., 1983), and triterpenoid acids (Pradhan et al., 1984). An anecdotal report of allelopathy (Gresham, 1986) is at odds with all experimental studies conducted to date, which indicate allelopathy does not play a role in Chinese tallow invasion success. Studies with Chinese tallow foliar extracts, litter, and soil have all found no allelopathic effect, and often a facilitative effect, on growth on native species, such as little bluestem (Keay et al., 2000), and native trees including bald cypress and black willow *(Salix nigra* Marshall) (Conway et al., 1997, 2002; Rua et al., 2008).

3.7. Propagules: Pressure, supply, and dispersal

Propagule pressure refers to the absolute number of individuals

released during any one release event and the number of discrete release events (Lockwood et al., 2005). As the number of individuals released or the number of events increases, so does propagule pressure and the likelihood of invasion success of a non-native species (Lockwood et al., 2005; Simberloff, 2009). Factors such as number of introductions, seed production and viability, and mode of dispersal could significantly affect propagule pressure and thus the likelihood that a propagule will reach a safe site and become established. Though required for invasion, propagule availability does not guarantee invasion success, especially in habitats with stressful or marginally suitable habitats (Simberloff, 2009). For example, Gabler and Siemann (unpublished data) found that adding Chinese tallow seeds to 11 previously tallow-invaded sites across a moisture gradient increased invasion success at most sites, but had no effect on Chinese tallow abundance in those sites at the extreme wet or dry ends of the soil moisture range. It is in marginally suitable sites where the frequency or number of introduction events is particularly important (perhaps more so than the number of individuals introduced) to local invasion success (Simberloff, 2009). Since its first introduction in 1772, Chinese tallow has been separately introduced multiple times into the southeastern US, with multiple, more diverse, early introduction events in South Carolina and Georgia. Later introductions were fewer and more genetically homogenous in the rest of the southeastern US which may additionally contribute to variations in potentially adaptive traits among genotypes (DeWalt et al., 2011). In its native country of China, Chinese tallow has been cultivated for 14 centuries as a seed crop (Bruce et al., 1997). The invasive success of Chinese tallow could be a result of artificial selection for seed production prior to its introduction to North America (Butterfield et al., 2004). The long history of introduction events to the southeastern US and the cultivation of Chinese tallow for fruit production may have led to locally high levels of propagule pressure in recipient communities.

Chinese tallow invests in producing many large seeds, with a mean seed weight between 112 and 121 mg (Lin et al., 1958) and a mean seed diameter of 7–8 mm (McCormick, 2005). Woody plant invasions are often correlated with small seed size (< 50 mg) perhaps due to high seed numbers, with larger seeds typically associated with extended habitat compatibility (Burke and Grime, 1996). Larger-seeded invasive plants have a higher likelihood of being successful in undisturbed, late-successional plant communities (Rejmanek et al., 2005). An established woodland of Chinese tallow may produce up to 4000 kg ha^{-1} yr^{-1} of seeds (Scheld et al., 1984). Renne et al. (2000) found that seed crop sizes in spoil areas were larger than in forests and were larger in clustered trees than in isolated ones. Seed crops were able to reach 325,000 seeds/cluster in a mature Chinese tallow cluster in spoil areas where the high light environment promoted increased growth and contributed to larger individuals (Renne et al., 2000).

Time to maturation is also important to propagule pressure. In the coastal prairies of Texas, Scheld et al. (1984) reported that half of Chinese tallow populations flowered by the third growing season. In common garden experiments in Texas, Siemann and Gabler (unpublished data) have observed Chinese tallow flower development as early as the second growing season.

Chinese tallow germination rates are sometimes low (0–10%) in field conditions (Conway et al., 2000; Siemann and Rogers, 2003b, 2006) indicating specific cues for germination. In a study with a range of soaking and chilling times, germination rates were low among all treatments (Conway et al., 2000). In another study, Chinese tallow seeds only germinated when exposed to day-night temperature variation, with little germination in constant warm or cold temperatures, even with day-night light variation (Nijjer et al., 2002). Indeed, application of mulch from Chinese tallow stands reduced temperature variation at the soil surface and suppressed Chinese tallow germination in both laboratory (Donahue et al., 2004) and field restoration studies (Donahue et al., 2006). The seeds of Chinese tallow may retain viability in the soil seed bank for at least 5 years (Cameron et al., 2000).

