

Lower resistance and higher tolerance of invasive host plants: biocontrol agents reach high densities but exert weak control

YI WANG,^{1,2} WEI HUANG,^{1,2} EVAN SIEMANN,³ JIANWEN ZOU,⁴ GREGORY S. WHEELER,⁵ JULI CARRILLO,³
AND JIANQING DING^{1,6}

¹Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Institute|Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, Hubei 430074 China

²Graduate University of Chinese Academy of Sciences, Beijing 100049 China

³Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005 USA

⁴College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing 210095 China

⁵Invasive Plant Research Laboratory, United States Department of Agriculture, Agricultural Research Service, 3225 College Avenue, Fort Lauderdale, Florida 33314 USA

Abstract. Invasive plants often have novel biotic interactions in their introduced ranges. Their defense to herbivory may differ from their native counterparts, potentially influencing the effectiveness of biological control. If invasive plants have decreased resistance but increased tolerance to enemies, insect herbivores may rapidly build up their populations but exert weak control. Moreover, resource availability to plants may affect the efficacy of biological control agents. We tested these predictions using Chinese tallow tree (*Triadica sebifera*) and two specialist herbivores (*Heterapoderopsis bicallosicollis* and *Gadirtha inexacta*) that are candidates for biological control. We performed a pair of field common garden experiments in China in which *Triadica* seedlings from the native or introduced range were grown in low or high light conditions and subjected to different levels of herbivory by each herbivore in a factorial design. We found that *Heterapoderopsis* achieved greater densities on tallow trees from the introduced range or when trees were grown in high light conditions. When *Gadirtha* was raised in the lab on tallow tree foliage we found that it performed better (larger pupal size) when fed foliage from introduced populations. However, introduced populations generally had greater herbivore tolerance such that the impact of each agent on plant performance was lower than on native populations despite higher herbivore loads. Tallow trees grew more slowly and achieved smaller sizes in lower light levels, but the impact of biological control agents was comparable to that found for higher light levels. Plants from introduced populations grew larger than those from native populations in all conditions. Our results suggest that reduced resistance and increased tolerance to herbivory in introduced populations may impede success of biological control programs. Biological control practitioners should include plants from the introduced range in the prerelease evaluation, which will help predict insect impact on target weeds.

Key words: biological invasions; Chinese tallow tree; EICA; *Gadirtha inexacta*; herbivory; *Heterapoderopsis bicallosicollis*; light; specialist; *Triadica sebifera*.

INTRODUCTION

Success in the biological control of invasive plants depends on the ability of host-specific natural enemies to suppress the growth and reproduction of their host plant. Understanding interactions between insect biological control agents and host plants is critical for forecasting the impact before the insects are introduced, and for improving our knowledge of the mechanisms driving success or failure of the released agents. Though many approaches for evaluation have been developed in recent decades, including scoring systems (Harris 1973, Goeden 1983), climate matching (Wapshere 1985), and demographic models (Shea and Kelly 1998, McEvoy

and Coombs 1999), the biological control success rate has not been high (McFadyen 1998). Many introduced insects establish populations on their target invasive plant; however, their impact is not sufficient to curb the invasion. Further work is needed to improve our ability to predict likely control efficacy prior to release (Crawley 1989, Lawton 1990, McEvoy and Coombs 1999, Denoth et al. 2002).

Recent theories on the defense of invasive plants to herbivory may help bridge such gaps and further explain the interactions between insect agents and their host plants in biological control programs (Franks et al. 2004, 2008a). For example, the evolution of increased competitive ability (EICA) hypothesis predicts that coevolved specialist enemies that are potential biological control agents should show improved performance on the invasive plants, if invasive plants have reallocated

Manuscript received 30 December 2009; revised 15 July 2010; accepted 6 August 2010. Corresponding Editor: S. M. Altizer.

⁶ Corresponding author. E-mail: dingjianqing@yahoo.com

resources away from herbivore defense towards growth and reproduction in the absence of specialist herbivores in the introduced range (Blossey and Nötzold 1995). As predicted by EICA, increased growth and reproduction but decreased defense in invasive plants from populations in their introduced range, relative to conspecifics in their native range, have been reported in several plant systems (Bossdorf et al. 2005, Hull-Sanders et al. 2007, Franks et al. 2008a, Cano et al. 2009) but not in other studies (Bossdorf et al. 2005, Franks et al. 2008b, Ridenour et al. 2008). With respect to the population dynamics of biological control agents, Müller-Schärer et al. (2004) predicted that “plants that have evolved increased vigor in the exotic range will experience a particularly fast population buildup of biological control agents.”

Plant defense against herbivores can involve both resistance and tolerance strategies. Resistance is a plant trait that reduces the preference or performance of herbivores, whereas tolerance is the ability of a plant to withstand and survive a fixed amount of herbivore damage without a corresponding reduction in fitness (McNaughton 1983, Paige and Whitham 1987). By further comparing the difference in defense mechanisms between resistance and tolerance to herbivory in invasive plants, Müller-Schärer et al. (2004) also predicted that the impact of insect agents on plant performance “will depend on the levels of resistance and tolerance evolved during the invasion process in the absence of specialist herbivores.” In other words, less resistant plants could experience lower impacts by herbivores owing to increased levels of tolerance. This idea may help explain why a high abundance of some insect biological control agents has been found on invasive populations relative to their abundance in the native range yet these high number of insects failed to control the invader (Müller-Schärer et al. 2004). Knowledge of tolerance vs. resistance of exotic populations may also help forecast the impact of biocontrol agents prior to their release for biological control. To our knowledge, however, studies have rarely tested this issue in biological control programs.

