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Differences in cold hardiness between introduced populations of an invasive tree

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Abstract The potential for populations of exotic invasive plants to differ in their response to stressful environmental conditions is an underexplored issue in determining invasive species' range limits. Introduced genotypes may differ in response to climatic, edaphic, or biotic factors within their introduced range leading to differences in potential ranges among populations. We examined differences in cold hardiness (resistance and tolerance to winter conditions and freeze events) among Chinese tallow tree (*Triadica sebifera* (L.) Small) seeds and seedlings from two genetically distinct populations in the northernmost portion of its introduced U.S. range (North Carolina and South Carolina). Seed germination from these two sources was compared between fall plantings (mimicking natural dispersal timing) and spring plantings (occurring post-frost) as well as among areas within and inland of Chinese tallow's core coastal distribution in South Carolina. Overwinter seedling survival and damage were also assessed among seedlings planted in the piedmont of South Carolina and following artificial freeze events in the lab. Seeds and seedlings from South Carolina sources showed greater reductions in germination success by inland winters, greater winter damage in field plantings in the piedmont, and lower survival after prolonged freezes than those from North Carolina. These results indicate that differences in cold hardiness exist among introduced populations of Chinese tallow and suggest that genotypes from North Carolina possess greater potential for expansion into areas with more severe winters. Differences among introduced populations should be considered when evaluating the potential range expansion of Chinese tallow and other invasive species.

Keywords Germination · Invasive species · Range limitation · *Triadica sebifera* (L.)

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Introduction

Understanding the factors that limit plant species' ranges is a subject of great importance for predicting the potential of recently introduced species to expand into new areas as well as range shifts driven by global climate change. Climatic conditions, such as mean

annual rainfall, seasonality of rainfall, and minimum daily temperature, are generally considered the predominant factors determining the high-latitude limits of plant species' ranges (Morin et al. 2007; Woodward 1987). Seed dispersal, herbivory, parasitism, and competition can also affect species ranges but in most cases are considered secondary in importance (Case et al. 2005; Primack and Miao 1992) at high latitudes, where tolerance of low temperatures often drives local selective processes (Loehle 1998). Ecotypic differences in morphological, physiological, and life history traits in response to local climatic conditions are recognized for many plant species (Keller et al. 2009; Loehle 1998; Nardini et al. 2000; Wagner and Simons 2008), but the potential for different introduced populations of exotic invasive species to expand beyond their original sites of introduction at different rates or to different extents have not been thoroughly investigated. In most cases, the invasive range of a species has been predicted by describing the climatic conditions that contain the native range and determining which areas within the possible invasive range fit within that climate envelope (Peterson 2003). These methods may not be sufficient if there are differences among introduced populations that affect their range limits (Beaumont et al. 2009).

Populations of exotic invasive species may differ in their potential to expand beyond their sites of introduction for myriad reasons. Founder effects, such as the number of individuals introduced, their identity (i.e. particular source populations), and the amount of genetic variation introduced, could determine the physiological suitability and ability to adapt to local climatic conditions. The degree to which the climate in the introduced range matches the native range may also determine the success of the introduction, the rate of expansion, and the eventual extent of the introduced range. In addition, evolution after introduction in physiological or morphological traits may lead to divergence of populations in response to various environmental stress factors (Caño et al. 2008; Donohue et al. 2005; Evans and Cabin 1995; Maron et al. 2007; Rogers and Siemann 2004) and environmental variation (Keller et al. 2009; Leger and Rice 2007; Montague et al. 2008). Such differences among introduced populations could result in certain populations having greater or lower potential for range expansion.

In this paper, we examine whether there are differences in the seed germination and seedling

survival in response to winter conditions (minimum temperatures and freeze events) between two genetically distinct, regional populations of the invasive species Chinese tallow tree (*Triadica sebifera* (L.) Small, Euphorbiaceae; previously known as *Sapium sebiferum*) in its introduced range in North America. We use Chinese tallow because the northern portion of its range in the United States (U.S.) is believed to be limited by winter conditions (Pattison and Mack 2009) and genetically determined differences in allocation to herbivory defense and growth have been found among different introduced populations in the southeastern U.S. (Siemann and Rogers 2001). Different populations within the introduced range experience different selective pressures (Siemann et al. 2006) and stem from different introductions (DeWalt et al. 2011) such that they may also differ in their cold hardiness (i.e. resistance and tolerance to damage due to cold and freezing temperatures).

