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EFFECTS OF SIMULATED HERBIVORY AND RESOURCES ON CHINESE TALLOW TREE (*SAPIUM SEBIFERUM*, EUPHORBIACEAE) INVASION OF NATIVE COASTAL PRAIRIE[1]

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Trade-offs associated with maintaining herbivory resistance and herbivory tolerance are frequently inferred in plant life histories. Invasive success for many non-native plants is often attributed to novel resistance that repels native herbivores. Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) is a non-native invader that threatens ecosystems throughout the southeastern United States, including imperiled coastal prairie regions. Low herbivore loads due to costly resistance are generally assumed to give *Sapium* a competitive advantage over native plants. We predicted that if *Sapium* experienced higher damage levels it would show significant decreases in growth and reduced ability to compete with native prairie vegetation. We conducted full-factorial, paired greenhouse and field experiments designed to assess the effects of simulated leaf herbivory on *Sapium* growth in the presence of prairie vegetation at different levels of light and nitrogen. Contrary to our expectations, neither low-intensity, chronic defoliation nor high-intensity, acute defoliation negatively affected *Sapium* seedlings in any resource combination in either experiment. These studies reveal that *Sapium* possesses considerable phenotypic plasticity, and herbivory tolerance is a newly appreciated trait that likely contributes to its invasive potential.

Key words: acute defoliation; Chinese tallow tree; chronic defoliation; compensatory plant growth; Euphorbiaceae; exotic invader; herbivory tolerance; nitrogen fertilization; shade tolerance; *Sapium sebiferum*; woody encroachment.

Non-native species introductions are a threat to the biological integrity of ecosystems worldwide (Cronk and Fuller, 1995; Mack et al., 2000; Pimentel et al., 2000). Although deliberately introduced perennial woody species are among the least common invasive plants (Baker, 1974; Reichard and Hamilton, 1997), they are frequently the most aggressive invaders of natural habitats (Vitousek and Walker, 1989; Schierenbeck, Mack, and Sharitz, 1994; Fleischmann, 1997; Richardson, 1998). *Sapium sebiferum* [(L.) Roxb., Euphorbiaceae, Chinese tallow tree] is a major woody invader in the southeastern United States (Bruce, Cameron, and Harcombe, 1995; Jubinsky and Anderson, 1996). Once established, it aggressively displaces native plants and forms monotypic woodland thickets (Bruce et al., 1997; Grace, 1998).

Phenotypic plasticity and differences in resource acquisition abilities have been identified as fundamental traits contributing to the invasiveness of introduced plants (Bazzaz, 1986; Dukes and Mooney, 1999; Alpert, Bone, and Holzapfel, 2000; Davis, Grime, and Thompson, 2000). The rapid decomposition of *Sapium* litter makes available nitrogen concentrations under *Sapium* trees nearly double those beneath native prairie vegetation (Cameron and Spencer, 1989), which creates nutrient feedbacks that potentially contribute to the invasion of coastal grasslands. Also, the ability to grow efficiently in a wide range of light conditions may partially explain *Sapium*'s successful invasion of a variety of different habitats (Jones and McLeod, 1989; Rogers and Siemann, 2002). *Sapium* seedlings are capable of rapid growth in full sunlight and sustained, moderate growth under low light levels, where their growth rates are frequently higher than many native, shade-tolerant tree species (Jones and McLeod, 1989, 1990).

