16 The Role of Insect Herbivores in Exotic Plant Invasions: Insights Using a Combination of Methods to Enhance or Reduce Herbivory

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16.1 Summary

Exotic plant invasions are threatening biodiversity and altering fundamental ecosystem properties and processes worldwide. Escape from native insect herbivores is believed to be one of the primary causes contributing to the successful invasion of many introduced plants. With biotic homogenization increasing globally, studies that examine the effects of herbivores on both native and introduced species are essential for understanding the influence of exotic species invasions on community dynamics and ecosystem function. While collecting field observations and life history characteristics of an exotic plant can be useful, it is experimental manipulations that will most clearly reveal the mechanisms responsible for the dominance of an aggressive invasive species. Employing a variety of methodological approaches that both increase and decrease insect herbivory will best elucidate the population ecology and ecosystem impact of an exotic plant invader. There is a pressing need to develop effective management strategies to lessen the effects of exotic invaders on a variety of threatened species and imperiled ecosystems. Such experiments will not only increase basic ecological knowledge, but also provide useful insights to land managers pressed with addressing a large and growing problem with tremendous societal, economic and environmental costs.

16.2 Introduction

Numerous biases and inherent problems are associated with the different methods of experimentally manipulating herbivore damage (Hendrix 1988; Baldwin 1990; Osterheld and McNaughton 2000; Hjältén, Chap. 12, this Vol.; Lehtilä and Boalt, Chap. 13, this Vol.; Schmitz, Chap. 14, this Vol.; Siemann et

al., Chap. 15, this Vol.). Perhaps the best manner of dealing with these short-comings is to concurrently perform a variety of experiments that approach herbivory questions using several of the methodologies described herein and compare and contrast the findings from these different studies. Together the results of several approaches should be richer and more reliable than any method used in isolation. In this chapter, we outline a variety of methodological techniques for assessing and comparing the effects of insect herbivory on exotic invaders and native plants. Specific reference will be made to studies we have conducted examining the role of herbivores in invasions of *Sapium sebiferum* in North America and Hawaii. In aggregate, these studies will provide other researchers with examples and a framework for pursuing questions related to the accumulation dynamics of herbivores on plants, mechanisms of community assembly and coevolutionary interactions of herbivores and their hosts.

16.3 The Role of Herbivores in Exotic Plant Invasions

Invasions by exotic plant species are considered to be one of the greatest contemporary and future threats to the integrity of ecosystems worldwide (Coblentz 1990; Soule 1990; Chapin et al. 2000; Pimentel et al. 2000). Despite the importance of the problem, ecologists are still in the early stages of understanding the mechanisms underlying exotic plant invasions. Nevertheless, because invasive plants typically experience low losses to herbivores in their introduced range (Elton 1958; Tucker and Richardson 1995; Yela and Lawton 1997; Maron and Vila 2001), the assertion that herbivores are important in mediating plant competition is nearly ubiquitous in the invasion literature (Groves 1989; Mooney and Drake 1989; Tucker and Richardson 1995; Williamson 1996; Keane and Crawley 2002). In general, insect herbivores need not consume a large amount of plant material to have a large effect on plant community composition, they need only reverse the outcome of competition (e.g. Louda et al. 1990; Grover 1994; Leibold 1996; Crawley 1997).

The Enemy Release Hypothesis predicts that when exotic plants are introduced with few or none of the specialist herbivores from their native habitat and are not a preferred choice of generalist herbivores in their introduced range they will suffer low rates of attack by enemies and thereby gain a competitive advantage over native plants (Schierenbeck et al. 1994; Williamson 1996; Keane and Crawley 2002; Wolfe 2002; DeWalt et al. 2004). With reduced damage, resources normally lost to enemies or used for the production of defences may be allocated to growth and/or reproduction by a plastic phenotypic response (Bazzaz et al. 1987; Tilman 1999; Alpert et al. 2000; Stowe et al. 2001; Schlichting and Smith 2002). Since relatively small amounts of leaf herbivory can have major detrimental effects on plant growth and survival (Mar-

quis 1992), this release from enemies can greatly benefit exotic species competing with native plants.

16.4 Focal Plant Species

Chinese tallow tree [*Sapium sebiferum* (L.) Roxb, Euphorbiaceae] is a major invader throughout the southeastern United States (Bruce et al. 1997; Grace 1998; Siemann and Rogers 2003a). Originally introduced to North America in 1772, *Sapium* has become naturalized from the southern Atlantic coast to the Texas Gulf coast (Bruce et al. 1997). It aggressively displaces native plants and forms monospecific stands. First established in Texas in the early 1900s, in the past 50 years much of the coastal prairie, abandoned agricultural fields and floodplain forests along the Texas Gulf coast have been converted to *Sapium*-dominated woodlands (Bruce et al. 1997; Grace 1998). It is monecious, has insect-pollinated flowers from April to June and fruits ripen from August to November (Bruce et al. 1997). Seeds are dispersed by many bird species. It is a deciduous tree that loses its leaves in autumn and has range limits largely determined by winter temperatures and aridity (Bruce et al. 1997). Rapid growth, colourful autumn foliage, abundant flowers and seeds rich in oils have encouraged widespread plantings that readily escape from cultivation.

16.5 Experimental Methods for Assessing Herbivory Effects

Designing an experimental study so that the exotic species of interest is paired with a similar native species can provide a better understanding of the mechanisms responsible for invasion (Barrett and Richardson 1986; Schierenbeck et al. 1994; Mack 1996; Sakai et al. 2001; Keane and Crawley 2002; Daehler 2003). Ideally, the native and exotic species would be congeners, but many introduced species are taxonomically isolated, making pairing difficult. In such instances, an ecologically similar native species can be used for comparisons. In our studies, *Sapium sebiferum* is the only woody member of its genus in the region and there are no native Euphorbiaceae trees in Texas. By using both *Sapium* and a native tree species that shares multiple morphological, physiological and phenological characteristics, we can monitor similarities and differences between *Sapium* and native plants that are unrelated to their site of origin. This is especially important in grassland invasions because *Sapium* is a woody plant competing with herbaceous functional groups. As such, experiments that incorporate both the exotic tree and a native tree species will more likely reveal the mechanisms responsible for successful invasions and competitive dominance.