Estimates of Chinese tallow's potential invasive range made using the climate model CLIMEX, which match climate parameters from the native range to conditions in North America, suggest that it is capable of expanding 500 km northward and inland of its current southeastern U.S. distribution (Pattison and Mack 2008). This predicted expansion is primarily because Chinese tallow grows naturally in colder climates within its native range than its current U.S. range (Lee 1956). Successful germination of seeds collected in South Carolina and planted beyond Chinese tallow's current introduced range in the southeastern U.S. supported these climate-based range estimates (Pattison and Mack 2009). However, Chinese tallow in North Carolina, which represents the northernmost portion of Chinese tallow's current range in the southeastern U.S., was found to be distinct from neighboring South Carolina populations based on Bayesian clustering analysis of six microsatellite loci (DeWalt et al. 2011) and may pose an additional risk of inland or northward expansion.

To examine whether introduced populations near the northernmost limit of Chinese tallow's current range in the southeastern U.S. may pose different possibilities of expansion into northern or inland areas that experience colder conditions than within its current range, we studied the response of seeds and seedlings from North Carolina and South Carolina populations to winter conditions in areas within the species' current core range in the coastal region of

South Carolina, as well as in the colder midlands and piedmont regions beyond its current range. As these populations represent the northernmost portion of Chinese tallow's range in the U.S., they likely pose the greatest threat of northward expansion beyond their current range. We asked the following questions: (1) do seeds of Chinese tallow from North Carolina and South Carolina populations differ in their germination success across the three major edaphic and climatic regions of South Carolina (coastal, midlands, and piedmont), (2) are differences in germination across these regions driven by winter conditions, (3) do seedlings grown from seed collected from different populations differ in the extent of cold-induced stem damage, budbreak timing, or overwinter survival rate under different winter regimes or freeze durations, and (4) are differences in cold-hardiness among these populations sufficient for differences in range limits to occur? To address these questions, we conducted two field experiments and one lab experiment.

We examined seeds and seedlings because these life history stages are under strong selective pressure, particularly as they relate to climatic factors. Unsuitable timing of germination can result in exposure of seedlings to fatal freeze events (Marshall 1968; Woodward et al. 1990), and plants are most vulnerable to cold temperatures and other environmental stresses at the seedling stage (Larcher 2003). Additionally, the presence of profuse seed production among isolated Chinese tallow transplanted as saplings to sites well beyond its current invasive range (I. Park, personal obs.) indicates that later life history stages are unlikely to exclude its northward expansion.

Methods

Study species

Chinese tallow is an invasive species of Chinese origin that was first introduced into the U.S. in the late eighteenth century to Savannah, Georgia (Bell 1966) and Charleston, South Carolina (Elliott 1824; Hunt 1947; Michaux 1803; Schoepf 1911). In the early twentieth century, the Foreign Plant Introduction Division of the Bureau of Plant Industry helped establish plantations of Chinese tallow across the southeastern U.S. to make soap from the sarcotesta surrounding the seeds (Jamieson and McKinney 1938). It has naturalized along the Gulf Coast and East Coast of the southeastern U.S. from east Texas to southern North Carolina, where it has become a dominant species primarily in coastal ecosystems (Bruce et al. 1997). It is also found in small, scattered stands in non-coastal areas. Chinese tallow utilizes generalist pollinators (Hayes 1979) and is extensively dispersed both by birds (Renne et al. 2000, 2002) and by humans as an ornamental and agricultural plant (Bruce et al. 1997; Hayes 1979). Chinese tallow tends to have lower levels of herbivory than native trees of similar life-history strategy (Siemann and Rogers 2003) and displays increased survivorship and growth in soils not previously colonized by conspecifics (Nijjer et al. 2007). Additionally, Chinese tallow has been shown to thrive under a wide variety of moisture regimes (Barrilleaux and Grace 2000, Butterfield et al. 2004) in both direct sun and full shade (Jones and McLeod 1989) and is tolerant of a wide variety of soil types and drainage conditions (Bruce et al. 1997).

Field germination

For the purposes of this experiment, South Carolina was divided into three areas that correspond to major transitions in soil type and minimum daily temperatures: piedmont, midlands, and coastal regions. Currently, Chinese tallow has large, established populations only in the coastal region of South Carolina. The midlands region represents a low, inland sandy region with reduced temperatures compared to the coastal region. The piedmont region represents the coldest and most inland region, as well as an area of higher elevation and topographic relief as compared to midlands or coastal areas. Within each region, three sites were identified in hardwood forest near water sources in locations with analogous light and moisture availability to coastal sites in which Chinese tallow was commonly observed. One piedmont field site was flooded during the course of the experiment, and therefore this site was omitted from all analyses.

Seeds were collected from trees in various sites of South Carolina and North Carolina. In South Carolina, seeds were collected in November 2005 from 18 trees in the Ace Basin National Wildlife Refuge, the cities of Monk's Corner and Mt. Pleasant, and the Hobcaw Barony Wildlife Refuge (approximately 120 km apart). Seeds were collected in North Carolina at the same time from 17 trees in and around the city of

Wilmington. All collection sites were located within 50 km of the coastline. North Carolina collection sites were located at approximately 34.2°N, and South Carolina sites were located between 32.5° and 33.4°N (Table 1). We refer to all collections in each state as a "source population" for ease of discussion even though they represent several populations collected over a large geographic area, particularly in South Carolina. In addition, South Carolina individuals are genetically similar to each other but distinct from the Wilmington, North Carolina population according to microsatellite markers (DeWalt et al. 2011). Chinese tallow tree does not currently occur in large stands north or inland of Wilmington.