Here, we test these predictions using Chinese tallow tree (*Triadica sebifera* [L.] Small [synonyms: *Sapium sebiferum* (L.) Roxb.] [Euphorbiaceae]) as a model species (hereafter referred to as *Triadica*). Native to China, *Triadica* is a deciduous tree, with a well-documented invasion history (Bruce et al. 1997). Previous studies suggest that *Triadica* has evolved to be a faster-growing and less herbivore-resistant plant in response to low herbivore loads in its introduced range (Siemann and Rogers 2001, 2003a, b, Siemann et al. 2006), consistent with the EICA hypothesis. Recent studies also indicate that invasive populations of *Triadica* tolerate herbivory more effectively relative to native populations (Rogers and Siemann 2004, 2005, Zou et al. 2008a, b). There is also evidence of greater plasticity in growth of invasive *Triadica* in response to

light conditions (Zou et al. 2009). Therefore, the reallocation of resources in invasive populations could result in *Triadica* showing higher tolerance to herbivory and greater plasticity to varying light conditions.

Light-dependent growth and survival functions are key predictors of forest understory dynamics (Pacala et al. 1996). All else being equal, species with the highest growth rates and lowest mortality at a given light level will dominate sites with such light levels if they are not recruitment limited (Hurt and Pacala 1995). Indeed, this may help explain the spectacular success of *Triadica* in invading bottomland hardwood forests. A two-year field experiment found that germination was higher in open-canopy microhabitats. Furthermore, low light levels in closed-canopy microhabitats reduced plant performance but did not prevent establishment (Pattison and Mack 2009). *Triadica* has a more rapid growth rate than the tested native tree species at light levels over 3% and mortality rates lower than native tree species at light levels over 10% ambient light (Lin et al. 2004). Indeed, at the highest light levels, *Triadica* has a growth rate that is twice that of the next fastest growing species tested in this study. One explanation for this spectacular advantage of *Triadica* is its greater plasticity to variations in light conditions, possibly as an evolutionary consequence of release from insect herbivores in the introduced range. Therefore, it is critical to understand how biological control agents impact plant performance along light gradients for tree species such as *Triadica*, which are both grassland and forest invaders.

In this study, we conducted laboratory and common garden experiments to examine the performance of two specialist herbivores, *Heterapoderopsis bicallosicollis* (Voss) (Attelabidae) and *Gadirtha inexacta* Walker (Noctuidae), on *Triadica* native and invasive populations, and predict their biological control impact. Based on the literature reviewed above, we predicted that (1) insect population buildup will be faster on genotypes from invasive *Triadica* populations than on those from native populations (lower resistance in the introduced range); (2) under the same herbivore load, invasive *Triadica* populations will perform better than native populations (higher tolerance in the introduced range); and (3) under shaded conditions, invasive populations will show similar tolerance patterns to those in ambient light conditions in response to herbivory (greater plasticity in introduced range).

MATERIALS AND METHODS

Study system

Triadica seedlings and adult trees aggressively displace native plants and form monospecific stands in the southeastern United States (Bruce et al. 1997). This species has the potential to spread 500 km northward beyond current invaded areas (Pattison and Mack 2008). In its native range in China, the plant is very common, growing in cultivation and in the wild.

Seedlings appear in late April or May and grow rapidly (Zhang and Lin 1994). Flowering occurs from July to August and seeds mature in late September.

Heterapoderopsis bicallosicollis is a leaf-rolling weevil, having four to five generations per year in the Hubei Province, China. Adults feed on leaves and lay eggs inside rolled leaves (nidi). One nidus usually contains two eggs. Larvae and pupae live inside the nidus until they emerge as adults. *Gadirtha inexacta* is a noctuid moth. The eggs of the moth overwinter on branches or leaves and hatch in May. The larvae feed on leaves where they can cause severe damage, especially in the last three instars. Host range tests in China show both insects are host-specific to *Triadica*, thus both are being considered as potential biological control agents against this weed in the United States (Wang et al. 2009).

Plant seed and insect collections.—In late November 2007, we collected seeds from five populations across south China (hereafter referred to as native populations) and five populations from the southeastern United States (referred to as invasive populations; Appendix A). Previous genetic analysis suggests that Chinese tallow trees from Jiangsu Province, the northernmost one sampled, may be the source of non-Georgia/South Carolina U.S. genotypes, while the Georgia and South Carolina genotypes may be derived from Guangdong Province in the south of China (DeWalt et al. 2006; S. J. DeWalt, E. Siemann, and W. E. Rogers, unpublished data); as such, we consider the populations used in this experiment to be representatively native and invasive.

For each population, seeds were collected from four to 10 haphazardly selected *Triadica* trees. To evaluate the potential impact of seed provisioning on seedling performance, 20 seeds from each population were weighed. No difference was detected in seed weight of invasive and native populations (nested ANOVA, $F_{1,8} = 1.831$, $P = 0.213$). All seeds' waxy coats were removed by soaking in water with laundry detergent (10 g/L) for 2 days since coats do not provide resources to the embryo. The seeds were then buried in sand at a depth of 5–10 cm and placed in a refrigerator (4°C) for 60 days.

On 5 April 2008, seeds from all 10 populations were planted into 115 mL containers (Stuewe and Sons, Corvallis, Oregon, USA) filled with sterilized growing medium (50% field soil and 50% sphagnum peat moss) and maintained in a greenhouse for four weeks. On 4 May 2008 similar-sized seedlings were transplanted individually into pots containing sterilized growing medium (50% field soil and 50% sphagnum peat moss) in a field common garden at the Wuhan Botanical Garden, Chinese Academy of Sciences, Hubei, China (30°32' N, 114°24' E). Each pot contained one plant seedling that was enclosed by a nylon cage (100 cm height; 27 cm diameter) to exclude herbivores.

We field-collected about 150 newly emerged adults or larvae of *H. bicallosicollis* and 200 larvae of *G. inexacta* in Luotian, Hubei Province in June 2008 and reared them on *Triadica* (Wuhan population) in field cages at

Wuhan Botanical Garden. We used first generation offspring from these collections in the experiments.