An alternative experimental method is to incorporate seedlings derived from seeds collected in both the native and introduced ranges. Such studies can provide valuable insights into genetic change as a potential mechanism causing invasiveness. Evolutionary change is increasingly being recognized as an important factor contributing to the success of exotic invaders (Blossey and Nötzold 1995; Thompson 1998; Mack et al. 2000; Keane and Crawley 2002; Mooney and Cleland 2001; Sakai et al. 2001; Lee 2002; Stockwell et al. 2003).

16.5.1 Common Garden/Reciprocal Transplant Studies

Reciprocal seedling transplants in common garden and greenhouse pot studies can be used to assess the effects of genetic change on invasive characteristics relative to the effects of phenotypic and developmental plasticity. Although the Enemy Release Hypothesis has been widely accepted to explain the invasive success of many exotic plant species, an alternative hypothesis, the Evolution of Increased Competitive Ability (EICA; Blossey and Nötzold 1995), proposes that invasive plants evolve reduced allocation to defence and increased allocation to growth and/or reproduction because they are seldom attacked by enemies (Thompson 1998; Willis et al. 1999; Willis et al. 2000). Because allocation to defence may be as costly as herbivore damage (Bazzaz et al. 1987; Simms 1992; Baldwin 1998; Strauss et al. 2002), plants that escape their enemies in an introduced range would gain a selective benefit from decreasing their defensive investment. While the Enemy Release Hypothesis predicts that both native and invasive genotypes would benefit from low levels of herbivore damage in the introduced range, the EICA hypothesis suggests that invasive genotypes would achieve an additional benefit derived from reduced allocation to energetically expensive defences. Some studies confirm differences in growth and competitive ability of invasive and native genotypes (Blossey and Nötzold 1995; Willis and Blossey 1999; Leger and Rice 2003), while others are inconclusive (Willis et al. 1999, 2000; Thebaud and Simberloff 2001).

Using long-term common garden and greenhouse experiments, we have recently shown genetic differences in growth and defence among native and introduced genotypes of *Sapium sebiferum* that likely contribute to its invasiveness (Siemann and Rogers 2001, 2003b, c). In a long-term common garden planted in east Texas, invasive genotypes of *Sapium* from North America had significantly higher growth rates, earlier and greater seed production but lower foliar tannin concentrations than native *Sapium* genotypes from Asia (Fig. 16.1). All genotypes had uniformly low amounts of leaf area removed by insect herbivores and damage was independent of genotype (Siemann and Rogers 2001). This outcome is unlikely to be explained by the Enemy Release Hypothesis since both native and invasive genotypes should have similarly displayed a plastic phenotypic reallocation from defence to growth in the
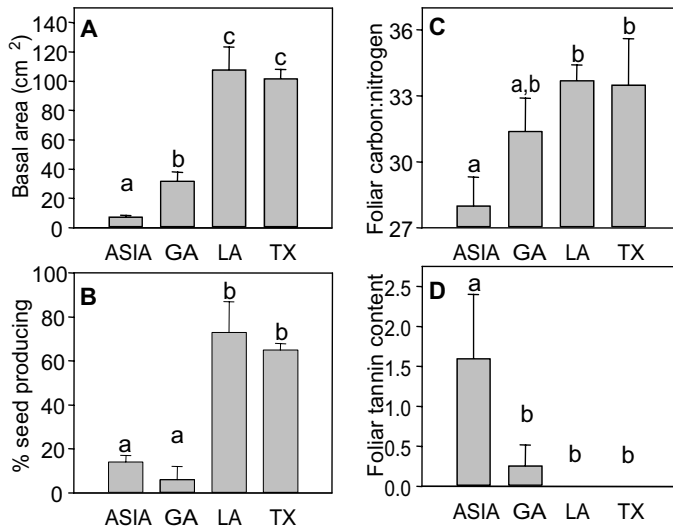
Fig. 16.1. Genotypes of *Sapium sebiferum* grown in a 14-year common garden in Texas differed in A growth, B seed production, C leaf chemistry and D defence chemicals [foliar tannin content measured as tannic acid equivalents (mg) per 100 mg tissue dry weight]. *ASIA* Native range; *GA* Georgia (site of North American introduction); *LA* Louisiana; *TX* Texas (areas colonized later). All trees had low levels of herbivore damage. *Different letters on bars* indicate significant statistical differences at *P*<0.05. (Modified from Siemann and Rogers 2001)

introduced range where herbivores are absent. Rather, the EICA hypothesis postulates an evolutionary mechanism for reallocation of resources from defence to growth in response to low herbivory and is consistent with these patterns for native and invasive genotypes of *Sapium* (Blossey and Nötzold 1995). In this scenario, there is little increase in the rate of herbivory on exotic plants with lower allocation to defence, whereas, for native plants, herbivory is expected to increase strongly as defences decrease. Reductions in defence likely lead to greater competitive ability only when the additional costs of herbivore damage do not exceed the reduced costs of defence (Coley et al. 1985; Bazzaz et al. 1987; Simms and Rausher 1987; Maschinski and Whitham 1989; Louda et al. 1990; Herms and Mattson 1992; Hunter and Price 1992; Mauricio 1998; Agrawal 2000). According to the EICA hypothesis, the discrepancy in growth rates between native plants and invasive exotics arises from the unique combination of low herbivory and low defence that native plants are unable to achieve.

We recently reinforced this interpretation by examining a companion long-term common garden study established in Hawaii that used *Sapium* seed collected from many of the same source trees as the east Texas common garden (Siemann and Rogers 2003 c). In Hawaii, the native Asian genotypes had

less leaf damage and grew significantly larger than invasive Texas genotypes (Fig. 16.2A,B). This was contrary to our findings in the Texas common garden where invasive genotypes outperformed native genotypes. We believe this reversal of growth patterns for the different genotypes is due to Asian herbivores, which were inadvertently introduced to Hawaii, feeding more heavily on poorly defended Texas *Sapium* genotypes (Fig. 16.2). As a result, *Sapium* is currently not invasive on any of the Hawaiian islands despite being present for several decades.