The waxy sarcotesta surrounding all seeds was removed by stirring seeds in a water and soap mixture (Alconox, White Plains, NY). The removal of the sarcotesta of Chinese tallow seeds simulates passage through a bird's digestive system, which removes most of the sarcotesta (Renne et al. 2001). In addition,

it has been found to reduce the germination time and result in a higher germination during the first year (E. Siemann and W. E. Rogers, unpublished data).

In late November 2006, 21 pieces of 20-cm long, 15-cm diameter PVC pipe were placed in a 1-m interval grid at each site. These pipes were buried so that 2.5–3.5 cm remained above ground, and the removed soil was placed in the pipes at the same level as the soil surrounding the pipe. Soil was removed in a plug, and topsoil and litter remained on top and were largely intact when replaced in the pipe. In each pipe, five seeds from one source population were buried 1.5 cm below the soil surface. Planting at this depth has been shown to be within the optimal range of planting depth to stimulate germination of Chinese tallow (Donahue et al. 2004; Renne et al. 2001). Seed from the two populations were assigned to pipes in a completely randomized design for each site with a total of 10 replicate pipes for each source population. Hardware cloth was fixed over the mouth of all pipes

Table 1 Characteristics of the seed collection sites and field sites used to test germination success of Chinese tallow in three regions of South Carolina

Sites	Min. temp. 1970–2010 (°C)	Min. temp. 2007 (°C)	MAP (mm)	Latitude	Longitude	Min. soil temp. (°C)
Collection sites						
North Carolina						
Wilmington	−4.21	–	1194	34.20°	−77.90°	–
South Carolina						
Hobcaw	2.57	–	1369	33.38°	−79.90°	–
Moncks Corner	1.81	–	1202	33.19°	−80.01°	–
Ace Basin	3.21	–	1251	32.52°	−80.30°	–
Field sites						
Piedmont						
Clemson	−0.62	1.67	1217	34.62°	−82.80°	1.14
Greenwood	−0.72	1.57	1158	34.11°	−82.12°	2.59
Midlands						
Peedee	0.45	3.02	1203	34.30°	−79.30°	3.64
Sandhills	0.32	2.47	1166	34.13°	80.87°	4.13
Edisto	1.18	3.41	1168	33.35°	81.32°	2.87
Coastal						
Hobcaw	2.57	6.31	1368	33.20°	79.16°	5.64
Coastal	3.68	6.04	1230	32.47°	80.40°	5.38
Nemours	2.11	5.17	1254	32.60°	80.73°	3.65

Mean minimum temperature of the coldest month between 1970 and 2010 (Min. Temp. 1970–2010), minimum temperature in 2007 (Min. Temp. 2007) and mean annual precipitation (MAP) were taken from 1970 to 2010 Prism climate data (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 23 May 2011.) Minimum soil temperature data in January 2007 were collected at each site using three Hobo pendant sensors planted throughout each site at similar depth to outplanted seeds

to prevent rodents, birds, or other animals from removing seeds.

To determine whether germination was driven by winter temperatures as opposed to edaphic or biotic differences among regions, we compared germination rates of the fall plantings placed in the ground in November 2006 with spring plantings placed in the ground in mid-March 2007, after the last frost. For spring plantings, additional pipes with a similar but independently randomized design were placed adjacent to each existing site. Germination success was recorded and resulting seedlings removed through October 2007 for both spring and fall plantings. Second-year germination was recorded in August 2008, at which point all remaining material was removed from each site. Seedlings that died left behind distinctive stems and were easily detected, although seedling death prior to observation was rare. Lower germination for fall than spring plantings in a region would indicate that cold temperatures were responsible for the reduction in germination.

Germination occurred primarily in the first year of planting, before October 2007. No second-year germination occurred in four sites after this point, and post-October germination of more than one seed was detected in only two sites. As second-year germination was rare and its addition did not alter the significance or interpretation of the results, these data were excluded from all analyses.

Hobo[TM] pendant temperature sensors (Onset Computer Corp., Pocasset, MA) were buried inside and adjacent to a pipe at one site from each region (Clemson, Sandhills, and Coastal R.E.C.) in order to examine the extent to which the pipes provided insulation for the seeds. No significant differences were detected between temperature sensors placed within and adjacent to pipes ($F_{1,461} = 0.00$, $P = 0.98$).