Different resource availabilities also affect herbivore selectivity and the ability of plants to respond to herbivores (Bazzaz et al., 1987; Trumble, Kolodny-Hirsch, and Ting, 1993; Stowe et al., 2000; Lill and Marquis, 2001). *Sapium*'s success as an invader is frequently attributed to a lack of pests and pathogens (Scheld and Cowles, 1981; Harcombe, Cameron, and Glumac, 1993; Jubinsky and Anderson, 1996; Bruce et al., 1997), and its leaves purportedly contain secondary metabolites that maintain resistance to both native vertebrate and invertebrate herbivores (Russell, Schwartz, and Dollahite, 1969; Cameron and Spencer, 1989; Jubinsky and Anderson, 1996). Repeated observations confirm that *Sapium* experiences very low levels of herbivory in its introduced range (Scheld and Cowles, 1981; Siemann and Rogers, 2001). Ecological theory holds that a trade-off exists between herbivory resistance (i.e., mechanisms that reduce the probability of defoliation) and herbivory tolerance (i.e., mechanisms that facilitate regrowth following defoliation) (van der Meijden, Wijn, and Verkaar, 1988; Herms and Mattson, 1992; Simms, 1992; Fineblum and Rausher, 1995). Thus, herbivory-resistant plants invest resources and energy that would otherwise be used for growth or reproduction into producing and maintaining chemical or physical herbivore deterrents, while herbivory-tolerant plants rapidly regrow following defoliation and compensate for mass lost to herbivore damage via high growth rates.

Because *Sapium* leaves are believed to possess costly antiherbivore defenses we expected artificially damaged seedlings to show significant decreases in growth while competing for resources with native vegetation. We also proposed that decreased *Sapium* growth due to leaf damage could be partially compensated for by increasing light and soil nutrients because fertile conditions are known to reduce the negative effects of

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TABLE 1. Treatments in greenhouse experiments and in field studies conducted at the University of Houston Coastal Center, Texas, USA.

Greenhouse experiment	Field experiment
Shade	
S0 = high light (ambient greenhouse)	S0 = high light (58.6% increase with tiebacks)
S1 = low light (87% reduction with cloth)	S1 = low light (ambient prairie understory)
Nitrogen	
N0 = no nitrogen fertilization	N0 = no nitrogen fertilization
N1 = 14 g N/m^2 added as NH_3NO_4	N1 = 14 g N/m^2 added as NH_3NO_4
Simulated herbivory	
CNT = control, no simulated herbivory	CNT = control, no simulated herbivory
LCD = low-intensity, chronic defoliation	LCD = low-intensity, chronic defoliation
HAD = high-intensity, acute defoliation	HAD = high-intensity, acute defoliation

herbivores (Coley, Bryant, and Chapin, 1985; Mashinski and Whitham, 1989; Louda, Keeler, and Holt, 1990; Hunter and Price, 1992). To test these predictions, we conducted paired greenhouse and field experiments designed to assess the effects of different types of defoliation at different levels of light and nitrogen on *Sapium* seedlings grown in the presence of native coastal prairie.

MATERIALS AND METHODS

Study species—*Sapium sebiferum* was originally introduced to the United States in 1772, but has only recently become an invader of many habitats throughout the southeastern United States (Bruce, Cameron, and Harcombe, 1995; Jubinsky and Anderson, 1996). It is monecious and has insect-pollinated flowers from April through June (Bruce et al., 1997). Fruits ripen from August to November, and seeds are dispersed by many bird species (Barrow et al., 2000; Renne, Gauthreaux, and Gresham, 2000). 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, colorful fall foliage, abundant flowers, and seeds rich in oils have encouraged extensive planting of *Sapium* for ornamental purposes, biomass production, industrial oils, and a nectar crop (Scheld and Cowles, 1981). It readily escapes cultivation throughout the southeastern United States, and *Sapium* invasions seriously threaten many native ecosystems, including endangered coastal prairies (Bruce, Cameron, and Harcombe, 1995; Grace, 1998; Barrileaux and Grace, 2000). Once established, it is capable of aggressively displacing native plants and transforming diverse habitats into biotically depauperate woodland thickets (Bruce et al., 1997; Grace, 1998).