Experimental design

Experiments on the leaf-rolling weevil.—To test for differences in population dynamics of *H. bicallosicollis* on native and invasive populations and their impact on plant performance, we conducted a field common garden experiment from late July to early December 2008. Naturally mating pairs (unoviposited females) of *H. bicallosicollis* reared in the field cage were released into a cage containing one individual *Triadica* plant. To obtain different insect population sizes we established three distinct densities: 0 (control), one, and two adult pairs per plant at the start of the experiment. To examine the effect of shade on plant and insect performance, nylon-caged plants were either exposed to ambient light (light treatment) or covered with black polypropylene shade cloth (shade treatment). The nylon cage intercepted 30% of photosynthetically active radiation as measured by weekly midday readings with a PAR ceptometer (GLZ-A, Tuopu Ltd., Hangzhou, China), so plants in the light treatment received 70% of the ambient light. The black shade cloth and nylon cage intercepted 88% of the photosynthetically active radiation, therefore, plants in shade treatment received 12% of the ambient light. Each treatment was replicated six times, yielding a total of 360 seedlings (2 continents \times 5 populations \times 3 insect densities \times 2 light/shade \times 6 replicates) in the experiment.

Insects were added to cages on 29 July 2008 and their survival was checked daily from 29 July to 5 August. If adults were found dead during this period, new adults were added to replace them. Insect populations were measured by counting the total number of nidi and adults every two weeks from 29 July to 3 December 2008. At harvest (3 December), we measured height and stem diameter of each seedling. Plants were dried at 80°C for 3 days and weighed.

Experiments on the noctuid moth.—We examined differences in the development time and pupal size of moths reared on native vs. invasive populations as a proxy for the moth population growth rate, as pupal size is generally strongly correlated to adult fecundity (Honek 1993, Calvo and Molina 2005). As each female moth can lay more than 300 eggs (Y. Wang, unpublished data) and those offspring larvae require abundant food resources, it is extremely difficult for seedlings to support multiple generations in an enclosed experiment.

We conducted the experiment in insectariums at Wuhan Botanical Garden from August to September in 2008. One fully expanded leaf (third or fourth position from the tip) was excised from a plant of each population (five native and five invasive populations, each replicated 10 times), and then placed on moist filter paper in a Petri dish (inner diameter 9 cm). A newly hatched larva was transferred to the leaf. Petri dishes were closed and incubated in the lab at 24°C and a 14:10

h light : dark photophase. Food was changed as necessary. During the experiment, we recorded the pupal weight and development time.

To examine the different effects of the moth on native and invasive plants under light and shade conditions, we conducted a field common garden experiment. The experimental design was the same as the weevil experiment, i.e., a factorial design (2 light states \times 3 insect densities \times 2 continents \times 5 populations) including six replicates for each factor. Thus, a total of 360 potted seedlings from native and invasive populations were used. We stocked cages with second instar larvae at the densities of 0 (control), four, and eight per plant on 5 August. We removed adults when they emerged, then seedlings were allowed to regrow for more than two months before harvest. The experiment ended on 24 November 2008, when we measured seedlings' stem height and diameter and harvested, dried, and weighed all seedlings.

STATISTICAL ANALYSIS

For the field experiments on the weevil and moth, we conducted a nested analysis of variance (ANOVA) to examine the effects of light, insect density, continent (plant origin), and population as well as their interactions on growth variables of *Triadica* seedlings. The model included light, insect density and plant origin as fixed factors and population nested within origin as a random effect. Thus tests of origin differences used the corresponding population term as the associated error term.

We examined herbivory tolerance using the slope of regression of herbivore load on seedling height and biomass. In the regression analyses, the slope represents herbivory tolerance (the negative impacts of herbivory) with a shallower negative slope representing higher tolerance to herbivores (Strauss and Agrawal 1999, Stowe et al. 2000, Agrawal et al. 2004). We conducted a separate set of ANCOVAs in Proc Mixed (SAS 9.1; SAS Institute 2004) on seedling height and biomass to examine the relationship between insect number (measured weevil density or number of moth larvae stocked) and plant performance for each combination of continent and light treatments. We parameterized this model to fit separate intercepts and slopes for the I-L, I-S, N-L, and N-S treatments (I-L, invasive populations in light conditions; I-S, invasive populations in shade conditions; N-L, native populations in light conditions; N-S, native populations in shade conditions). We used adjusted means contrasts to conduct pairwise tests of differences in slopes and intercepts.

We used a GLM repeated measures analysis of variance (ANOVA) to assess the impact of continental origin, light, insect density, and sample date on the number of weevils (total number, including adults, eggs, and larvae) over the experimental season from July to December 2008 (more than 100 days). We conducted similar nested tests for effects of origin as we did for plant performance response variables. We also used

nested ANOVAs to examine the effect of continental origin and population on moth pupal weight and larval development duration. The model included plant origin as a fixed factor and population nested within origin as a random effect.

RESULTS

Experiment on leaf rolling weevil

Effects of plant origin on insect population buildup.—*H. bicallosicollis* always had higher numbers on plants from invasive populations of *Triadica* than on plants from native populations (Fig. 1; Appendix B). Four weeks after insects were stocked into the cages, weevil populations reached their peak densities. For example, on 26 August, in the low-density treatment (one pair released per plant) the number of insects (including weevil and nidi; 7.0 ± 0.3 [mean \pm SE]) on each invasive plant was about 28% more than the number of insects on each native plant (5.9 ± 0.5) under ambient light conditions (Fig. 1a). Insect numbers were always greater on invasive plants than on native plants until the end of the field season (starting from late October). The same general patterns were also found in the high-density treatments (two pairs released per plant; Fig. 1b).

Effects of shade and starting density on weevil populations.—Weevil populations significantly decreased under shade conditions, compared with those under light conditions (Appendix B) regardless of their host plant origin. In the low-density treatments, 15% more weevils were supported by plants in light conditions than those in shaded conditions. A similar pattern was found for the high-density treatment and the interaction between density and light was not significant.