Although Chinese tallow trees are able to establish a persistent soil seed bank, seed viability was found to be higher for freshly collected seeds than one year-old seeds, and seed viability was markedly reduced after 5 years (Renne et al., 2001).

The mode and rate of seed dispersal are important for informing the dynamics of spread and range expansion of invasive species. The types of dispersal agents, including wind, water, and fauna are determinants in dispersal distance from parent tree and may potentially influence seed germination and viability. Birds are important dispersal agents for invasive trees (Pyšek et al., 2014), especially regarding their ability to reach new and distant sites. Chinese tallow seeds are consumed in large numbers by many different bird species, including native species of the southeastern US, and diverse bird assemblages use Chinese tallow seeds heavily as a food source regardless of the habitat type (Renne et al., 2000, 2001; Baldwin et al., 2008; Gifford and Armacost, 2012). As a result, Chinese tallow trees may compete with native plants for dispersal agents (Renne et al., 2001), because lipid-rich fruits are often favored by birds as winter approaches and energy demands increase (Herrera, 1982). The lipid-rich seeds of Chinese tallow become available when many native, lower lipid content fruits mature [e.g., blackgum, dogwood (*Cornus florida* L.), yaupon (*Ilex vomitoria* Aiton), American holly (*Ilex opaca* Aiton), sugarberry or hackberry (*Celtis* spp.), greenbriers (*Smilax* spp.) and many ericaceous shrubs] (Renne et al., 2000). Seeds that had been defecated by birds and buried had higher germination relative to those unhandled and not buried, however, most emergent seedlings came from freshly collected, defecated seeds (Renne et al., 2001). High consumption and dispersal rates by specific bird species helps contribute to the invasive success of Chinese tallow throughout the coastal plain and surrounding areas (Renne et al., 2000). Endozoochorous dispersal by mammals, such as white-tailed deer, has not been found for Chinese tallow (Pile et al., 2015). However, hydrochory, especially after extreme flood events, may be a significant factor in long range dispersal and a contributor to seed bank potential in lowland areas for Chinese tallow (Bennett et al., 2015; Henkel et al., 2016).

Flowering periods early in the growing season or extended flowering periods are commonly cited as a trait that promotes invasiveness in plants (Pyšek and Richardson, 2007; Küster et al., 2008; Godoy et al., 2009; Pyšek et al., 2014). However, the significance of flowering period has not been established for Chinese tallow in the USA. Reports of phenology have been documented for invasive populations in India (Jaryan et al., 2014), but was not compared to native species phenology. However, phenological observations reported leaf emergence occurring in March with leaf fall in December, flowering from April to May, seed ripening in September, and dehiscing in late November (Jaryan et al., 2014).

3.8. Litter decomposition

Chinese tallow is considered a transformer species in the communities it invades (Richardson, 2011b) because invasion alters the continuity of fuel for fires and enhances nutrient cycling through rapid leaf decomposition (Cameron and Spencer, 1989; Grace et al., 2005). Annual biomass from leaf fall of Chinese tallow is similar to that of native deciduous trees, but the leaves decompose more rapidly and nutrients are turned over more rapidly in Chinese tallow forests than native deciduous forests (Cameron and Spencer, 1989). Chinese tallow litter and shading together impact fuel accumulation and continuity in grassland invasions (Grace et al., 2005). Chinese tallow may enhance productivity in the invaded ecosystems by rapid addition of nutrients, particularly in coastal prairie ecosystems that have few native deciduous trees (Cameron and Spencer, 1989). Total lignin content and the ratio of lignin to initial nitrogen concentration, which are highly correlated to the rate of decomposition for hardwood tree species, were low for Chinese tallow (10.5% lignin content and a lignin:initial N ratio of 0.10) compared to black willow (23.7% lignin) and other temperate

deciduous hardwoods (12–27% lignin and 0.13 and 0.26 lignin:initial N ratio) (Meentemeyer, 1978; Melillo et al., 1982; Shure et al., 1986; Cameron and Spencer, 1989). The initial concentrations of nitrogen and calcium in Chinese tallow leaves were also found to be nearly twice that of native tree species (Cameron and Spencer, 1989).