Greenhouse experiment—In December 1999, 48 clonal bunches of *Schizachyrium scoparium* were excavated from the University of Houston Coastal Center, a research area located approximately 50 km southeast of Houston, Texas, USA (see below for site description). The excavated bunches were reduced to fit into 9-L pots (24-cm diameter) and transferred to an unheated greenhouse at Rice University. After the grasses senesced in January 2000 (typical for Texas Gulf Coast graminoids), we clipped the vegetation 2.5 cm above the soil surface. This material was dried and weighed. In the same greenhouse, we germinated *Sapium* seeds collected from trees at the Coastal Center in November and December 1999. Following 1 mo of *Schizachyrium* regrowth, we planted a single newly sprouted *Sapium* seed into the middle of each clonal bunch on 18 February 2000. *Sapium* seedlings all had true leaves after less than 1 mo of growth in the pots. 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).

We initiated the 15-wk experiment on 15 March 2000 and recorded initial *Sapium* stem heights, diameters, and leaf numbers. We measured stem height of each seedling from the soil surface to the tip of the apical meristem and measured stem diameter at the soil surface with a digital caliper. Each pot was randomly assigned a full-factorial treatment combination involving shade, nitrogen fertilization, and simulated leaf herbivory on the *Sapium* seedlings (Table 1). Plants in the shade treatment were placed under a black polypropylene shade cloth that intercepted approximately 87% photosynthetically active radiation present in the greenhouse as measured by weekly readings with a Decagon Accupar Linear Ceptometer (Decagon Devices, Pullman, Washington, USA). Unshaded plants received ambient greenhouse light that was reduced to 75% outdoor sunlight due to attenuation by glass panes. We rotated plants within each shade treatment frequently. Plants in nitrogen fertilization treatments received 14 g/m^2 of nitrogen added as ammonium nitrate in weeks 1, 3, 5, 7, 9, 11, and 13 (2 g N/m^2 per addition).

Although infrequently observed, small holes presumably created by chewing insects are the most common form of leaf damage observed on naturally growing *Sapium* seedlings (W. E. Rogers, personal observation). Thus, we simulated leaf herbivory with a steel paper hole punch (6.3 mm diameter). 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). However, this type of simulated leaf herbivory can provide an adequate representation of the decreased leaf area and mass loss experienced by herbivore-damaged tree seedlings (Hendrix, 1988; Marquis, 1992; Stowe, 1998; Tiffin and Inouye, 2000).

Hole punches were randomly and independently assigned to leaves. If possible, we did not punch midveins to prevent unintended magnification of the damage, and new leaves near the top of each seedling were excluded to protect apical meristems and avoid affecting branching dynamics (Marquis, 1992). Because partial herbivory rarely leads directly to the mortality of a seedling (Fenner, 1987), two types of simulated leaf herbivory treatments were used to defoliate *Sapium* seedlings to assess which caused the greatest reduction in competitive ability (Hendrix, 1988). The first treatment was a low-intensity, chronic defoliation (LCD; Table 1). We punched six leaf holes per seedling during weeks 4, 6, 8, 10, and 12 for a cumulative total of 30 leaf punches. Approximately 20% leaf area was removed initially, but as the seedlings grew larger, subsequent defoliations removed less area. The second simulated herbivory treatment was a high-intensity, acute defoliation (HAD) designed to simulate an outbreaking insect (Table 1). For the HAD treatment we punched 30 leaf holes in the *Sapium* seedlings during week 8. This constituted a mean of $>$60% estimated leaf area removed. Although the same number of leaf holes were punched for LCD and HAD treatments, the tempo and potential effect of the damage differed considerably.

Throughout the experiment, non-*Schizachyrium* plants (mostly forbs and sedges) that germinated in the pots were removed. In order to prevent uncontrolled background herbivory, we periodically sprayed esfenvalerate (tradename Asana XL, DuPont Agricultural Products, Wilmington, Delaware, USA) on the plants. We have conducted separate phytotoxicity tests and found no negative effects of this insecticide on *Sapium* or *Schizachyrium* plant mass (E. Siemann, unpublished data). All pots were watered daily or as needed.