The initial number of insects released significantly affected weevil populations (Appendix B). Regardless of host plant origin and light treatment, weevils maintained higher populations in the high-density treatment than in the low-density treatment until the end of the field season (Fig. 1a, b).

Growth of native and invasive plants.—Seedlings from invasive populations always grew larger than those from native populations (total biomass and height), regardless of herbivore numbers. However, the number of insects negatively affected plant growth for both invasive and native populations (Fig. 2; Appendix C). Light availability and plant origin influenced plant tolerance patterns in response to the increased weevil numbers. Under light conditions, the impacts of the weevil on the total biomass and height of the invasive populations were significantly less than its impacts on the native populations, indicated by the differences in the slopes of regression lines (Fig. 2; I-L vs. N-L in Appendix D). Shade suppressed plant growth of both the native and invasive populations (Fig. 2; Appendix C). Under shaded conditions, there was no difference in the effects of weevil numbers on total biomass between invasive and native populations, although a significant difference remained for height (Fig. 2; I-S vs. N-S in Appendix D).

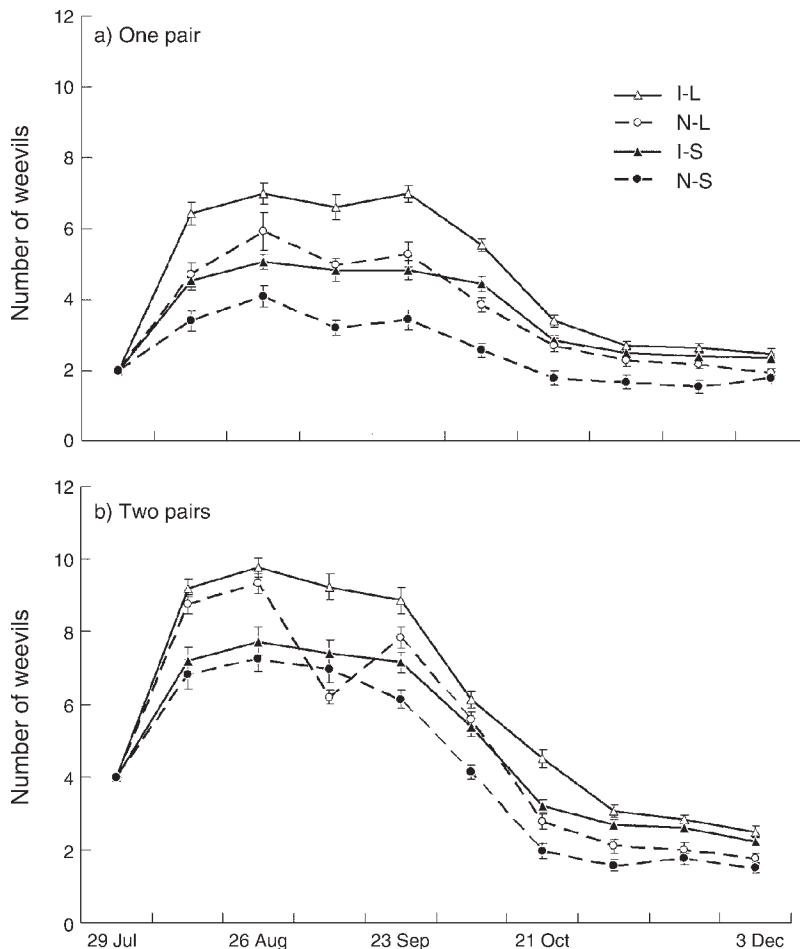


FIG. 1. Population dynamics of the leaf-rolling weevil, *Heteropoderopsis bicallosicollis* affected by *Triadica* plant origin (invasive vs. native), light (shade and ambient light), and the number of insect released (a, one pair; b, two pairs). Treatments are: I-L, invasive populations in light conditions; I-S, invasive populations in shade conditions; N-L, native populations in light conditions; N-S, native populations in shade conditions. Values are means \pm SE.

Light availability did not affect tolerance patterns in invasive populations, in terms of total biomass and height (Fig. 2a, b; I-L vs. I-S in Appendix D). However, the tolerance patterns of native populations were affected by light as the slope for height under shade was steeper than the light treatment; the slopes for total biomass were not affected by light (Fig. 2a, b; N-L vs. N-S in Appendix D).

Experiment on the noctuid moth, *G. inexacta*

Larval development on native and invasive populations.—The biomass of *G. inexacta* pupae reared on leaves from invasive populations was significantly greater than when they were reared on leaves from native populations ($F_{1,8} = 14.566$, $P = 0.005$; Fig. 3a). However, pupal development time was not affected by continental origin of tallow tree populations ($F_{1,8} = 0.779$, $P = 0.403$; Fig. 3b).

Growth of native and invasive plants.—Similar to the impact of the weevil, increasing moth larval numbers

negatively affected plant growth (total biomass and height) for both native and invasive populations (Appendix E). Native and invasive populations each tolerated herbivory better under shade as compared to light conditions when measured based on total mass (non-parallel lines in Fig. 4a; I-L vs. I-S and N-L vs. N-S in Appendix F). However, for measures of height, tolerance to herbivory did not vary between shaded and light conditions (Fig. 4b; I-L vs. I-S and N-L vs. N-S in Appendix F). Under light conditions invasive populations tolerated herbivory better than native populations for measures of both total biomass and height, indicated by the shallower slopes of regression lines (Fig. 4a, b; I-L vs. N-L in Appendix F). Under shade conditions the tolerance patterns were similar between invasive and native populations for measures of total biomass, however, the invasive populations tolerated herbivory better than native ones when measured based on height (Fig. 4a, b; I-S vs. N-S in Appendix F).