4. Invasibility – Community traits

The degree to which a community can be successfully invaded by a non-native species is referred to as *invasibility*. The invasibility of a community is dependent on the amount of available resources at the time of invasion, which is closely linked to the local disturbance regime (Davis et al., 2000), levels of biotic competition for resources, whether the invading species may fill a niche for resources that is not currently used by the recipient community, and the presence of herbivores, pathogens, and predators that can act to constrain the establishment of a new species (Pyšek and Richardson, 2010). The invading species may also benefit from mutualisms or facilitative effects from resident biota. These community factors, coupled with highly competitive traits commonly associated with invasive plants, can help to drive invasive species dominance.

4.1. Empty niche hypothesis

The empty niche hypothesis is based on the invaders ability to occupy a niche not currently filled by the resident community. A niche opportunity is provided for an invading species if it results in a positive rate of increase from low to high densities (Shea and Chesson, 2002). There are no documented novel traits of Chinese tallow but rather Chinese tallow's success may be attributed to a suite of traits and community characteristics that contribute to invasiveness.

4.2. Disturbance hypothesis

Disturbance is commonly cited as a facilitator and driver of non-native species invasion (Lockwood et al., 2013). Human-mediated disturbance appears to play a role in Chinese tallow invasion, and was found to have a significant association with the probability of occurrence (Paudel and Battaglia, 2015). In South Carolina, the sites with the largest and highest density of reproductive Chinese tallow trees were predominantly on spoil dredge areas and in other highly disturbed sites (Renne et al., 2001). Forest harvesting operations, including thinning, increases Chinese tallow abundance (Johns et al., 1999; Pile et al., 2017a). Following harvest of three tracts of plantation pine for the restoration of bottomland hardwoods, Chinese tallow changed from a minor component to the most dominant species (Johns et al., 1999). Pine plantation establishment on former agricultural lands and subsequent forest thinning were found to increase the presence and abundance of Chinese tallow in comparison to remnant maritime forests on Parris Island in South Carolina (Pile et al., 2017a). Indirect anthropogenic disturbances may also facilitate Chinese tallow invasions. Potential indirect drivers of invasions include nitrogen deposition, changes in rainfall amounts or patterns, increased ground level ozone, increased UV, and increased CO_2; however, of these drivers only nitrogen deposition appears to strongly increase Chinese tallow invasive success. Anthropogenic nitrogen deposition increases invasion success (Siemann and Rogers, 2003a, 2007; Siemann et al., 2007), whereas with the other factors have comparatively little effect on Chinese tallow performance or invasion success (Siemann and Rogers, 2003b; Siemann et al., 2007; Zhang et al., 2017). Natural disturbances have also been found to increase Chinese tallow abundance in forested ecosystems. Seventeen years after Hurricane Andrew (1992), Chinese tallow represented 25% of all tree stems in ridge community plots in Louisiana when no Chinese tallow existed prior to the hurricane (Conner et al., 2014). Following Hurricane Rita (2005), Chinese tallow had accelerated growth into the canopy in east Texas (Harcombe et al.,

2009), and rapidly recruited into adult size classes (> 10 cm dbh) 6 years following Hurricane Katrina (Henkel et al., 2016). In contrast, studies in Texas grasslands indicate that Chinese tallow is also able to establish without disturbance (Bruce et al., 1997; Grace, 1998; Siemann and Rogers, 2003a,b, 2007; Siemann et al., 2007). In addition, the invasion of feral hogs, who disturb soil, alter forest floor chemistry, and reduce forest regeneration diversity, may facilitate the invasion of Chinese tallow [e.g., invasional meltdown (Simberloff and Von Holle, 1999; Simberloff, 2006)]. In a Texas field experiment, Chinese tallow was twice as abundant on sites with feral hogs than within hog exclosures (Siemann et al., 2009).

4.3. Enemy release and increased competitive ability

The enemy release hypothesis states that, when a non-native species encounters its introduced range, it will increase in distribution and abundance resulting from a decrease in control from herbivory and other natural enemies (Keane and Crawley, 2002). The evolution of increased competitive ability hypothesis posits that non-native species will reduce their allocation to herbivore defenses when not attacked in their introduced range and reallocate them those resources to growth and reproduction (Blossey and Nötzold, 1995). This theory has been extended to include evolutionary changes in defenses against specialist vs. generalist herbivores (Joshi and Vrieling, 2005; Huang et al., 2010) and in the ability to prevent vs. tolerate herbivore attack (Strauss and Agrawal, 1999).