At the end of 15 wk (105 d) we measured final *Sapium* stem heights, diameters, leaf numbers, and leaf area. Leaf area was estimated from the length and width of three leaves systematically selected near the top, middle, and bottom of each seedling. This measure strongly correlates with computerized leaf scans due to the obovate shape of *Sapium* leaves (W. E. Rogers, unpublished data). *Sapium* stems and *Schizachyrium* shoots were clipped at the soil base, *Sapium* leaves were removed from the stems, and roots were gently washed from the soil. *Sapium* and *Schizachyrium* roots were visually distinguishable and carefully separated. *Sapium* root growth did not reach the bottom of any pot; thus, none of the tree seedlings appeared to be growth-limited by rooting space. Leaves, stems, and roots of *Sapium* and shoots and roots of *Schizachyrium* were dried at 60°C for at least 72 h and weighed separately.

Field experiment—A companion field study was designed to complement the greenhouse study. This experiment was conducted in a *Schizachyrium*-dominated coastal prairie at the University of Houston Coastal Center that was last mowed in May 1999. The regional climate is semitropical with 1200-mm mean rainfall and a 250-d growing season (Scheld and Cowles, 1981; Harcombe, Cameron, and Glumac, 1993). Soils are Lake Charles clay (fine, montmorillonitic, thermic Typic Pelludert) containing a 40–60% clay content (Anonymous, 1988). The annually mowed coastal grassland areas primarily consist of perennial grasses (75% of mass) with vegetation cover dominated by *Schizachyrium scoparium* (34%), *Paspalum plicatum* (10%), and *Tripsacum dactyloides* (6%) (Harcombe, Cameron, and Glumac, 1993). A diverse assemblage of graminoids, perennial forbs, and shrubs comprise the remaining plant cover except unmowed or unburned areas are predominantly monospecific *Sapium* woodlands (Harcombe, Cameron, and Glumac, 1993; Bruce, Cameron, and Harcombe, 1995).

Sapium seeds were individually germinated in an unheated greenhouse in single-celled, 100-mL conetainers (Stuewe and Sons, Corvallis, Oregon, USA) containing surface soil collected from the Coastal Center. After growing in the greenhouse for approximately 1 mo, the seedlings were transferred outdoors, placed beneath a 50% shade cloth for 2 wk, and watered daily.

We established a grid of 1-m^2 plots in the prairie and transplanted a *Sapium* seedling in the center of alternating plots so that all seedlings were a minimum of 2 m apart. A total of 48 *Sapium* seedlings were transplanted. The plots were watered periodically to minimize transplant mortality. One seedling died and was replaced the first week after transplanting. We initiated the 15-wk experiment on 17 May 2000, 2 wk after transplanting *Sapium* seedlings into the field, and recorded initial *Sapium* stem heights, diameters, and leaf numbers. Experimental treatments were analogous to the greenhouse experiment, but field contingencies required some changes in the manipulations (Table 1). In particular, rather than erecting shade cloths over plots in the field we manipulated light by pulling back the herbaceous prairie vegetation using wire tomato cages (S0). This increased light to the *Sapium* seedling by approximately 58.6% compared with the shaded conditions beneath the undisturbed prairie canopy (S1). Nitrogen additions were similar to the greenhouse experiment, except the ammonium nitrate was dissolved in approximately 8 L of water and applied equally to the entire 1-m^2 plot. Control plots received equal amounts of water. Simulated herbivory treatments were administered in the same way as in the greenhouse experiment.

In order to minimize the effects of a prolonged drought in East Texas and improve comparisons with the daily watered greenhouse experiment, we erected sprinklers on site and watered the plots once weekly. Again, we periodically sprayed esfenvalerate on the vegetation to prevent uncontrolled background herbivory.

At the end of 15 wk (105 d) we measured final *Sapium* stem heights, diameters, leaf numbers, and leaf area. *Sapium* stems were clipped at the soil base, and leaves were clipped from stems. A 0.1-m^2 frame was used to clip aboveground prairie vegetation in each plot. Leaves and stems of *Sapium* and clipped prairie mass were dried at 60°C for 72 h and weighed separately.