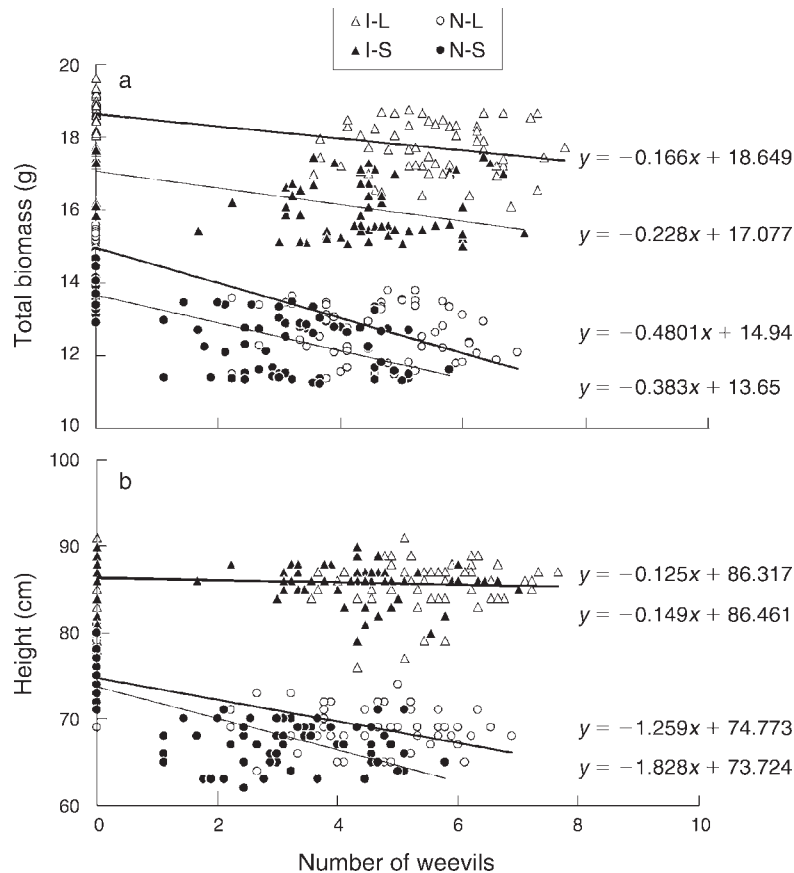


FIG. 2. Regression of the (a) total biomass and (b) height against the number of weevils of *Heterapoderopsis bicallosicollis* for *Triadica* native and invasive populations under shade and light conditions.

DISCUSSION

In this study, we compared the responses of invasive and native *Triadica* populations to herbivory by two specialist herbivores. We found that the weevil, *H. bicallosicollis*, achieved greater densities on seedlings from invasive populations but caused lower impacts (compared to seedlings from native populations). We observed a similar pattern in *G. inexacta* in terms of its performance and impact. Moth larvae reared on invasive plants achieved greater pupal size than those reared on native plants (Fig. 3), suggesting that this specialist moth may produce more offspring on invasive populations than on native ones. Insect body size is considered positively correlated with fecundity (Honek 1993, Calvo and Molina 2005). Like the weevils, moths had lower impacts on plants from invasive populations compared to those on plants from native populations.

Invasive plants always grew larger than natives, independent of herbivore load (Fig. 2). Previous studies revealed a higher tolerance to herbivory in invasive *Triadica* populations than that in natives (Zou et al. 2008b). We found that under light conditions the invasive populations tolerated herbivory better than their native counterparts, but under shade conditions

(12% of the ambient light in our experiments) their tolerance appeared to be similar. Together with the improved insect performance (greater insect numbers) on invasive populations, the results of this study support the hypothesis that herbivore-tolerant genotypes of invasive plants will support a rapid population buildup of biological control agents but experience lower impact on their growth.

The decreased resistance and increased tolerance to herbivores in invasive *Triadica* populations (Zou et al. 2008b) may reflect differences in the insect community between ranges. Given that many *Triadica* herbivores in the native range (both specialists and generalists) and the introduced range (only generalists) are defoliators, the invasive and native plant populations may share similar compensatory mechanisms in response to their corresponding natural enemies. Thus, although the specialists are absent, generalist herbivores in the introduced range could select for the maintenance of increased tolerance to herbivory in invasive populations. In another study, we found a greater tolerance of the invasive *Triadica* populations to herbivory by generalists than by specialists (Huang et al. 2010). In addition, increased growth rate may explain the high levels of

herbivore tolerance in invasive *Triadica* populations (Zou et al. 2008a). We observed a rapid leaf regrowth of *Triadica* in our study. Although plants in the high insect density treatment were 100% defoliated by *G. inexacta*, we observed that they were able to generate new leaves after only three weeks. Thus, though we used one-year-old seedlings for our defoliation experiments, all the plants, including those 100% defoliated, still survived to the end of the growing season. With regard to herbivore resistance, invasive *Triadica* populations are reported to have lower tannin content relative to native genotypes (Siemann and Rogers 2001). Thus, decreased tannin content may enhance food palatability of the invasive genotypes, supporting a larger herbivore population.

The differing responses to herbivores we observed across *Triadica* populations may indicate altered patterns of selection for defense in the introduced range. Trade-offs between resistance and tolerance to herbivory damage have been reported in both agricultural and wild plants (see Leimu and Koricheva 2006), but generally have not been considered in terms of biological invasions or biological control programs. In fact, though many biotic and abiotic factors have been implicated in the failure or low impact of biological control agents (McFadyen 1998), plant tolerance to herbivory is only recently regarded as one of them. Evolved increased tolerance due to changes in growth rate in invasive plants may be a common phenomenon. For example, the European plant *Centaurea maculosa* Lam. is an invasive weed in North America that has high tolerance to herbivory by two introduced gall flies (Müller-Schärer et al. 2004). Though the biological control agents have established populations at a 100-fold density compared with their density in their native Europe, they have failed to control the plant in North America (Pearson and Callaway 2003, Müller-Schärer et al. 2004). In the prerelease evaluation of biological control programs, very few studies have attempted to forecast the impact of the agents by examining and comparing tolerance difference between native and invasive genotypes (Hinz and Schwarzlaender 2004, Morin et al. 2009). With respect to *Triadica*, our study predicts that (1) *H. bicallosicollis* and *G. inexacta* may establish populations rapidly in the southeastern United States once they are introduced and released, unless there are extenuating factors affecting their population buildup; (2) high tolerance to high herbivore loads in invasive U.S. populations will limit their impact on plant growth; and (3) repeated defoliations over several growing seasons will be necessary to effectively suppress plant regrowth, at least for the *Triadica* adult trees. Additionally, though we did not examine the effects of sequential bouts of defoliation, repeated defoliation events may be more likely with multivoltine biocontrol agents, such as *H. bicallosicollis* and *G. inexacta*, as opposed to univoltine biocontrol agents.