In North America, Chinese tallow is rarely attacked by herbivores (Bruce et al., 1997; Siemann and Rogers, 2001; Siemann et al., 2017). In response, it appears that Chinese tallow has evolved a reduction in defense allocation and an increase in allocation to growth and/or reproduction (Siemann and Rogers, 2001, 2003d,c). In comparisons between invasive populations in North America ('invasive ecotypes') and native populations in China ('native ecotypes'), invasive ecotypes grew more vigorously regardless of herbivory or neighbor effects from competition and the ability to reallocate carbon to tissue growth than native ecotypes (Zou et al., 2007; Huang et al., 2012a). In addition, invasive ecotypes have lower levels of defense chemicals such as tannins (Huang et al., 2010, 2012b, 2013; Wang et al., 2012b, 2016; Yang et al., 2013; Li et al., 2016). These patterns are thought to underlay the greater damage and/or higher performance of numerous herbivores from the native and introduced ranges (including candidate biocontrol agents, aboveground and belowground herbivores, and generalist herbivores from the native and introduced ranges) when they feed on Chinese tallow from invasive populations versus native populations (Siemann and Rogers, 2003d,c; Lankau et al., 2004; Huang et al., 2010; Wang et al., 2011b, 2012b, 2016; Yang et al., 2015b; Li et al., 2016). Invasive ecotypes of Chinese tallow were also found to have more rapid compensatory regrowth following herbivory and greater herbivore tolerance (Rogers et al., 2000, 2003; Rogers and Siemann, 2002, 2004; Zou et al., 2008; Wang et al., 2011b, 2016; Carrillo et al., 2014; Carrillo and Siemann, 2016). There appears to be specificity in the responses of Chinese tallow to types of herbivores (generalists vs. specialists, aboveground vs. belowground, feeding mode) in terms of tolerance and induced defenses including extrafloral nectar (Carrillo et al., 2012, 2014; Yang et al., 2013, 2015b).

4.4. Facilitation and enhanced mutualisms

Non-native invasive species may have greater establishment success due to facilitation by native species, which may either directly or indirectly make environmental conditions more favorable (Bruno et al., 2003). Chinese tallow was highly abundant and was more likely to be present in dense wax myrtle (*Morella cerifera* L. Small) shrub thickets than in surrounding floating marsh vegetation, suggesting that wax myrtle may have an overall facilitative effect on the invasion of Chinese tallow in similar ecosystems (Battaglia et al., 2009). The woody canopy

of wax myrtle provides perches and a food source for birds, and may facilitate dispersal of Chinese tallow seeds and other bird-dispersed species, thereby establishing a foci for Chinese tallow recruitment (Battaglia et al., 2009). The co-occurrence of Chinese tallow and wax myrtle may also be driven in part by overlapping periods of fruit ripening (Clark et al., 2004). However, once established Chinese tallow growth was inhibited by wax myrtle via competition for light (Battaglia et al., 2009). Chinese tallow seedlings have a competitive advantage over grasses when competing under the canopy of parent trees where light levels are lower and nitrogen levels are higher (Siemann and Rogers, 2003a).

Non-native invasive plants may have enhanced facilitation by soil biota in the introduced range compared to biota in the native range (Reinhart and Callaway, 2006). Niijer et al. (2008) found that Chinese tallow seedlings experienced significantly stronger positive interactions (growth and aboveground biomass) with active soils (non-sterilized) receiving fertilization, and had significantly higher mycorrhizal colonization levels in fertilized soils when compared to native species (sweetgum, blackgum, and water oak). Such unusual growth benefits outside of its native soil biota and from fertilized soils, the potential mycorrhizal mutualisms may provide Chinese tallow with a performance advantage over natives in the forest understory and may especially aid in its success in invading sites with increased anthropogenic nitrogen inputs (Niijer et al., 2008). In part, the high benefits from interactions with soil may reflect stronger mycorrhizal associations (Yang et al., 2015b), but they may also reflect enemy release from soil pathogens (Yang et al., 2013).