Data analyses—For both experiments, *Sapium* growth rates [ln(final measurement/initial measurement)] were calculated for stem height and stem diameter. New *Sapium* leaves added were calculated by subtracting final leaf numbers from initial leaf numbers. We examined the data for normality and used analysis of variance to compare among experimental treatments (StatView 5.0, SAS Institute, Cary, North Carolina, USA). *Sapium* seedlings that died in the greenhouse experiment were included as zeros for mass but excluded from growth rate analyses.

RESULTS

Greenhouse experiment—All newly germinated *Sapium* seeds placed in the *Schizachyrium* pots became established and grew vigorously for 4 wk prior to initiating shade, nitrogen, and herbivory treatments. While we expected some *Sapium* seedlings receiving the high-intensity, acute defoliation treatment (HAD) would suffer mortality due to the negative effects of simulated herbivory, none of the seedlings in this treatment died, but rather regrew vigorously and quickly replaced lost leaves. Unexpectedly, several control seedlings died late in the experiment. None of the seedlings that died looked unhealthy prior to their rapid wilting and death. This phenomenon has also been observed for both transplanted and naturally established *Sapium* seedlings in field conditions (W. E. Rogers, personal observation).

At the end of 15 wk, *Sapium* height growth rate was significantly increased by nitrogen additions ($F_{1,31} = 5.56$; $P = 0.025$), but not affected by shade, simulated leaf herbivory, or any interactions among experimental variables (Fig. 1A). *Sapium* diameter growth rate was not significantly affected by any experimental variables (not shown). Only shade significantly increased the number of new *Sapium* leaves added ($F_{1,31} = 6.11$; $P = 0.019$; Fig. 2A) and mean leaf area ($F_{1,31} = 22.09$; $P < 0.0001$; Fig. 2B). *Sapium* shoot (leaves + stem) mass was not significantly affected by any experimental variables as main effects or in interaction, although there was a trend for additional nitrogen to increase shoot mass ($F_{1,31} = 3.10$; $P = 0.087$; Fig. 3A). Shade significantly decreased both *Sapium* root mass ($F_{1,36} = 5.48$; $P = 0.025$; Fig. 3B) and *Sapium* root : shoot mass ratio ($F_{1,36} = 53.4$; $P < 0.0001$). A significant nitrogen by herbivory interaction also revealed that simulated herbivory increased *Sapium* root : shoot mass without nitrogen, but simulated herbivory decreased root : shoot mass with additional nitrogen ($F_{2,36} = 5.78$; $P = 0.007$). Shade significantly decreased *Schizachyrium* shoot mass ($F_{1,36} = 11.38$; $P = 0.002$; Fig. 3C), root mass ($F_{1,36} = 11.66$; $P = 0.002$; Fig. 3D), and root : shoot mass ratio ($F_{1,36} = 9.41$; $P = 0.004$). The ratio of *Sapium* mass : total plant mass (*Sapium* + *Schizachyrium*), a measure of post-invasion success, was significantly increased by nitrogen additions (Table 2).

Field experiment—All *Sapium* seedlings survived the 15-wk field experiment. Seedlings that did not receive simulated herbivory sustained less than 3% natural leaf damage by the end of the study. As in the greenhouse experiment, *Sapium* height growth rate was significantly increased by nitrogen ($F_{1,36} = 6.32$; $P = 0.017$), but shade, simulated leaf herbivory, and interactions among experimental variables had no significant effects (Fig. 1B). Again, *Sapium* diameter growth rate was not significantly affected by any experimental treatments (not shown). Nitrogen significantly decreased the number of new *Sapium* leaves added ($F_{1,36} = 4.77$; $P = 0.036$; Fig. 2C) while significantly increasing mean leaf area ($F_{1,36} = 15.85$; $P = 0.0003$; Fig. 2D). Nitrogen significantly increased both *Sapium* shoot mass ($F_{1,36} = 6.59$; $P = 0.015$; Fig. 4) and aboveground *Sapium* mass : aboveground total plant mass (Table 2).