Combined, these long-term common garden experiments in Texas and Hawaii with *Sapium* from its native range and areas where it is invasive suggest that post-introduction evolutionary change has occurred in response to an absence of herbivores. This may potentially explain *Sapium*'s current invasive status in Texas where Asian herbivores are non-existent and *Sapium*'s rel-
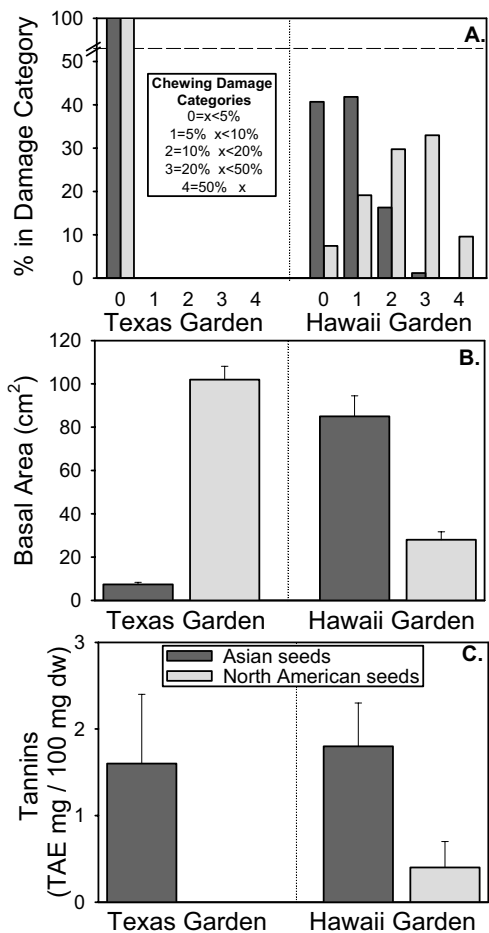

Fig. 16.2. Long-term common garden experiments in Texas and Hawaii, USA, with *Sapium* from its native range (Asia) and areas where it is invasive (North America) demonstrate that post-introduction evolutionary change promotes invasiveness in Texas, but not in Hawaii where Chinese herbivores are abundant. **A** In Texas, where *Sapium* is invasive, herbivory levels are low in the common garden. In Hawaii, where *Sapium* is not invasive, North American genotypes suffered greater herbivore damage than native Asian genotypes. **B** Invasive genotypes grew significantly larger than native genotypes in Texas, but the opposite occurred in Hawaii. **C** Foliar tannin content [measured as tannic acid equivalents (TAE, mg) per 100 mg tissue dry weight (dw)] was significantly greater in native genotypes compared to invasive genotypes regardless of common garden location. (Modified from Siemann and Rogers 2003 c)

ative scarcity in Hawaii where the herbivore *Adoretus sinicus* (Chinese rose beetle) is abundant (Siemann and Rogers 2003 c). In Texas, where *Sapium* is invasive, herbivores avoided feeding on all plants in the common garden. With uniformly low herbivory, fast-growing, poorly defended invasive genotypes outperformed slower-growing, better defended native genotypes. In Hawaii, where *Sapium* is not invasive, *A. sinicus* caused greater damage to Texas genotypes, which may be responsible for Asian genotypes being superior.

The reversal of growth patterns for native and invasive genotypes due to native herbivores being either present or absent emphasizes the importance of establishing common garden studies in both the introduced range where the species is invasive and in an area where native herbivores are present, preferably in the native range that contributed the original introduced source populations. Because insect herbivory pressures and plant resistance traits covaried across time and space, our insights into the genetic differences of invasive and native *Sapium* would have been greatly reduced without established gardens in both Texas and Hawaii. As a result, it is highly recommended that future common studies be concurrently established in the native and introduced range and include plant genotypes from both sources. We are currently pursuing studies that will establish common gardens of multiple *Sapium* genotypes at sites across a biogeographical gradient of invasion in several regions of the southeastern United States, sites in the native range of China, and sites in Hawaii where it has been introduced but is currently not invasive.

Another finding from these common garden studies is that *Sapium* derived from seed where it has been present longer as an introduced species is more similar in growth and defence to genotypes from the native Asian range than in North American areas where it has more recently invaded (Fig. 16.1). Within 300 years after introduction, invasive plants often support diverse insect communities similar to those on native plants (Strong et al. 1984). *Sapium* from Georgia, the site of original introduction, may more closely approximate the situation in Hawaii with Asian herbivores than that of Texas where herbivores are relatively inexperienced with the novel plant. The intermediate position of Georgia genotypes may reflect smaller genetic change compared to Texas genotypes. Alternatively, Georgia genotypes are potentially being recognized by native herbivores as an edible resource and are beginning to be selected for increased levels of defence as they accumulate a higher pest load and suffer greater amounts of damage. *Sapium* invasions present an ideal opportunity to conduct multiple common garden studies and various herbivore manipulations in order to examine native herbivores and an invasive plant in different stages of adjustment to a novel environment. The intriguing possibility that the ecological success of *Sapium* may be attributed to rapid post-introduction evolutionary change in competitive ability and defence against herbivores establishes a model system for investigations into the role of enemies in the success of other exotic plant species.

16.5.2 Reducing Herbivory on Target Plants Using Insecticide Sprays

There is a long history of debate in the ecological literature regarding top-down herbivore regulation of plant population dynamics, community structure and net primary productivity (e.g. Hairston et al. 1960; Strong et al. 1984; Crawley 1989; Brown and Gange 1990; Louda et al. 1990; Hunter and Price 1992; Schmitz, Chap. 14, this Vol.). In spite of this controversy, a central prediction of the Enemy Release Hypothesis is that if introduced plants suffer less damage than the native flora, removing herbivores should result in significantly greater damage reductions to natives than to exotic species. If differences in pest loads are responsible for the greater growth and lower mortality of introduced plants, removing herbivores should also minimize growth and survival differences between exotics and natives (Sakai et al. 2001; Keane and Crawley 2002).

Insect herbivores can be excluded by regular spraying of foliage on target plants with a variety of readily available insecticides, many of which have been successfully used for other ecological studies (reviewed by Siemann et al., Chap. 15, this Vol.). Plants not receiving insecticide should be sprayed with an equal amount of water. To avoid unintentional treatment of control plants with insecticide, sprays should be administered only on days when there is no wind.

Phytotoxic effects could potentially cause methodological artifacts. Companion studies in controlled environments should always be performed to discount the possibility of plant growth being directly affected by the chemical spray per se. Further, degree of toxicity to non-target organisms, residence time on vegetation and in the soil and nutrient levels (many insecticides contain trace amounts of nitrogen and phosphorus) need to be considered when designing studies involving the application of chemical sprays. While there is considerable utility in employing insecticides for disrupting insect herbivory on target plants, if concerns of toxicity or nutrient additions are warranted the more labour-intensive method of manually removing larger, sessile herbivores is also an effective manipulation (Karban and Strauss 1993; Agrawal 1998).