Statistical analyses testing for differences in germination success were conducted using Proc GLIMMIX in SAS/Stat v9.1 (SAS, Cary, NC). Region of planting (coastal, midlands, piedmont), planting season (fall or spring), and source population (North Carolina or South Carolina) were examined as main effects on seed germination, while site within region of planting (2–3 depending on the region) and all interactions with site were treated as random effects. The response variable was the number of seeds out of five per pipe that germinated. Because each seed either germinated or failed to germinate, the data were analyzed using a binomial response distribution and a logit link function. Denominator degrees of freedom for all tests were calculated using the Kenward-Rogers adjustment, which is recommended for unbalanced data and inclusion of among-site random effects (Littell et al. 2006). This method resulted in non-integer denominator degrees of freedom in many cases. To reduce the Type I error rate, the P values for all effects were adjusted according to Sidak's inequality.

Seedling field response to winter conditions in the piedmont

Overwinter mortality in Chinese tallow occurs primarily in plants under 30 cm tall (Renne 2001), suggesting that the seedling stage is critical in limiting expansion into areas with winter conditions colder than coastal areas. To determine the effects of winter conditions on the growth and survival of Chinese tallow seedlings, 20 seedlings from each source population were planted in October 2007 in a forested site at the South Carolina State Botanical Garden in Clemson, SC, which is in the piedmont region. Seedlings were planted in the field in a 1-m spaced grid using to a completely randomized design. The study site was in an area in which naturalized Chinese tallow seedlings were found. All experimental seedlings were obtained from seeds that were sown 13 mo earlier and kept in a growth chamber at 25 °C until transplantation.

Height of all seedlings was recorded before the first freeze, which occurred on 18 December 2007. All seedlings were between 7 and 13.5 cm in height at the time of transplant. No differences in post-germination mortality or seedling height were detected between populations prior to initial observation of winter damage. Survival, stem damage, and bud status of these seedlings were monitored until June 2008. The most visible damage from freeze events occurred as top-down tissue damage, which resulted in a reduction in the height of each seedling. Therefore, stem damage was monitored through repeated measurement of living stem tissue height. When possible, measurements were taken immediately before and immediately after freeze events. Additionally, survival and budbreak of seedlings were measured 6 weeks after last frost.

We used a repeated-measures analysis with a normal probability distribution in Proc GLM to compare height loss between source populations across measurement periods. Differences between

the two populations in post-winter survival and bud-break, which were inherently binomial in response, were analyzed using Proc LOGISTIC.

Seedling lab response to extended freeze durations

We also investigated the effect of freeze duration on the survival, growth, and damage of Chinese tallow seedlings from the two source populations. Seeds from both populations were sown simultaneously, and resulting seedlings were grown at 25 °C under a 12-h light cycle for 9 mo. All seedlings were then exposed to 5 days of alternating temperatures of 25 °C when under light and 5 °C under dark conditions and measured for height. Seedling height averaged 10.9 cm, and no significant differences in the height of seedlings from different source populations were detected prior to treatment. Seedlings were then placed in a 5 °C chamber for 24 h, and the temperature was dropped to −7 °C at a rate of 1° per h. Seedlings were maintained at −7 °C for one of five freeze durations: 6, 48, 96, 192, or 384 h in separate trials. Sample sizes differed among source populations because of differences in availability of seed. In each freeze duration treatment, sample sizes were 11–12 for North Carolina and 6–7 for South Carolina.

After treatment, temperature was returned to 5 °C in the same fashion, and seedlings were maintained at 5 °C for 24 h. Height was recorded, and seedlings were returned to 25 °C. After 6 weeks, seedling height and survival were recorded again, and changes in height were contrasted across treatments and source populations. Regression (height) and logistic regression (survival) analyses were conducted using Proc GLM and Proc LOGISTIC respectively.

Sample sizes for the seedling field and lab experiments were relatively small, but the results were consistent with those of the seed field experiment, which had robust sample sizes. For all statistical tests, significant differences were determined at the $P < 0.05$ level.

Results

Field germination

Across planting seasons and regions, North Carolina seeds had higher germination success than South Carolina seeds (Table 2; Fig. 1). However, there were

Table 2 Type 3 test of fixed effects for germination of Chinese tallow seeds collected from different source populations (North Carolina or South Carolina) and planted in piedmont, midlands, or coastal regions of South Carolina in the fall or spring season

Effect	df	F	P
Population (P)	1, 305	13.58	**<0.001**
Planting region (R)	2, 9.95	2.41	0.140
Planting season (S)	1, 9.95	2.28	0.162
P * R	2, 305	8.81	**0.002**
P * S	1, 305	4.63	**0.032**
R * S	2, 9.95	0.32	0.732
P * R * S	2, 305	1.14	0.321

Significant P values are in boldface

significant population × planting season and population × planting region interactions. For seeds planted in the fall, those from the North Carolina source population had higher germination success than those from South Carolina in piedmont sites, but germination success between source populations was similar in midlands and coastal regions (Fig. 1a). For seeds planted in the spring after the last frost, no differences in germination were detected between North Carolina and South Carolina seeds planted in any of the three regions (Fig. 1b). In fall plantings, germination of South Carolina seeds was significantly lower in piedmont than coastal sites (Fig. 1a), whereas no significant differences were detected in germination of South Carolina seeds among regions in spring plantings (Fig. 1b). Germination of North Carolina seeds was lower in midlands sites than coastal or piedmont sites regardless of planting season.