5. Management practices

5.1. Herbicide

Invasive plant management often involves the use of herbicide as a main control treatment, and many studies have tested how different herbicide types and the method and timing of application could affect the control efficacy. When targeting large individuals of Chinese tallow, injection appeared to be a more effective method of herbicide application than foliar applications (Johns et al., 1999), and the highest plant mortality occurred when herbicide was assimilated into perennating buds and organs (Bóo and Pettit, 1975; Wilson et al., 1975; Sosebee, 1983). In a study investigating several herbicide treatment methodologies for Chinese tallow (cut stump, basal bark, and foliar) using aminocyclopyrachlor (DuPont, Wilmington, DE), aminopyralid (Milestone VM™, Dow AgroSciences), fluroxypyr (Vista XRT™, Dow AgroSciences, Indianapolis, IN), imazamox (Clearcast™, BASF, Research Triangle Park, NC), triclopyr amine (Garlon 3A™, Dow AgroSciences), and triclopyr ester (Garlon 4™, Dow ArgoSciences), only triclopyr (ester and amine formulations) did not provide consistent control of root collar and lateral root sprouting (Enloe et al., 2015). In a study on the efficacy of imazapyr, triclopyr, and glyphosate using 'hack and squirt' application methodology, Gresham (2010) found that all three herbicides were effective on Chinese tallow with no residual effects on untreated native live oak (*Quercus virginiana* Mill.) within the experimental area.

The timing of herbicide application significantly affects the efficacy of herbicide for controlling invasive plants. Total nonstructural carbohydrate (TNC) accumulation in roots is a metric based on the fundamental ecophysiological process of carbohydrate storage (Glerum, 1980; Hopkins and Hüner, 1995), and it is often correlated with phenological development and is used to develop recommendations for effective herbicide treatments (Conway et al., 1999). For example, the timing of foliar herbicide application should occur when there is an increased downward translocation of TNC. Total nonstructural carbohydrate concentrations in Chinese tallow were found to be highest during leaf fall and lowest during leaf and seed development (Conway et al., 1999). Root carbohydrate sources supply energy for the increased

metabolic costs associated with the break in dormancy, bud break, and root and leaf development in the spring, which results in decreased root TNC levels (Hopkins and Hüner, 1995; Conway et al., 1999). Root TNC levels in Chinese tallow increase as the seeds begin to ripen and mature, with maximum levels prior to leaf fall and after fruit maturation (Conway et al., 1999). Therefore, greatest mortality should occur when foliar herbicide is applied during seed maturation and leaf fall.

5.2. Prescribed fire

Native forest ecosystems across the southeastern US invasion range of Chinese tallow are historically characterized by frequent, low intensity surface fires. Prescribed fires have therefore been tested for controlling the invasion of Chinese tallow. Chinese tallow can be damaged, and when small, killed by fire. However, Chinese tallow is considered a fire suppressor in the communities that it invades (Richardson, 2011b). The bark of Chinese tallow becomes thicker with age; indicating an increased fire resistance with age. As an aggressive sprouter, Chinese tallow can also survive fire as root-sprouts after top-kill (Grace, 1998). However, there is some evidence that prescribed fire might be an effective management option for Chinese tallow, especially following prior control treatments (Pile et al., 2017b). Studies have shown that if sufficient fuels are present, fire can reduce germination probability, and growing season burns may be hot enough to top-kill even larger trees (Grace, 1998; Burns and Miller, 2004). For example, a relatively low-temperature and fast-moving fire in a healthy coastal prairie in Texas reduced germination of Chinese tallow seeds at the soil surface by more than 50% compared to unburned controls or seeds buried 2, 5, or 10 cm below ground (Gabler, unpublished data). It is possible that hotter fires could also reduce the germination of buried seed as well. The ability of Chinese tallow to suppress fuels under its own canopy may suggest that only isolated trees or populations at an early stage of invasion can be controlled with fire unless additional control methods such as chemical or mechanical treatments are also applied (Grace et al., 2005).

5.3. Mastication

In addition to herbicide and fire, mechanical treatments are also applied to control Chinese tallow. Mastication in Chinese tallow dominated stands may reduce seed germination by reducing day-night temperature variation at the soil surface. However, reduced germination rates were only observed when the mulch depths resulting from mastication exceeded 5 cm (Donahue et al., 2004). Due to their large size and adequate nutritional resources, Chinese tallow seeds can emerge from deep mulch depths prior to requiring energy from photosynthesis if they do germinate (Bonner, 1989; Donahue et al., 2004). Because Chinese tallow facilitates rapid litter decomposition, mastication treatments can increase the horizontal continuity of the fuel bed, especially in communities where Chinese tallow is abundant (Grace et al., 2005). The wood of Chinese tallow may also be highly flammable (Tiller, 2015), providing an increased fuel source for fire following mastication. Given that prescribed fires have been frequently applied for the purpose of ecosystem restoration in southern forests, it is desirable to integrate prescribed fires into the management of Chinese tallow or other invasive species.