We have recently completed a 3-year test of the Enemy Release Hypothesis (Siemann and Rogers 2003a). Using chemical sprays, we suppressed insect herbivores on transplanted seedlings of *Sapium* and *Celtis laevigata*, a native tree, in forests and prairies in east Texas where *Sapium* is invading. Although not taxonomically related, pairing *Sapium* with the ecologically similar native tree *Celtis* established a control for woody establishment and encroachment in the absence of insect herbivory that is unrelated to the geographical origin of the species and should better reveal the mechanisms responsible for successful invasions.

As predicted by the Enemy Release Hypothesis, results from our study showed that insect herbivores caused greater damage to unsprayed native

seedlings than unsprayed *Sapium* seedlings. However, contrary to predictions of the Enemy Release Hypothesis, suppression of insect herbivores caused significantly greater increases in survivorship and growth of *Sapium* compared to native seedlings (Siemann and Rogers 2003a). It was only due to common garden studies (mentioned above) and additional companion experiments that manipulated herbivore damage in alternative ways (see sections below) that we were able to explain these counterintuitive results and repeatedly obtain results consistent with the EICA hypothesis. We are currently pursuing studies using common garden plantings and factorial insecticide spray treatments on native plant species and native and invasive *Sapium* genotypes in a variety of biogeographical locations to further explore the role of genetic change in exotic species in response to the presence or absence of a herbivore load.

16.5.3 Reducing Herbivory on Community Assemblages Using Insecticide Sprays

Another method of assessing herbivore effects on native and exotic plants is to chemically treat the entire plant community in experimental plots. Other researchers have had dramatic success with this technique in native herbaceous communities (Brown et al. 1988; Carson and Root 1999, 2000). Again, if enemies strongly facilitate exotic plant invasions, removing herbivores from entire plant communities containing native and exotic species should reduce damage to native plants significantly more than exotics. The resultant competitive release caused by spraying should also reduce the growth of exotics relative to the growth of native plants in areas where herbivores are abundant. We recently completed a 3-year experiment chemically treating 2-m^2 prairie plots containing a mixture of native and invasive woody and herbaceous plant species. Surprisingly, no significant patterns in plant community composition or productivity were observed (Siemann and Rogers, unpubl. data). This type of study is likely most effective when implemented over longer time periods, particularly in instances where outbreaking insects occur (Carson and Root 1999, 2000).

The effect of belowground herbivores on exotic plant species and native plant community dynamics can also be manipulated by soaking insecticides into the soil of experimental plots. Belowground herbivory can have strong effects on plant community structure and the competitive environment of a plant often influences its response to belowground herbivory (Anderson 1987; Brown and Gange 1990; Mortimer et al. 1999; Rogers and Hartnett 2001; Verschoor et al. 2002). Several studies have found the impact of belowground insect herbivory to be greater when the host plant was competing with other plant species (e.g. Müller-Schärer 1991; Nötzold et al. 1998). Above- and belowground herbivores often damage plants simultaneously and complex

interactions between different types of tissue damage frequently become manifest in varied growth responses (Seastedt et al. 1988; Moran and Whitham 1990; Müller-Schärer and Brown 1995; Houle and Simard 1996; Maron 1998; Masters et al. 2001; Masters, Chap. 5, this Vol.). Other studies have shown that root herbivory has a greater negative effect on plant growth and reproduction than foliar herbivory (Reichman and Smith 1991; Strong et al. 1995; Maron 1998; but see Moran and Whitham 1990; Houle and Simard 1996). Several root-feeding insects associated with *Sapium* have been identified in its native Asian range (Zhang and Lin 1994), but the effects of root damage on invasive North American genotypes and its effect on plant competition have not been previously examined. Despite belowground herbivores frequently having greater effects on plant community composition and productivity than aboveground herbivory, we are not aware of any studies to date that utilize insecticide manipulations to specifically examine the interactions between native and exotic plants with respect to root-damaging herbivores.

At the other end of a plant's life history, chemically removing insect herbivores from adult trees presents multiple logistic difficulties. Chemically fogging tree canopies has been successfully used in assessing insect species diversity in tropical rainforests (Erwin 1982; Basset 2001) and to control eruptive herbivores in European and North American forests (Perry 1994). Herbivore densities and effects on native and exotic adult trees could also be assessed by experimentally employing similar techniques in both the native and introduced range.

16.5.4 Factorial Manipulations of Herbivory, Resources and Competition

It is possible that herbivores exert their influence on exotic plant invasions by mediating resource competition. The negative effects of herbivory can be particularly pronounced with low nutrient availability and are frequently mitigated by an increased supply of limiting resources (Brown and Gange 1990; Louda et al. 1990; Maschinski and Whitham 1989; Steinger and Müller-Schärer 1992; Verschoor et al. 2002). Factorial experiments that simultaneously manipulate other environmental conditions such as soil resources, water, light availability and/or intensity of competition while concurrently manipulating herbivore damage will provide additional insights into the role of herbivores in facilitating exotic plant invasions. Recent reviews have emphasized the utility of making comparisons between native and invasive plants under multiple growing conditions and suggest context dependence for the invasiveness of many species (Alpert et al. 2000; Sakai et al. 2001; Keane and Crawley 2002; Daehler 2003). This strategy has been particularly fruitful in our studies with *Sapium* (Rogers et al. 2000, 2003; Rogers and Siemann 2002, 2003, 2004; Siemann and Rogers 2003d).

16.5.5 Simulating Herbivory Via Mechanical Leaf Damage

Realistic simulation of herbivory by mechanical means is problematic because many aspects of insect chewing cannot be accurately duplicated (Hendrix 1988; Karban and Baldwin 1997; Agrawal 1998; Hjältén, Chap. 12, this Vol.; Lehtilä and Boalt, Chap. 13, this Vol.). Artificial defoliation typically results in tissues being removed indiscriminately, whereas natural herbivory is frequently more selective. However, simulated damage can suitably represent the decreased leaf area and mass loss experienced by herbivore-damaged tree seedlings (Hendrix 1988; Marquis 1992; Stowe 1998; Tiffin and Inouye 2000). The advantages of simulated herbivory over other manipulations of herbivores include the ability to remove exact amounts of tissue, specify spatial and temporal patterns of removal and randomize controlled damage treatments with resource manipulations and competitive interactions.