Seedling field response

Overall seedling mortality was 60.3 % in the piedmont field site, and there were no significant differences between source populations in survival ($F_{1,38} = 1.85$, $P = 0.17$) or date of budbreak ($F_{1,19} = 0.89$, $P = 0.36$). Beginning in mid-winter, however, South Carolina seedlings suffered significantly more stem damage than North Carolina seedlings ($F_{1,38} = 6.25$, $P = 0.017$; Fig. 2). Height loss was greatest in December and January. During the spring, South Carolina seedlings were also significantly less likely to successfully break bud than those from North Carolina
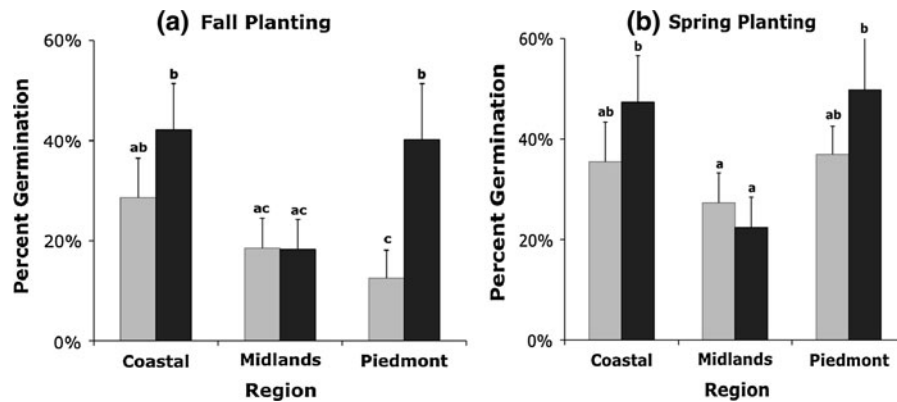
(a) Fall Planting

(b) Spring Planting

Fig. 1 Germination of North and South Carolina seeds by region of planting for fall (**a**) and spring plantings (**b**). Different *lowercase letters* denote significant differences between source populations among planting regions for each planting season as determined by LS means comparisons. *Gray bars* represent South Carolina seeds, while *black bars* represent North Carolina seeds
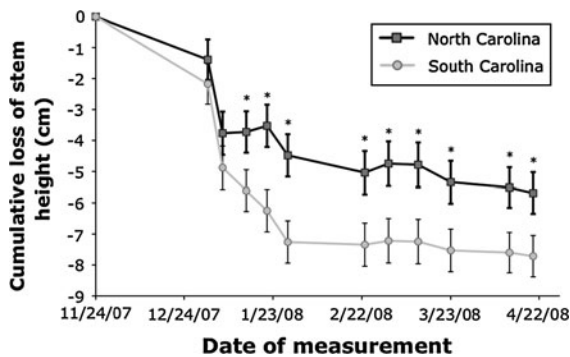

Fig. 2 Relative height loss of seedlings planted in the South Carolina State Botanical Garden, Clemson, SC. *Asterisks* denote dates for which significant differences between source populations were detected. Measurements began before the first frost, which was 2 weeks after initial planting, and continued until budbreak began in late April, well after the last frost

Fig. 3 Survival rate of Chinese tallow seedlings 6 weeks after exposure to 6, 48, 96, 192, or 384 h at −7 °C. Significant differences between populations were found for all freeze durations

($F_{1,38} = 5.32$, $P = 0.027$), possibly due to the higher levels of stem damage they sustained.

Seedlings response to extended freeze durations

Significant main effects of source population ($F_{1,79} = 7.54$, $P = 0.006$) and artificial freeze duration ($F_{1,79} = 21.63$, $P < 0.001$) but not their interaction ($F_{1,78} = 1.42$, $P = 0.24$) were detected on seedling survival in the lab experiment (Fig. 3). Six weeks after freeze events, survivorship of seedlings from both source populations was significantly lower for the longer duration freezes. North Carolina seedlings had significantly higher survivorship than South Carolina seedlings for freezes longer than 96 h
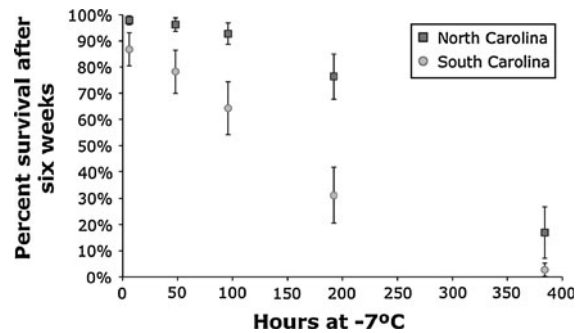
duration (Fig. 3). Height loss, as measured on plants that survived 6 weeks after freezing, did not significantly differ between populations ($F_{1,78} = 0.37$, $P = 0.54$).