5.4. Biological control

Biological control can be an effective and low cost method for managing invasive plant species (Müller-Schärer et al., 2004). Several potential biological control agents with high host specificity and plant fitness impacts have been identified for Chinese tallow, including foliage feeders, root feeders, and gall formers (Zheng et al., 2005; Wheeler and Ding, 2014). Specifically, a classical biological control agent of Chinese tallow, the flea beetle [*Bikasha collaris* Baly

(Coleoptera: Chrysomelidae)], native to China was found to be specific to Chinese tallow, completing development only on the target weed (Huang et al., 2011; Wheeler et al., 2017). Damage by this species occurs both below and above ground as the larvae damage roots and the adults feed on leaves (Huang et al., 2011; Li et al., 2016). Host range testing of this species has been completed, and a USDA/APHIS technical advisory committee has recommended release (USDA/APHIS, 2016). Another species, *Gadirtha fusca* Pogue (Lepidoptera: Nolidae), is currently being evaluated and also shows promise as a safe and effective classical biological control agent (Wang et al., 2012c; Pogue, 2014). Other species are also being tested for biological control but not all will be safe for release (Steininger et al., 2013; Fung et al., 2017). Due to the reduced defense mechanisms of invasive ecotypes of Chinese tallow but their higher tolerance of damage, it is possible that biocontrol agents may reach high densities but not provide effective control of invasive populations (Wang et al., 2011b).

The recent emergence of a specialist herbivore in North America may increase the effectiveness of biocontrol of Chinese tallow. Already present throughout much of the invaded range, an adventive moth (*Caloptilia triadicae* Davis; Lepidoptera: Gracillariidae), believed to be of Chinese origin, was first discovered in the US in 2004 (Fox et al., 2012). This species was not an intentionally-introduced species but fortuitously has a limited host range in the US (Duncan et al., 2016). However, this moth may damage native populations of one native plant species (oysterwood; *Gymnanthes lucida* Sw.) as demonstrated in garden plots and ornamental plantings (Duncan et al., 2016).

5.5. Forest ownership patterns and land management

Land ownership and land management activities may increase or decrease the invasibility of forest communities. It was reported that private lands had more Chinese tallow invasion than public lands because private lands are less closely monitored, more frequently harvested, and lack policy incentives to implement invasion prevention measures (Colton and Alpert, 1998; Gan et al., 2009). Models evaluated by Gan et al. (2009) indicate that artificially regenerated forest stands could lower the risk of Chinese tallow invasion. However, timber harvesting will generally enhance the probability of tallow invasion by exposing mineral soil, creating an opening and reducing competition from dominant species (Johns et al., 1999; Pile et al., 2017a). Site preparation and artificial regeneration on harvested sites were suggested to reduce the likelihood of future invasions by Chinese tallow (Wang et al., 2014), but this not been tested experimentally.

5.6. Integrated management

Application of a series of treatments in combination may be most effective in the management of Chinese tallow, especially when using an integrated approach that combines treatments to suppress the invader while promoting the resistance of the community to invasion. For example, in slash pine (*Pinus elliottii* Engelm.) dominated maritime forest stands, a combination of mastication applied in the spring, followed by a fall application of foliar herbicide to target regeneration, and a growing season prescribed fire two-years later was the most effective combination tested in terms of reducing Chinese tallow while also promoting understory diversity and reducing shrub density (Pile et al., 2017b). Despite Chinese tallow's high competitive ability, actively promoting native plant diversity and abundance through native seed or plant addition can enhance community resistance to invasion. Even in an early restoration context, where open, disturbed areas are exposed to full sun and natives are present only as seed (where Chinese tallow's advantage should be greatest), competition with native plants can nevertheless reduce Chinese tallow invasion success, especially in stressful habitats. Competition between Chinese tallow and native grass and forb species, when all species were initially present only as seed, significantly reduced Chinese tallow germination, survival, seedling