Before initiating a mechanical defoliation study, it is useful to examine natural types and levels of herbivory. Preliminary examinations of insects on *Sapium* in Texas and Louisiana showed that the few herbivores observed on the foliage are generalists that also feed on a variety of native species in both forests and prairies (Johnson and Allain 1998; Hartley; Rogers and Siemann, unpubl. data). Although infrequent, small chewing holes are the most common form of leaf damage observed on naturally growing *Sapium* seedlings (Rogers et al. 2000). As a result, we used a steel paper hole punch to simulate the effects of leaf herbivory on *Sapium* while growing in various resource and competitive conditions (Rogers et al. 2000; Rogers and Siemann 2002, 2003). In the first study, seedlings were grown in pots and exposed to factorial combinations of three light treatments, three soil fertility treatments and three simulated herbivory treatments (control, moderate and high). Native *Celtis laevigata* tree seedlings were also subjected to the treatments for comparison. Hole punches were randomly and independently assigned to leaves twice during the growing season. New leaves near the top of each seedling were excluded to protect apical meristems and avoid affecting branching dynamics.

Focusing on early life-history stages has a greater capacity for revealing mechanisms that regulate community dynamics because young seedlings are frequently more susceptible to environmental stress than older plants (Fenner 1987; Meiners and Handel 2000). Regardless, partial herbivory rarely leads directly to the mortality of a seedling (Fenner 1987; Hendrix 1988). As a result, we have also manipulated the temporal patterns of leaf herbivory on *Sapium* (Rogers and Siemann 2003). We were able to concurrently assess the effects of casual herbivore consumption using a low-intensity, chronic defoliation treatment and the effects of an outbreaking insect using a high-intensity, acute defoliation treatment. Although the same number of leaf holes were punched for both simulated herbivory treatments in this study, the tempo and potential effect of the damage differed considerably. Again, the defoliation treatments were crossed factorially with light and soil fertility manipulations and the

experiment was performed in both field and greenhouse settings (Rogers and Siemann 2003).

In another set of paired field and greenhouse studies simulating leaf herbivory on *Sapium* we used scissors to increase the damage severity by removing the front half of every full leaf blade twice during the growing season (Rogers et al. 2003). The scissors were sterilized with an alcohol wipe after defoliating each seedling to prevent the spread of disease or secondary allelochemicals. Clipped leaves that remained on seedlings were cut in half a second time as were all newly added leaves. In this and other studies, damaging the plants a second time allowed us to magnify the negative effects of artificial defoliation, particularly if the plants possess inducible defences that were activated by the initial leaf damage (Karban and Baldwin 1997; Rogers et al. 2003). Inducible defences can increase plant fitness in the presence of herbivores (Agrawal 1998), but can be costly if it does not deter future herbivore attacks. Unexpectedly, all of our studies involving simulated herbivory manipulations on invasive *Sapium* revealed that seedlings derived from seed collections obtained in the introduced range of east Texas were capable of rapidly compensating for all levels and types of tissue damage we imposed.

The success of *Sapium* as an invader is frequently attributed to an absence of pests (Bruce et al. 1995; Jubinsky and Anderson 1996) with the connotation that *Sapium* is resistant to native herbivores. Our results from these and other studies suggest that North American *Sapium* is a herbivory-tolerant plant that rapidly compensates for mass lost to defoliation. Consistent with the predictions of EICA, *Sapium*'s success as an invader may be that as a herbivory-tolerant species without an appreciable herbivore load, it is experiencing the benefits of a herbivore-resistant plant without incurring the associated costs of resistance (e.g. van der Meijden et al. 1988; Simms 1992; Rosenthal and Kotanen 1994; Strauss and Agrawal 1995; Stowe et al. 2001). In other words, invasive genotypes of *Sapium* are not experiencing a trade-off between herbivory resistance and tolerance like other native plant species because it has escaped the 'to grow or defend' dilemma of plants in its introduced range by allocating resources to growth rather than defence (Herms and Mattson 1992).

The predictions of the EICA hypothesis require that simulated herbivory be more costly to native genotypes of *Sapium* than to invasive genotypes. We conducted full-factorial, paired greenhouse and field experiments designed to assess the effects of soil fertility and simulated leaf herbivory using scissors on growth and survival of *Sapium* seedlings derived from seed collections obtained from the species' native range in China and introduced range along the Texas Gulf coast. Artificially defoliating *Sapium* significantly decreased the growth of Asian *Sapium* genotypes whereas Texas *Sapium* genotypes compensated for the leaf mass removed (Rogers and Siemann; Fig. 16.3). The negative effect of removing costly, defended leaves in native genotypes compared to substantial regrowth potential in poorly defended invasive geno-

Fig. 16.3. Experimental defoliation of *Sapium* with scissors had a greater negative effect on native Chinese genotypes than on invasive Texas genotypes (Rogers and Siemann, unpubl. data). *n.s.* Not significant
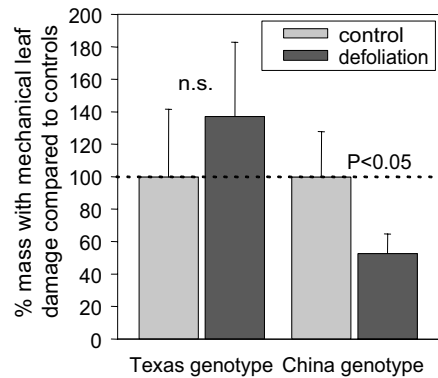
types provides further support for EICA predictions that invasive genotypes of *Sapium* have undergone a post-introduction evolutionary change from a herbivore-resistant species to a fast-growing, herbivore-tolerant species that rapidly compensates for tissue damage.