DISCUSSION

Our results support claims that the invasive potential of *Sapium sebiferum* is due to both a lack of herbivore regulation

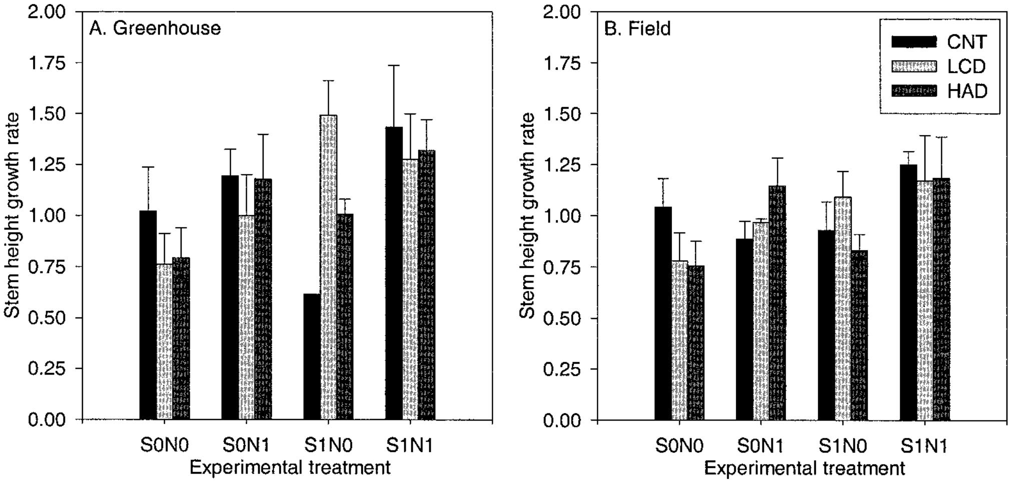

Fig. 1. Mean stem height growth rate (+1 SE) for (A) greenhouse-experiment ($N = 43$) and (B) field-experiment ($N = 48$) *Sapium* seedlings grown in full-factorial combinations of shade, nitrogen, and simulated leaf herbivory.

Figure abbreviations: CNT, control, no simulated herbivory; HAD, high-intensity, acute defoliation; LCD, low-intensity, chronic defoliation; N0, no nitrogen fertilizer; N1, 14 g N/m^2 added; S0, high light; S1, low light.

and an ability to thrive in a variety of resource conditions (Scheld and Cowles, 1981; Jubinsky and Anderson, 1996; Bruce et al., 1997; Siemann and Rogers, 2001). However, while previous assertions regarding the lack of herbivore regulation imply that herbivores are deterred by costly herbivory resistance (Russell, Schwartz, and Dollahite, 1969; Cameron and Spencer, 1989; Jubinsky and Anderson, 1996), our current studies suggest that herbivory tolerance, expressed as phenotypic plasticity and rapid compensatory regrowth, is an additional explanation for *Sapium*'s success. Phenotypic plasticity has been identified as a fundamental trait contributing to the invasiveness of many non-native plants (Bazzaz, 1986; Alpert, Bone, and Holzapfel, 2000), hence *Sapium*'s resilience is likely a key factor in its success.

There was marked similarity between results for the greenhouse and field experiments. Although there were some statistical differences, the majority of measured variables in both studies observed commensurate responses to experimental