The results of this study have implications for improving the current evaluation methodology for

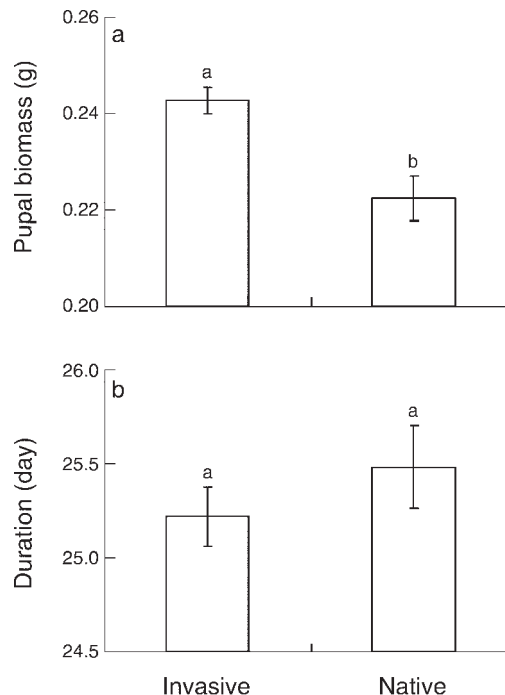


FIG. 3. (a) The biomass of pupae and (b) the developmental duration of larvae and pupae (from the first instar to adult emergence) reared on the excised leaves from native and invasive populations in laboratory tests. Values are means \pm SE. Means with the same letters were not significantly different at $P \leq 0.05$.

biological control efficacy in the prerelease study when screening insects in their native range. To predict the efficacy of potential biological control agents, many experiments are designed to test the effects of insects on growth and reproduction of the plant in the native range (McClay and Balciunas 2005, Morin et al. 2009). However, the test plant materials are mostly from the native populations, rather than the invasive populations. If the invasive populations have a higher tolerance to herbivory than native populations, the results of tests that only include native plants may overestimate the control efficacy of the insect agents. Thus, we recommend that tests should be conducted on plant materials originating from the designated biological control sites (Hinz and Schwarzlaender 2004).

Furthermore, resource availability (light, water, nutrients, etc.) that can influence the growth and reproduction of invasive plant species (Dukes and Mooney 1999, Davis et al. 2000, Rogers and Siemann 2003), and differences in resource usage of native and invasive populations may also affect the outcome of biological control (Blumenthal et al. 2009, Sun et al. 2009). In this study, seedlings from invasive populations had similar tolerance patterns under shade and ambient light conditions (except for the total biomass of the moth with marginal difference, see Appendix F), suggesting that their compensatory ability may not be greatly

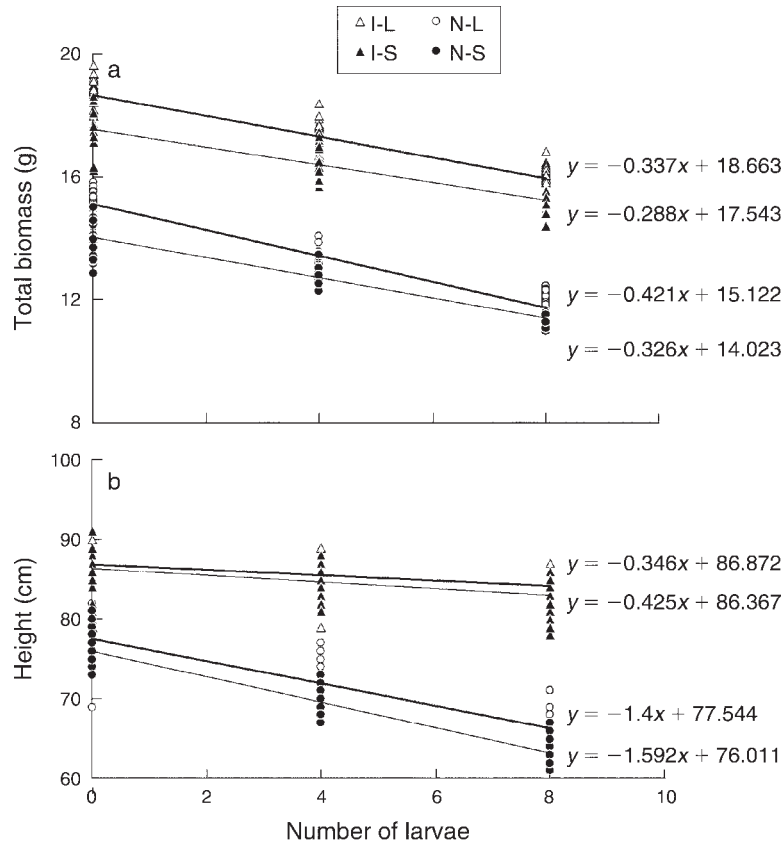


FIG. 4. Regression of (a) total biomass and (b) height against the number of larvae of *Gadirtha inexacta* for *Triadica* seedlings from native and invasive populations under shade and light conditions.

affected by light availability. Therefore, biological control of *Triadica* may be equally difficult in both shaded forests and open grasslands in the invaded range.