16.5.6 Simulating Herbivory Via Mechanical Root Damage

Less common than herbivory manipulations involving mechanical defoliation are studies that simulate belowground root herbivory. While field studies can be performed (Reichman and Smith 1991; Rogers and Hartnett 2001), severing root tissue in pot experiments is considerably more tractable given the inaccessibility of the belowground environment (Detling et al. 1980; Schmid et al. 1990; Houle and Simard 1996). We conducted a full-factorial pot experiment designed to assess the effects of simulated root herbivory, soil fertility and competition on *Sapium* seedlings derived from seeds obtained in the ancestral Chinese range and introduced Texas range. Roots were severed using a sharp serrated steel blade inserted into a narrow opening cut in the plastic pot. Test pots were used prior to initiating root herbivory to ensure the effectiveness of this method. Belowground competition was achieved by adding annual ryegrass seed (Lolium multiflorum Lam.) to the pots. The results, again consistent with EICA predictions, reveal that Chinese genotypes were negatively affected by root damage, while Texas genotypes were able to compensate for root herbivory (Rogers and Siemann,). Increased soil fertility promoted growth of Chinese genotypes, but did not reduce the negative effects of root herbivory enough to allow the seedlings to completely compensate for damage. Grass competition increased the height growth rate of Chinese genotypes, but did not affect shoot or root mass. In competitive conditions, the shoot and root mass of Chinese genotypes was lower than undamaged controls in both fertilized and unfer-
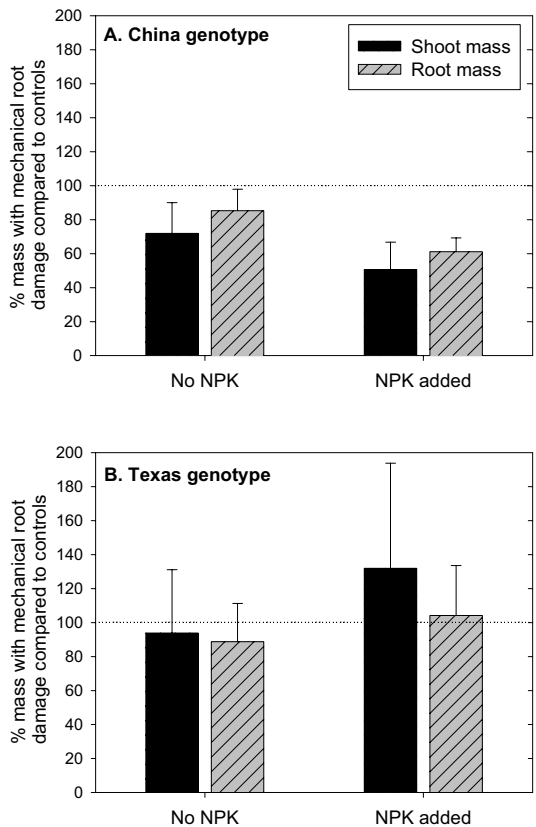
Fig. 16.4. Mass of potted *Sapium* seedlings grown in competition with ryegrass and receiving factorial combinations of fertilizer (*NPK*) and simulated root herbivory. Per cent *Sapium* shoot and root mass (mean +1 SE) of mechanically damaged seedlings relative to control seedlings (100 %) reveals that China genotype seedlings (**A**) were markedly less likely to compensate for simulated root herbivory than Texas genotype seedlings (**B**), especially with the addition of soil nutrients. (Modified from Rogers and Siemann, 2004)

tilized conditions (Fig. 16.4A). By contrast, the shoot and root mass of Texas genotypes compensated for simulated root herbivory relative to undamaged plants, particularly in fertilized conditions (Fig. 16.4B). These results provide additional support for previous studies indicating that invasive Texas *Sapium* has undergone a genetic shift away from possessing costly herbivore-defended tissues to producing relatively inexpensive tissues that are capable of rapidly compensating for damage.

16.5.7 Simulating Herbivory Using Herbicide Sprays

Species removal studies have a long history in ecological experiments (Connell 1961; Paine 1966). Many studies have used herbicides to selectively remove particular plant species and examine the subsequent community responses to altered competitive interactions (see reviews by Aarssen and Epp 1990; Goldberg and Barton 1992). These experiments are typically performed

on small scales in herbaceous ecosystems and involve the removal of dominant native species (McLellan et al. 1997; D'Antonio et al 1998; Smith et al. 1999; Cabin et al. 2002). Simulating insect herbivory via experimental removal of designated plants provides unique opportunities to investigate the role of a specific plant population on competitive interactions, community assembly dynamics and ecosystem function.

In order to assess whether *Sapium* invasions can be controlled by eliminating local seed production, we killed all mature *Sapium* trees in eight 16-ha plots in an east Texas bottomland floodplain forest. Eight 16-ha control plots were also established. This study was designed to represent a highly effective seed predator or devastating insect outbreak that causes tree mortality (Perry 1994). In the removal plots, all *Sapium* trees with a diameter at breast height (dbh) greater than 4.5 cm were killed by girdling and basal bark applications of Garlon herbicide in an oil base. In total, seed recruitment from nearly 14,000 mature *Sapium* trees was eliminated. Our preliminary findings suggest that killing seed-producing *Sapium* trees results in *Sapium* seedling density being reduced while seedling density of native trees is increased (Fig. 16.5A). Although these trends were not statistically significant, 4 years after initiating the herbicide treatments the ratio of native to *Sapium* seedling density was significantly greater in plots where mature *Sapium* trees had been killed (Fig. 16.5B). This shift could potentially alter the competitive balance back in favour of the native species. Mature native tree growth and native sapling growth also increased with *Sapium* removal (Siemann and Rogers, unpublished data). Because *Sapium* forms a short-statured, short-lived forest

Fig. 16.5. A Density of *Sapium* seedlings and all native tree seedlings in control plots of undisturbed floodplain forest and plots where all mature *Sapium* trees were killed with herbicide. **B** Ratio of native tree seedling density to *Sapium* seedling density. *Sapium* kill plots represent a 20-fold reduction in adult *Sapium* trees (Siemann and Rogers, unpubl. data). *Cross P<0.01; asterisk P<0.05; ns* not significant
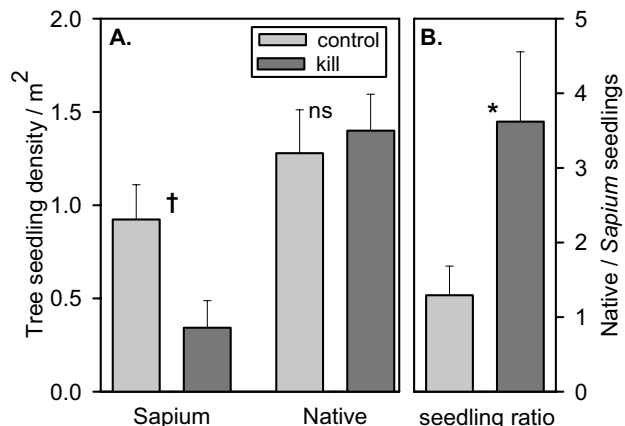
canopy compared to the native floodplain forest trees it displaces, there are also likely to be important differences in ecosystem processes, such as nutrient cycling and carbon sequestration, of forests dominated by exotic trees. Long-term monitoring of forest regeneration dynamics will be necessary to fully assess the effectiveness of this experiment, but these early results suggest that killing mature *Sapium* trees and reducing local seed supply, either through an outbreaking insect or field-worker efforts, would be a worthy strategy for conserving native forest communities imperiled by *Sapium* invasions. To our knowledge, other replicated experimental removals of a dominant invasive species have not been previously conducted on these large spatial and temporal scales.