abundance, and seedling performance in greenhouse experiments simulating flood- and drought-stressed communities (Gabler and Siemann, 2013b). Additionally Chinese tallow germination and survival, in general, and seedling abundance and performance, in some sites, in an 11-site field experiment spanning a moisture gradient were reduced (Gabler and Siemann, unpublished data). Although it has not been tested, the combination of successful biological control agents with other treatments aimed at reducing Chinese tallow populations or site invasion potential may effectively reduce the establishment and spread of Chinese tallow. The effectiveness of control will likely vary among sites and among years depending on the suitability of conditions for the target invasive plant (Gabler and Siemann, 2012). For Chinese tallow, reinvasion pressure is likely to be intense in most years in the most suitable sites but in sites with marginal conditions for young plants, reinvasion pressure may be light in most years; the latter may allow for highly effective and/or inexpensive control methods (Gabler and Siemann, 2012, 2013b,a). Furthermore, if sites or time periods with low reinvasion pressure can be identified ahead of time, strategically opportunistic management is possible where control methods scale with reinvasion intensity and site selection prioritizes low cost, high impact areas.

Management actions themselves are disturbances. Therefore, understanding which disturbances and conditions enhance or impede invasion is important not only to determine the drivers of invasion but also to identify the best options available for management (Hobbs and Humphries, 1995). Management of invasive species requires targeting treatments to the species and ecological conditions that favor the desired outcome for the community. For Chinese tallow, this will require understanding the site level factors and community traits that enhance invasion (Fig. 2). Managing for desired community structure, composition, and function may become even more important than single-species management as the establishment of one invasive species may lead to more invasions [i.e., invasional meltdown, (Simberloff and Von Holle, 1999; Simberloff, 2006)]. Management should be designed and implemented with consideration of the historical functions and processes that have characterized the target ecosystems, as these may be important to building invasion resistance in the community, or maintaining function in the face of invasion. Often, maintaining or restoring the structure and ecosystem processes known to favor native species can increase community resilience and resistance and thereby reduce invasion potential (D'Antonio and Chambers, 2006).
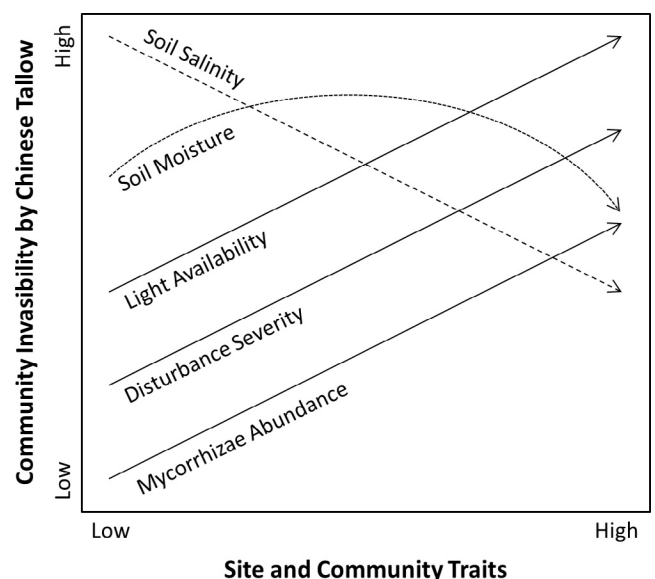
Fig. 2. Hypothesized relationship between site and community traits and community invasibility by Chinese tallow for forest and prairie ecosystems in the southern USA. Relationships are generalized from a wide body of literature cited in the text.

6. Future research and management needs

Despite increased application of control measures and management efforts, Chinese tallow invasions, and biological invasions in general, continue to degrade native ecosystems. Currently, assessing the impact of invasive species and developing practical solutions to invasion problems have lagged behind scientific studies on biogeographical patterns and ecological mechanisms (Pyšek and Richardson, 2010). There is a pressing need for research on repairing/restoring ecosystems following invasion and after control treatments, especially in context of legacy effects, secondary invasions, and variable ecosystem responses to different control treatments (Pyšek and Richardson, 2010; Gabler and Siemann, 2012). Therefore, we conclude our review by identifying some critical knowledge gaps in the invasion ecology and the management of Chinese tallow that should be addressed in future research.