Discussion

Source populations differ in cold hardiness

Our field and lab experiments all demonstrated that South Carolina seeds and seedlings had lower cold hardiness than those from North Carolina. Seeds from the South Carolina source population showed substantially lower germination success in the colder piedmont (12.5 %) than in the warmer coastal region (28.6 %), whereas germination of North Carolina

seeds was similar across regions. Winter conditions appeared to drive the lower germination of South Carolina seeds in inland sites as lower germination was only found among fall-planted and not spring-planted seeds. South Carolina seedlings also displayed greater overwinter stem damage in the piedmont and lower survival after artificial freezing events than North Carolina seedlings. As the northern border of Chinese tallow's invasive U.S. range is generally believed to be limited primarily by cold temperatures (Pattison and Mack 2008), these differences likely have implications for invasiveness and future range expansion. Additionally, as winter temperatures during this experiment were mild compared to average conditions (Table 2), this study likely represents a conservative estimate of cold restriction of Chinese tallow within this range.

Regional differences not associated with winter conditions were also detected, as germination of North Carolina seeds was significantly higher in coastal and piedmont sites than in midlands sites across both fall- and spring-plantings. Soils at midlands sites had a higher sand content than the piedmont and were more prone to desiccation than coastal sites (I. Park, personal observation). Although the germination success of North Carolina seeds was lower in the midlands than the other two planting regions, it was similar to the germination success of South Carolina seeds in coastal regions where Chinese tallow is abundant. Chinese tallow has also been found to survive on sandy soils and soils that exhibit periodic desiccation in other portions of its range (Bruce et al. 1997). Therefore, the lower germination success of North Carolina seeds in the midlands than on the coast or piedmont likely represents a competitive advantage by North Carolina seeds in coastal and piedmont areas rather than a disadvantage or exclusion of these genotypes from midlands sites. As all spring-planted seeds in the midlands showed similar germination to seeds located in coastal regions where it is highly invasive, it is highly unlikely that biotic or other local edaphic factors play a substantial role in restricting Chinese tallow from inland expansion by reducing germination success.

Explanations for differences between source populations in cold hardiness

The differences in cold hardiness between the two introduced source populations (North and South Carolina) as demonstrated with our field and lab experiments could result from maternal effects, founder effects, post-introduction evolution, or a combination of these factors. Differences in seed characteristics such as size, mass, and permeability of the seed coat due to different maternal growing conditions (maternal effects) can affect the germination requirements of seeds (Baskin and Baskin 1973; Nelson et al. 1970; Quinn 1977). Thus, seeds collected in North Carolina may have been less susceptible to winter temperatures and freezes because of the growing conditions of the maternal trees.

As winter temperatures are relatively similar across the areas inhabited by the North and South Carolina populations, it is unlikely that there was sufficient post-introduction selective pressure to explain the observed differences in cold hardiness. A more likely explanation is that the observed differences in cold hardiness among the introduced source populations are the result of founder effects, and that the founding individuals of the two populations possessed differing tolerance to cold. The specific introduction history of the North Carolina population is not known, but genetic analyses conducted using six microsatellite loci suggest that it arose from a different native source than the one that gave rise to the South Carolina populations (DeWalt et al. 2011). The North Carolina population is genetically more similar to populations in Texas, Louisiana, Alabama, Mississippi, and Florida than to those in South Carolina or Georgia (DeWalt et al. 2011). Preexisting differences in cold hardiness between native source populations may therefore be preserved in the introduced range. To distinguish between maternal effects or genetically determined differences in cold tolerance, an experiment would need to be conducted using seeds collected from a common garden containing trees grown from North Carolina and South Carolina stock. Whichever the reason for the differences in germination success and seedling performance, the conclusion is the same: seeds dispersed or planted from North Carolina sources were less adversely affected by winter conditions than those from South Carolina sources.