16.5.8 Assessing Herbivore Damage Using Exclosures and Enclosures

Experimental cages are a useful tool for comparing insect herbivore impacts on exotic plants and native plants. Cages can be constructed to serve as either exclosures to prevent herbivore access to target plants or they can be used as enclosures to ensure exposure of target plants to predetermined species and densities of insect herbivores.

Cages and fences used to prevent herbivore access are most effective at excluding vertebrate herbivores (Brown and Heske 1990; Jefferies et al. 1994; McNaughton et al. 1996; Ritchie et al. 1998; Knapp et al. 1999), but could be used to prevent access of insects to target plants or community plots (Schmitz, Chap. 14, this Vol.). Because of potentially strong microclimatic effects of cages on plant growth, control cages that contain large enough holes to provide access by insects should be also erected. Cages can also be used to examine trophic interactions by adding or excluding predators that feed on herbivorous insects (Price et al. 1980; Marquis and Whelan 1996; Schmitz 1998; Schmitz, Chap. 14, this Vol.).

For insect herbivory studies, experimental cages have been most successfully used by enclosing stocked herbivores on a single leaf, individual plant or assemblages of multiple species and individuals both in pots and under field conditions (Belovsky 1986; Ritchie and Tilman 1992; Schmitz 1993; Agrawal 1998; Lill and Marquis 2001). Cage enclosures are particularly useful in experimental manipulations with potted plants. Cages can easily be erected around aboveground plant tissues, allowing the investigator to control herbivore species, herbivore density and time of exposure to herbivory. Additionally, the pot itself can serve as an effective enclosure for stocking and manipulating belowground herbivores (Steinger and Müller-Schärer 1992; Blossey 1993; Nötzold et al. 1998). Other variables like resource availability and plant competition can be simultaneously manipulated in pot experiments with caged herbivores to examine how top-down and bottom-up interactions are affected by biotic and abiotic conditions. Pot experiments provide simple access to

multiple morphological and physiological measures of plant responses to damage including stem height and diameter, branch and leaf numbers, leaf area damage, water potential and photosynthesis rates. Potted plants are useful for obtaining data on measures that are frequently difficult to collect in field conditions such as both above- and belowground productivity at the termination of the experiment. Herbivore survival and performance are also easier to measure in controlled enclosure environments. In order to simultaneously examine the effects of plant competition, herbivore choice and community dynamics in controlled environments, larger foraging arenas using container mesocosms containing more diverse assemblages of plant species can be erected and stocked with herbivores.

Realism can be increased while only modestly sacrificing precision by erecting cages over transplants and/or existing vegetation in field settings and similarly stocked with herbivores. The focus can be a single target plant or a diverse community assemblage. Likewise, field studies with caged herbivores can be designed with factorial manipulations of resources and competitive interactions. Important additional insights regarding herbivory effects can be gained by conducting these bioassays with both generalist and specialist herbivores (Bernays and Chapman 1994; Marcel et al. 2002). Specialist herbivores are typically absent from exotic plant species because they have unique behavioural and physiological adaptations to their host species. Using exclosure bioassays to determine and eventually re-establish feeding relationships between exotic plants and their specialist herbivores is central to biological control efforts (McFayden 1998; Louda et al. 2003). Generalist herbivores lack specific adaptations to particular host plants and may avoid exotic plant species because they possess unusually toxic novel defences to which the herbivore is unaccustomed. Alternatively, the exotic plant may be suitable to native generalist herbivores, but the herbivores might lack behavioural adaptations necessary to recognize and utilize a new food source. Dietary experimentation is generally selected against because the risks of selecting a toxic plant often exceed the benefits of gaining an additional food source (Feeny 1975; Abrahamson and Weis 1997). Insects with many potential hosts are less efficient in their decisions and therefore suffer increased vulnerability to natural enemies. Thus, insects have evolved to quickly recognize specific chemical cues associated with suitable hosts and ignore or avoid plants that lack these cues (Bernays and Chapman 1994; Bernays 2001).

We have conducted several bioassay experiments using North American acridid grasshoppers exposed to native vegetation and exotic *Sapium* seedlings in both pot and field exclosures. In all of our studies we have found that, despite negligible herbivory damage on *Sapium* in natural grassland and forest conditions, when grasshoppers are placed in enclosures with *Sapium* they readily feed on its foliage and show strong preferences for it over native trees, forbs and grasses (Lankau et al. 2004; Fig. 16.6). We believe this indicates a behavioural barrier rather than a biochemical deterrent to utilization.
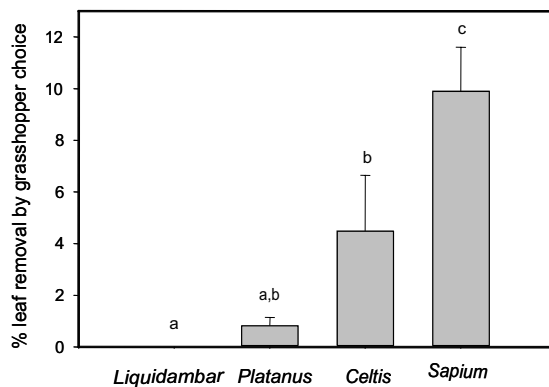
Fig. 16.6. Grasshopper (*Melanaplus angustipennis*) herbivory preferences determined by feeding trials in enclosures containing leaves of native (*Liquidambar styracifula*, *Platanus occidentalis* and *Celtis laevigata*) and an exotic (*Sapium sebiferum*) species. Grasshoppers consumed (estimated as mean percent leaf removal +1 SE) significantly more *Sapium* foliage than the native foliage in enclosures, suggesting a behavioural avoidance of the invasive species under field conditions. *Different letters on bars* indicate significant statistical differences at *P*<0.05. (Modified from Lankau et al. 2004)

Sapium is a potentially suitable food choice that is avoided because there is strong selection against host range expansion when new host plants may be toxic (Chew and Courtney 1991), temporally or spatially uncommon (Chew and Courtney 1991; Beccaloni and Symons 2000) or of limited use due to natural enemy influences (Camara 1997). We have also found that grasshoppers that were first conditioned on *Sapium* foliage in small cages fed more on the exotic tree after being introduced to multiple species mesocosms than grasshoppers first conditioned on native trees (Lankau et al. 2004). Together, these results suggest that behavioural constraints, rather than toxic novel defences, prevent generalist herbivores from more fully utilizing this abundant plant species.