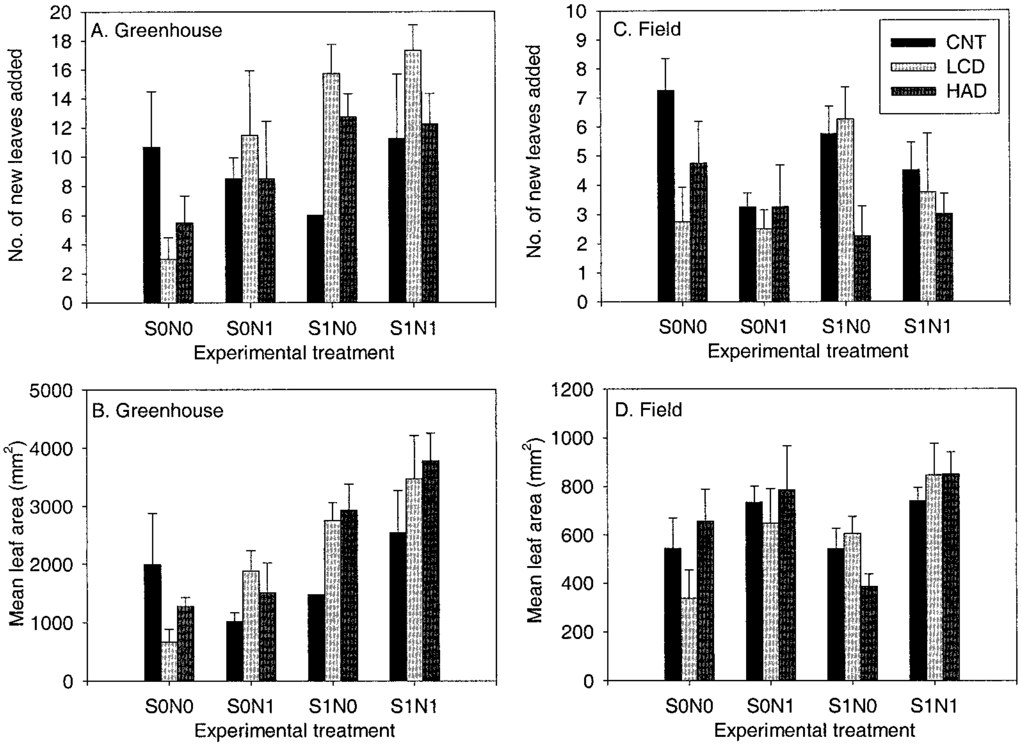

Fig. 2. Mean number of new *Sapium* leaves added (+1 SE) in (A) the greenhouse experiment ($N = 43$) and (C) the field experiment ($N = 48$) and mean *Sapium* leaf area (+1 SE) for (B) greenhouse-experiment ($N = 43$) and (D) field-experiment ($N = 48$) seedlings grown in full-factorial combinations of shade, nitrogen, and simulated leaf herbivory.