Implications for possible range expansion

The potential northern range of Chinese tallow tree is likely much more extensive than the current distribution along the coast in the southeastern U.S. Seeds of

Chinese tallow appear capable of germinating successfully throughout the coastal, midlands, and piedmont regions of South Carolina. These results are consistent with predictions that Chinese tallow is capable of germinating far north and inland of its current range in the U.S. based on the climate in the native range (Pattison and Mack 2008, 2009) and using spatially-explicit time-series projections (Wang et al. 2011). The novelty of our findings is that Chinese tallow from North Carolina appears less limited by cold than those from South Carolina. Thus, the potential invasive range of the North Carolina genotypes may extend into colder areas than previous field experiments conducted by Pattison and Mack (2009) using South Carolina genotypes indicated. Winter conditions in the piedmont likely reduce the likelihood of initial establishment but may not be sufficient to prevent expansion after the establishment of a few individuals capable of producing an intense seed rain (Siemann and Rogers 2006). Although additional factors may exist that could play a role in the northward expansion of these populations, the differences in seedling damage and germination success among fall-planted seeds appear to be the result of differing tolerance to winter conditions among North and South Carolina populations. As cold hardiness is commonly found to be a limiting factor to the fitness of temperate tree species near their northern range limits (Loehle 1998) and Chinese tallow currently established in North Carolina appear to be less vulnerable to winter conditions in inland areas, management efforts should prioritize control of the North Carolina population to prevent the spread of Chinese tallow.

This study shows that ecologically important physiological differences can exist between introduced populations of invasive species, even when those populations exist in close proximity and inhabit similar climate conditions. Phenotypic differences among introduced populations have been detected for other invasive plants (Keller et al. 2009; Maron et al. 2004; Parker et al. 2003) and may play a role in the ability of invasive species to expand into novel habitats (Dlugosch and Parker 2008; Parker et al. 2003). Thus, when studying post-invasion selection and determining the potential invasive range of a species, it is necessary to consider not only physiological differences between native and invasive populations but also differences among invasive populations that could lead to different range limits (Beaumont et al. 2009). Management plans based on characteristics of plants from one population may not hold true for plants drawn from another population.

References

Barrilleaux TC, Grace JB (2000) Growth and invasive potential of *Sapium sebiferum* (Euphorbiaceae) within the coastal prairie region: the effects of soil and moisture regime. Am J Bot 87:1099–1106

Baskin JM, Baskin CC (1973) Plant population differences in dormancy and germination characteristics of seeds: heredity or environment? Am Midl Nat 90:493–498

Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. Divers Distrib 15:409–420

Bell M (1966) Some notes and reflections upon a letter from Benjamin Franklin to Noble Wimberly Jones. Ashantilly Press, Darien

Bruce KA, Cameron GN, Harcombe PA, Jubinsky G (1997) Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L) Roxb. Nat Area J 17:255–260

Butterfield BJ, Rogers WE, Siemann E (2004) Growth and allometry of an invasive tree and four native species along a water gradient: avoidance of stress trade-offs. Tex J Sci 56:335–346

Caño L, Escarro J, Fleck I, Blanco-Moreno JM, Sans FX (2008) Increased fitness and plasticity of an invasive species in its introduced range: a study using *Senecio pterophorus*. J Appl Ecol 96:468–476

Case TJ, Holt RD, McPeek MA, Keit TH (2005) The community context of species' borders: ecological and evolutionary perspectives. Oikos 108:28–46

DeWalt SJ, Siemann E, Rogers WE (2011) Geographic distribution of genetic variation among native and introduced populations of Chinese tallow tree, *Triadica sebifera*. Am J Bot 98:1128–1138

Dlugosch KM, Parker IM (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Mol Ecol 17:431–449

Donahue C, Rogers WE, Siemann E (2004) Effects of temperature and mulch depth on Chinese tallow tree (*Sapium sebiferum*) seed germination. Tex J Sci 56:347–356

Donohue K, Dorn L, Griffith C, Kim E, Aguilera A, Polisetty CR, Schmitt J (2005) Niche construction through germination

cueing: life-history responses to timing of germination in *Arabidopsis thaliana*. Evolution 59:771–785

Elliott S (1824) Sketch of the botany of South Carolina and Georgia, vol 2. J. R. Schenck, Charleston

Evans AS, Cabin RJ (1995) Can dormancy affect the evolution of post-germination traits? The case of *Lesquerella fendleri*. Ecology 76:344–356

Hayes B (1979) Chinese tallow tree—artificial bee pasturage success story. Am Bee J 1979:848–849

Hunt KW (1947) The Charleston woody flora. Am Midl Nat 37:670–756

Jamieson GS, McKinney RS (1938) Stillingia oil. Oil Soap 15:295–296

Jones RH, McLeod KW (1989) Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. Bull Torrey Bot Soc 116:371–377

Keller SR, Sowell DR, Neiman M, Wolfe LM, Taylor DR (2009) Adaptation and colonization history affect the evolution of clines in two introduced species. New Phytol 183:678–690

Larcher W (2003) Physiological plant ecology. Springer, New York

Lee SK (1956) Genus *Sapium* in the Chinese flora. Acta Phytotaxon Sin 5:111–130

Leger EA, Rice KJ (2007) Assesing the speed and predictability of local adaptation in invasive California poppies (*Eschscholzia californica*). J Evolution Biol 20:1090–1103