Using grasshopper bioassays with potted *Sapium* seedlings derived from native China and invasive Texas seed, we have also shown significant herbivore preferences for invasive Texas foliage when offered a choice between native and invasive *Sapium* (Siemann and Rogers 2003b; Fig. 16.7A). The higher levels of consumption on native foliage caused significant decreases in the growth of China seedlings compared to the growth of Texas seedlings (Fig. 16.7B). Conversely, using the same seed sources, Texas *Sapium* seedlings grew 40% faster than Asia *Sapium* seedlings when grown in unmanipulated field conditions where herbivores remove less than 1% leaf area of both genotypes (Siemann and Rogers 2003b). When grasshoppers were stocked in cages with potted seedlings from the same continent, herbivory damage and *Sapium* growth rates were indistinguishable between the different genotypes

Fig. 16.7. A Asian genotypes of *Sapium* outgrew North American (*N. Am.*) genotypes of *Sapium* in direct competition in laboratory bioassays containing grasshoppers. Grasshoppers removed less leaf area of native Asian genotypes than invasive North American genotypes (percentage indicated in *bars*). B Conversely, a field study in east Texas with the same seed sources revealed that herbivory was uniformly low (percentage indicated in *bars*) and North American genotypes outgrew Asian genotypes. *Different letters on bars* indicate significant statistical differences at *P*<0.05. (Modified from Siemann and Rogers 2003b)
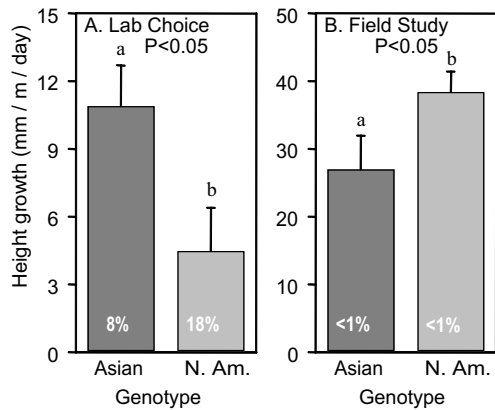
(Fig. 16.7). In a companion study, we allowed the *Sapium* seedlings 8 weeks to regrow after grasshoppers were removed. Texas genotypes were able to compensate for herbivory damage such that there was no statistical difference between the growth of damaged and undamaged trees (Rogers and Siemann, unpubl. data). By contrast, China genotypes exposed to grasshoppers in the same study had significantly reduced growth compared to undamaged plants despite 8 weeks of regrowth following herbivory (Rogers and Siemann, unpublished data).

These findings are further support for predictions of the EICA hypothesis. If the Enemy Release Hypothesis were correct, grasshoppers should have consumed or avoided seedlings from both regions similarly and growth rates for the different *Sapium* genotypes should have been indistinguishable within the same environmental conditions. In comparison, the EICA hypothesis predicts that even though herbivores in the introduced range avoid feeding on invasive plants in field settings, in controlled feeding trials they should overcome behavioural barriers and prefer fast-growing, less-defended invasive genotypes over slow-growing, better defended native genotypes.

16.6 Implications and Potential Significance

Invasions by exotic plant species are a large and growing environmental problem with tremendous societal costs. There is a pressing need to better understand the mechanisms responsible for exotic plant invasions and to develop

effective management strategies to lessen their effects on a variety of threatened species and imperiled ecosystems. In this chapter we have described a unique, complementary suite of experimental field and greenhouse studies examining the manner in which enhancing or reducing insect herbivory influences the success of an exotic plant species, *Sapium sebiferum*, which is aggressively invading a variety of habitats throughout the southeastern United States. Because invasion is a key step in community assembly, new studies like these with other problematic invasive species will provide valuable insights into the factors influencing successional dynamics, community structure and ecosystem stability and integrity.

Many of these studies were designed to experimentally test between two leading hypotheses, the Enemy Release Hypothesis and the Evolution of Increased Competitive Ability (EICA) hypothesis. The various experimental designs described above provide suggestions for differentiating between these hypotheses despite the differences in spatial and temporal scales of investigation. Experimental tests of the Enemy Release Hypothesis involve disrupting local patterns of insect herbivory and manipulating amounts of damage on different plants, whereas direct experimental tests of the EICA hypothesis involve disrupting geographical patterns of herbivory and manipulating evolutionary selection pressures. Nevertheless, it is important to note that the central premise of these hypotheses shares a similar origin. Evolution of invasiveness can only occur if exotic plants first experience an ecological release from enemies in their introduced range that strongly alters selection pressures and leads to genetic shifts away from defence allocation and toward greater growth and reproduction. The EICA hypothesis predicts that while genotypic changes in introduced species may contribute to their ecological success, it may also increase their susceptibility to herbivores introduced from their native range. In fact, it is possible that this phenomenon may explain the striking success of certain biological control efforts.

Successful biological control may be not only due to a re-establishment of feeding relationships with native herbivores, but also partially due to a host plant that has become unusually susceptible to its native herbivores because of a genetic shift away from chemical deterrents (Sakai et al. 2001). Invasive plants begin to support diverse insect communities similar to those on native plants within 300 years after introduction (Strong et al. 1977, 1984). If an invasive plant has evolved a reduction in herbivore deterrents, local herbivores in the introduced range may more likely begin to recognize and utilize the exotic species as a viable food alternative. While the introduction of an exotic species will by itself have profound effects on plant community composition and ecosystem processes like primary productivity, carbon sequestration and nutrient cycling, a shift in feeding preferences of native insect herbivores to the invasive exotic plant species will likely have equally dramatic consequences for community dynamics, trophic interactions and ecosystem function.

Although immediate action is required to suppress certain aggressive invaders (Simberloff 2003), a management strategy that encourages local herbivore recognition may be warranted considering the substantial risks associated with introducing biological control agents (Louda et al. 2003). Our results supporting the EICA hypothesis also suggest that commonly observed time lags from introduction to emergence as a problem invasive species may reflect a genetic adjustment period by the exotic plant and not merely demographic delays in recruitment and migration. This will greatly complicate the ability of horticulturists and land managers to identify and predict problem species a priori because the initial status of an introduced species may be a poor indicator of its future ecological success if the evolution of invasiveness is commonplace.

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