In this study, we focused on the effects of specialists on *Triadica* seedlings and the seedlings' defense, because previous studies suggest that the early seedling stage of *Triadica* plays an important role in its invasion success (Bruce et al. 1997). The results of this study, however, may also have implications for the management of older trees, as other investigations indicate that 14-year-old trees showed similar patterns of defense (both resistance and tolerance) as 2–3-year-old seedlings (Siemann and Rogers 2001, Huang et al. 2010).

In summary, insect herbivores performed better on invasive populations of *Triadica* relative to native populations. However, both potential biological control agents had lower impacts on the growth of plants from invasive populations compared to those from native populations. It is possible that due to differences in growth rate, invasive plants have increased tolerance to high herbivore loads of the two specialists, leading to a high ability to compensate for defoliation. For future biological control of *Triadica* using *H. bicallosicollis* and *G. inexacta* in the United States, should they be approved for release, post-release monitoring focusing

on plant regrowth should be a high priority. For prerelease evaluation in biological control of invasive plants, our results help to predict the impact of potential biological control agents on herbivore tolerant genotypes.

ACKNOWLEDGMENTS

We thank X. Lu and S. Feng for their assistance in lab and field work. We are grateful for comments by two anonymous reviewers, which improved the early version of the manuscript. This study was supported by the 100 Talent Program of the Chinese Academy of Sciences (to J. Ding), the U.S. National Science Foundation (DEB 0820560 to E. Siemann), U.S. NSF predoctoral and Ford Foundation fellowships (to J. Carrillo), the Florida Department of Environmental Protection (SL849 to G. Wheeler), and the foreign visiting professorship of the Chinese Academy of Sciences (2009S1-30 to E. Siemann).

LITERATURE CITED

- Agrawal, A. A., J. K. Conner, and J. R. Stinchcombe. 2004. Evolution of plant resistance and tolerance to frost damage. *Ecology Letters* 7:1199–1208.
- Blossey, B., and R. Nötzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* 83:887–889.
- Blumenthal, D., C. E. Mitchell, P. Pyšek, and V. Jarošík. 2009. Synergy between resource availability and pathogen release in plant invasion. *Proceedings of the National Academy of Sciences USA* 106:7899–7904.

- Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144:1–11.
- Bruce, K. A., G. N. Cameron, P. A. Harcombe, and G. Jubinsky. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese Tallow Tree, *Sapium sebiferum* (L.) Roxb. *Natural Areas Journal* 17:255–260.
- Calvo, D., and J. M. Molina. 2005. Fecundity–body size relationship and other reproductive aspects of *Streblote panda* (Lepidoptera: Lasiocampidae). *Annals of the Entomological Society of America* 98:191–196.
- Cano, L., J. Escarre, K. Vrieling, and F. X. Sans. 2009. Palatability to a generalist herbivore, defence and growth of invasive and native *Senecio* species: testing the evolution of increased competitive ability hypothesis. *Oecologia* 159:95–106.
- Crawley, M. J. 1989. The successes and failures of weed biocontrol using insects. *Biocontrol News and Information* 19:213–223.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88:528–534.
- Denoth, M., L. Frid, and J. H. Myers. 2002. Multiple agents in biological control: improving the odds? *Biological Control* 24:20–30.
- DeWalt, S. J., E. Siemann, and W. E. Rogers. 2006. Microsatellite markers for an invasive tetraploid tree, Chinese Tallow (*Triadica sebifera*). *Molecular Ecology Notes* 6:505–507.
- Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14:135–139.
- Franks, S. J., P. D. Pratt, F. A. Dray, and E. L. Simms. 2004. Selection for resistance in invasive plants. *Weed Technology* 18:1486–1489.
- Franks, S. J., P. D. Pratt, F. A. Dray, and E. L. Simms. 2008a. Selection of herbivory resistance and growth rate in an invasive plant. *American Naturalist* 171:678–691.
- Franks, S. J., P. D. Pratt, F. A. Dray, and E. L. Simms. 2008b. No evolution of increased competitive ability or decreased allocation to defense in *Melaleuca quinquenervia* since release from natural enemies. *Biological Invasions* 10:455–466.
- Goeden, R. D. 1983. Critique and revision of Harris' scoring system for selection of insect agents in biological control of weeds. *Protection Ecology* 5:287–301.
- Harris, P. 1973. The selection of effective agents for the biological control of weeds. *Canadian Entomologist* 105:1495–1503.
- Hinz, H. L., and M. Schwarzlaender. 2004. Comparing invasive plants from their native and exotic range: what can we learn for biological control? *Weed Technology* 18:1533–1541.
- Honek, A. 1993. Intraspecific variation in body size and fecundity in insects a general relationship. *Oikos* 66:386–388.
- Huang, W., E. Siemann, G. S. Wheeler, J. Zou, J. Carrillo, and J. Ding. 2010. Resource allocation to defense and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. *Journal of Ecology* 98:1157–1167.
- Hull-Sanders, H. M., R. Clare, R. H. Johnson, and G. A. Meyer. 2007. Evaluation of the evolution of increased competitive ability (EICA) hypothesis: loss of defense against generalist but not specialist herbivores. *Journal of Chemical Ecology* 33:781–799.
- Hurttt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitations: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176:1–12.
- Lawton, J. H. 1990. Biological control of plants: a review of generalisations, rules and principles using insects as agents. Pages 3–17 in C. Basset, L. J. Whitehouse, and J. A. Zabkiewicz, editors. *Alternatives to chemical controls of weeds*. FRI Bulletin 155. Ministry of Forestry, Rotorua, New Zealand.
- Leimu, R., and J. Koricheva. 2006. A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: combining the evidence from ecological and agricultural studies. *Oikos* 112:1–9.
- Lin, J., P. A. Harcombe, M. R. Fulton, and R. W. Hall. 2004. Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas. *Oecologia* 139:399–407.
- McClay, A. S., and J. K. Balciunas. 2005. The role of pre-release efficacy assessment in selecting classical biological control agents for weeds: applying the Anna Karenina principle. *Biological Control* 35:197–207.
- McEvoy, P. B., and E. M. Coombs. 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications* 9:387–401.
- McFadyen, R. E. C. 1998. Biological control of weeds. *Annual Review of Entomology* 43:369–393.
- McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40:329–336.
- Morin, L., A. M. Reid, N. M. Sims-Chilton, Y. M. Buckley, K. Dhileepan, G. T. Hastwell, T. L. Nordblom, and S. Raghu. 2009. Review of approaches to evaluate the effectiveness of weed biological control agents. *Biological Control* 51:1–15.
- Müller-Schärer, H., U. Schaffner, and T. Steinger. 2004. Evolution in invasive plants: implications for biological control. *Trends in Ecology and Evolution* 19:417–422.
- Pacala, S. W., C. D. Canham, J. A. J. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis, and dynamics. *Ecological Monographs* 66:1–34.
- Paige, K. N., and T. G. Whitham. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist* 129:407–416.
- Pattison, R. R., and R. N. Mack. 2008. Potential distribution of the invasive tree *Triadica sebifera* (Euphorbiaceae) in the United States: evaluating CLIMEX predictions with field trials. *Global Change Biology* 14:813–826.
- Pattison, R. R., and R. N. Mack. 2009. Environmental constraints on the invasion of *Triadica sebifera* in the eastern United States: an experimental field assessment. *Oecologia* 158:591–602.
- Pearson, D. E., and R. M. Callaway. 2003. Indirect effects of host-specific biological control agents. *Trends in Ecology and Evolution* 18:456–461.
- Ridenour, W. M., J. M. Vivanco, Y. Feng, J.-I. Horiuchi, and R. M. Callaway. 2008. No evidence for trade-offs: *Centaurea* plants from America are better competitors and defenders. *Ecological Monographs* 78:369–386.
- Rogers, W. E., and E. Siemann. 2003. Effects of simulated herbivory and resources on Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasion of native Coastal Prairie. *American Journal of Botany* 90:243–249.
- Rogers, W. E., and E. Siemann. 2004. Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. *Journal of Applied Ecology* 41:561–570.
- Rogers, W. E., and E. Siemann. 2005. Herbivory tolerance and compensatory differences in native and invasive ecotypes of Chinese tallow tree (*Sapium sebiferum*). *Plant Ecology* 181:57–68.
- SAS Institute. 2004. SAS 9.1. SAS Institute, Cary, North Carolina, USA.
- Shea, K., and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* 8:824–832.