Littell R, Milliken G, Stroup W, Wolfinger R, Schabenberger O (2006) SAS for mixed models, 2nd edn. SAS Institute Inc., Cary

Loehle C (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. J Biogeogr 25:735–742

Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. Ecol Monogr 74:261–280

Maron JL, Elmendorf SJ, Vilà M (2007) Contrasting plant physiological adaptation to climate in the native and introduced range of *Hypericum perforatum*. Evolution 61:1912–1924

Marshall JK (1968) Factors limiting the survival of *Corynephorus canescens* (L.) Beauv. in Great Britain at the northern edge of its distribution. Oikos 19:206–216

Michaux A (1803) Flora boreali-americana. Hafner Press, New York

Montague JL, Barrett SCH, Eckert CG (2008) Re-establishment of clinal variation in flowering time among introduced populations of purple loosestrife (*Lythrum salicaria*). J Evolution Biol 21:234–245

Morin X, Augspurger C, Chuine I (2007) Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? Ecology 88:2280–2291

Nardini A, Salleo S, Gullo MAL, Pitt F (2000) Different responses to drought and freeze stress of *Quercus ilex* L. growing along a latitudinal gradient. Plant Ecol 148:139–147

Nelson JR, Harris GA, Goebel CJ (1970) Genetic vs. environmentally induced variation in medusahead (*Taeniatherum asperum* [Simokai] *nevski*). Ecology 51:526–529

Nijjer S, Rogers WE, Lee C-TA, Siemann E (2007) The effects of soil biota and fertilization on the success of *Sapium sebiferum*. Appl Soil Ecol 38:1–11

Parker IM, Rodriguez J, Loik ME (2003) An evolutionary approach to understanding the biology of invasions: local adaptation and general purpose genotypes in the weed *Verbascum thapsus*. Conserv Biol 17:59–72

Pattison RR, Mack RN (2008) Potential distribution of the invasive tree *Triadica sebifera* (Euphorbiaceae) in the United States: evaluating CLIMEX predictions with field trials. Glob Chang Biol 14:813–826

Pattison RR, Mack RN (2009) Environmental constraints on the invasion of *Triadica sebifera* in the eastern United States: an experimental field assessment. Oecologia 158:591–602

Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. Q Rev Biol 78:419–433

Primack RB, Miao SL (1992) Dispersal can limit local plant distribution. Conserv Biol 6:513–519

Quinn JA (1977) Separating genotype from environment in germination ecology studies. Am Midl Nat 97:484–489

Renne IJ (2001) Invasion of Chinese tallow tree: causes, consequences, and forecast, Department of Biological Sciences, Clemson University, Clemson

Renne IJ, Gauthreaux SA, Gresham CA (2000) Seed dispersal of the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) by birds in coastal South Carolina. Am Midl Nat 144:202–215

Renne IJ, Spira TP, Bridges WC (2001) Effects of burial, age, and passage through birds on germination and establishment of Chinese tallow tree in coastal South Carolina. J Torrey Bot Soc 128:109–119

Renne IJ, Barrow WC, Randall LAJ, Bridges WC (2002) Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. Divers Distrib 8:285–295

Rogers WE, Siemann E (2004) Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. J Appl Ecol 41:561–570

Schoepf JD (1911) Reise durch einige der mittlern und sòdlichen vereinigten nordamerikanichen Staaten nach ost-Florida und den Bahama Inseln unternommen in den Jahren 1783 und 1784. Extracts from the translation by Alfred J Morrison Bull Lloyd Lib Bot Pharm Mat Med 16:1–39

Siemann E, Rogers WE (2001) Genetic differences in growth of an exotic tree species. Ecol Lett 4:514–518

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

Siemann E, Rogers WE (2006) Recruitment limitation, seedling performance and persistence of exotic tree monocultures. Biol Invasions 8:979–991

Siemann E, Rogers WE, DeWalt SJ (2006) Rapid adaptation of insect herbivores to an invasive plant. Proc R Soc Lond B Bio 273:2763–2769

Wagner I, Simons AM (2008) Intraspecific divergence in seed germination traits between high- and low- latitude populations of the arctic-alpine annual *Koenigia islandica*. Arct Antarct Alp Res 40:233–239

Wang HH, Grant WE, Swannack TM, Gan J, Rogers WE, Koralewski TE, Miller JH, Taylor JW (2011) Predicted range expansion of Chinese tallow tree (*Triadica sebifera*) in forestlands of the southern United States. Divers Distrib 17:552–565

Woodward FI (1987) Climate and plant distribution. Cambridge University Press, New York

Woodward FI, Fogg GE, Heber U (1990) The impact of low temperatures in controlling the geographical distributions of plants. Philos Trans R Soc Lond B 326:585–593