Our understanding of the degree to which Chinese tallow alters the plant communities it invades is limited. Knowledge gaps include the full effects of Chinese tallow invasion at multiple scales and levels of organization within communities and ecosystems. Chinese tallow is documented as an aggressive invader of coastal grassland communities, resulting in transformational changes to the structural and functional properties of grasslands into woodlands. However, less is known about the ecological impacts Chinese tallow has in forested ecosystems other than direct changes in stand structure and composition and basic nutrient cycling (Camarillo et al., 2015). Additionally, it is important to determine if Chinese tallow is a passenger or driver of ecological change in forested communities as this could have important underpinnings for management. We know Chinese tallow can establish under an intact forest community, but it is not well-understood whether Chinese tallow changes aspects of ecosystem function through its establishment and population growth, or if Chinese tallow is a symptom of ecological change prior to or at the time of invasion. For example, Chinese tallow can alter fuel characteristics and impede fire spread; however, it is not clear to what extent fire suppression has promoted invasions by Chinese tallow or to what extent invasions by Chinese tallow have led to functional changes in the community by reducing fire frequency.

The competitive ability of Chinese tallow in relation to native species in terms of long-term dominance and persistence is not clear. Although Chinese tallow has fast growth rates, it is also relatively short-lived and short in stature when compared to native tree species. Furthermore, buildup of soil pathogens in areas dominated by Chinese tallow can reduce Chinese tallow seedling survival and reduce its long-term success (Nijjer et al., 2007). It is unknown whether Chinese tallow will achieve and maintain a dominant position in the forest canopy through the competitive exclusion of other fast but slower growing, and longer-lived, larger-statured native tree species. In the single study of Chinese tallow stand persistence, it appeared that native trees have high per capita success compared to Chinese tallow but are recruitment limited (Siemann and Rogers, 2006). Recent advances have been made to quantify the growth and taper of Chinese tallow (Tian et al., 2017), however, they have not been compared to tree species in the introduced range.

There is a need to quantify ecological differences between the ecosystems and communities being invaded by Chinese tallow versus those that are resistant to invasion, which could help identify site-level conditions that aid in invasion success and reinvasion pressure. Recent modeling efforts (Gan et al., 2009; Wang et al., 2012a, 2014; Suriyamongkol et al., 2016) and observational studies (Gabler and Siemann, 2013b; Paudel and Battaglia, 2015; Pile et al., 2017a) have provided a framework for understanding invasion potential associated with biotic and abiotic conditions. However, more experimental and observational studies that make direct comparisons between communities are necessary to better understand community susceptibility to invasion. In addition, advancements in invasion science and applications of modeling invasion dynamics will require shifting from linear models of invasion to those that include a more complex socio-ecological network (Richardson, 2011a; Hui and Richardson, 2017). As outlined by Hui and Richardson (2017), this will require better data and statistical approaches that include adaptive cycles and network analyses.

There are few studies that attempt to compare the ecological processes that govern Chinese tallow populations in the native and invasive ranges. Studies that attempt to compare Chinese tallow population types have primarily focused on biotic interactions and the effect of abiotic biotic conditions on performance in short-term experiments. However, using a biogeographical approach to understand differences regarding the abundance, interaction strengths, and ecosystem impacts of Chinese tallow in native and invasive ranges may provide a broader level of ecological understanding for this species and for the foundations of invasion ecology.

Testing methods for the control of invasive species that are most relevant to managers by using an ecosystem management approach and determining which control methods produce desired gains in native plant cover, density, or biomass have been identified as major gaps in the evidence-based management of invaders. Current management approaches focus mostly on the efficacies of the prescribed treatments specifically in controlling Chinese tallow without considering the ecology of the plant communities subjected to the invasion control efforts. Future management should consider post-removal legacy effects, secondary invasions, and prediction of ecosystem response to different forms of manipulation (Pyšek and Richardson, 2010; Gabler and Siemann, 2012). In addition, frequent prescribed fire is cited as a potential management option to control Chinese tallow. However, this has not been tested experimentally. There is little information regarding the sprouting ability of Chinese tallow subjected to repeated top-kill, and it is not clear what type of prescribed fire regime (e.g., season, frequency, and intensity) would result in the most effective control of Chinese tallow while simultaneously restoring native communities.

As ecological communities are pushed further outside their range of natural variability because of increased human pressure on natural resources, climate change, and an era of increasing megadisturbances, more novel communities are likely to be encountered in the future (Hobbs et al., 2009; Millar and Stephenson, 2015). As a result, it also becomes important to understand how non-native species may potentially replace or augment lost or reduced ecosystem services or functions. Future research may need to determine how Chinese tallow could fill important ecological role in heavily infested communities that may be too expensive to restore. In addition, determining how climate change may influence the invasion dynamics, interactions, and competitive ability of Chinese tallow will be important for managing Chinese tallow in the future.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.08.023.

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