- Siemann, E., and W. E. Rogers. 2001. Genetic differences in growth of an invasive tree species. *Ecology Letters* 4:514–518.
- Siemann, E., and W. E. Rogers. 2003a. Increased competitive ability of an invasive tree may be limited by an invasive beetle. *Ecological Applications* 13:1503–1507.
- Siemann, E., and W. E. Rogers. 2003b. Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. *Oecologia* 135:451–457.
- Siemann, E., W. E. Rogers, and S. J. DeWalt. 2006. Rapid adaptation of insect herbivores to an invasive plant. *Proceedings of the Royal Society B* 273:2763–2769.
- Stowe, K. A., R. J. Marquis, C. G. Hochwender, and E. L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology, Evolution, and Systematics* 31:565–595.
- Strauss, S. Y., and A. A. Agrawal. 1999. Ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14:179–185.
- Sun, Y., J. Ding, and M. Ren. 2009. Effects of simulated herbivory and resource availability on the invasive plant, *Alternanthera philoxeroides* in different habitats. *Biological Control* 48:287–293.
- Wang, Y., J. Ding, G. S. Wheeler, M. F. Purcell, and G. Zhang. 2009. *Heterapoderopsis bicallosicollis* (Coleoptera: Attelabidae): a potential biological control agent for *Triadica sebifera*. *Environmental Entomology* 38:1135–1144.
- Wapshere, A. J. 1985. Effectiveness of biological control agents for weeds: present quandaries. *Agriculture Ecosystems and Environment* 13:261–280.
- Zhang, K., and Y. Lin. 1994. Chinese tallow. China Forest Press, Beijing, China.
- Zou, J., W. E. Rogers, and E. Siemann. 2008a. Increased competitive ability and herbivory tolerance of the invasive plant *Sapium sebiferum*. *Biological Invasions* 10:291–302.
- Zou, J., W. E. Rogers, and E. Siemann. 2009. Plasticity of *Sapium sebiferum* seedling growth to light and water resources: inter- and intraspecific comparisons. *Basic and Applied Ecology* 10:79–88.
- Zou, J., E. Siemann, W. E. Rogers, and S. J. DeWalt. 2008b. Decreased resistance and increased tolerance to native herbivores of the invasive plant *Sapium sebiferum*. *Ecography* 31:663–671.

APPENDIX A

Native and invasive populations of *Triadica sebifera* that were used in this study (*Ecological Archives* A021-037-A1).

APPENDIX B

Repeated-measures ANOVAs for effects of plant origin, population, light, initial insect density, and time on the weevil population size (*Ecological Archives* A021-037-A2).

APPENDIX C

Nested ANOVAs (three-way) for effects of weevil adult density, plant origin, population, and light on the growth of *Triadica* seedlings (*Ecological Archives* A021-037-A3).

APPENDIX D

Slope and intercept comparisons in the weevil experiment: differences in slopes and intercepts between treatments (*Ecological Archives* A021-037-A4).

APPENDIX E

Nested ANOVAs (three-way) for effects of moth larval density, plant origin, population, and light on the growth of *Triadica* seedlings (*Ecological Archives* A021-037-A5).

APPENDIX F

Slope and intercept comparisons in the moth experiment: differences in slopes and intercepts between treatments (*Ecological Archives* A021-037-A6).