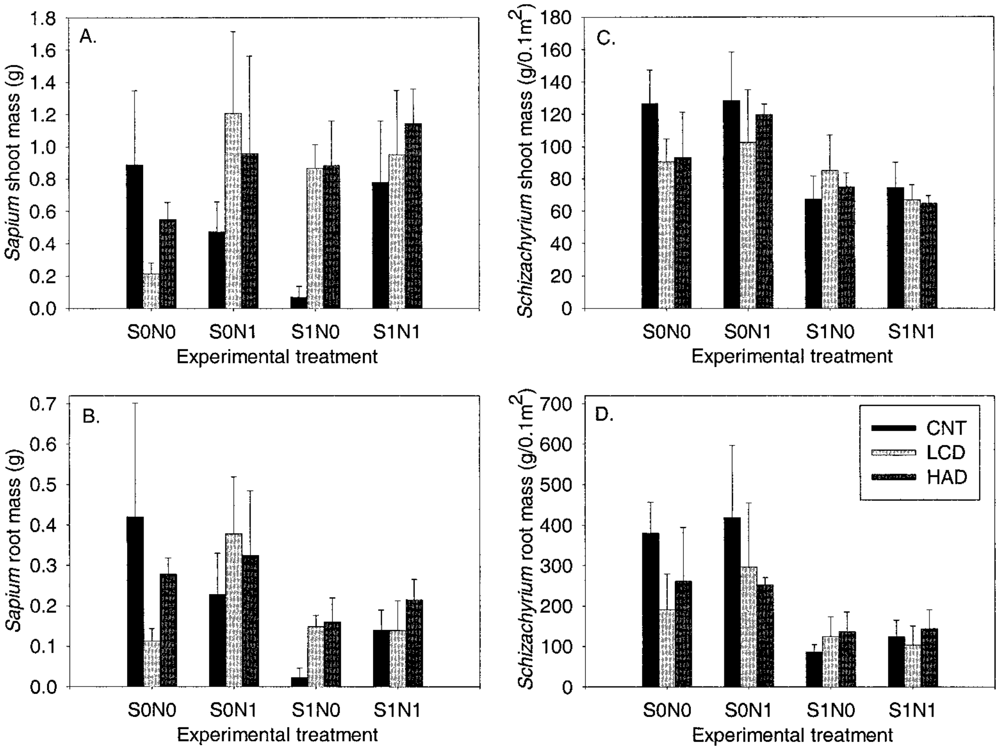

Fig. 3. Mass of greenhouse-experiment plants grown in full-factorial combinations of shade, nitrogen, and simulated leaf herbivory (see Table 1). Means (+1 SE; $N = 48$) for (A) *Sapium* shoot mass, (B) *Sapium* root mass, (C) *Schizachyrium* shoot mass, and (D) *Schizachyrium* root mass.

treatments. For instance, *Sapium* seedlings grew quite well without supplemental nutrients, but nitrogen fertilization significantly increased height growth rate in both greenhouse and field studies. Similarly, additional nitrogen significantly increased *Sapium* shoot mass in the field experiment and tended to increase shoot mass in the greenhouse study. Nitrogen did not affect the number of *Sapium* leaves or mean leaf surface area in the greenhouse study. However, in the field experiment nitrogen fertilization significantly decreased the number of *Sapium* leaves while significantly increasing mean leaf surface area possibly suggesting an allocation trade-off. Our study also revealed that elevated nitrogen levels in both experiments significantly increased *Sapium* mass relative to grassland vegetation, thereby suggesting coastal prairie sites are more susceptible to *Sapium* invasion with increased fertility. Davis, Grime, and Thompson (2000) provide an alternative explanation for the increased severity of invasion caused by additional nitrogen. Their theory suggests an invader need not be a better competitor for resources, but rather an increase in resource availability causes a temporary reduction in competitive interactions and provides opportunities for new species to become established (Davis, Grime, and Thompson, 2000; Davis and Pelsor, 2001). Additional studies are underway to determine the role resource fluctuations play in *Sapium* invasions.

Experimental light manipulations in the field experiment did not significantly affect any aspect of *Sapium* growth. *Sapium* seedlings grew equally well beneath the undisturbed prairie vegetation and with canopy tiebacks that increased light availability. Other research has shown that *Sapium* grows vigorously in a variety of light environments (Jones and McLeod, 1989, 1990; Rogers and Siemann, 2002). However, markedly lower light levels beneath the greenhouse shade cloth significantly affected both *Sapium* and *Schizachyrium* growth. Shade significantly increased both number and mean surface area of *Sapium* leaves in the greenhouse study. Accordingly, increased shade decreased *Sapium* root mass and root : shoot mass. Increased shade also decreased *Schizachyrium* shoot mass, root mass, and root : shoot mass.

While *Sapium*'s various responses to different resource conditions provide interesting new insights into its competitive ability, the most striking result from these combined studies is the absence of any appreciable effects of either defoliation treatment on *Sapium* growth. Despite the removal of considerable leaf area and mass, neither low-intensity, chronic defoliation nor high-intensity, acute defoliation had any statisti-

TABLE 2. Mean (±1 SE) effect and analysis of variance for the role of supplemental nitrogen in post-invasion success of *Sapium* as measured by total *Sapium* mass/(total *Sapium* + total *Schizachyrium* mass) in the greenhouse experiment ($N = 48$) and aboveground *Sapium* mass/(aboveground *Sapium* + aboveground prairie mass) in the field experiment ($N = 48$).

Experiment	No nitrogen added (N0)	14 g N/m^2 added (N1)	ANOVA
Greenhouse	0.003 ± 0.001	0.006 ± 0.001	$F_{1,36} = 4.36$; $P = 0.044$
Field	0.004 ± 0.001	0.006 ± 0.001	$F_{1,36} = 4.27$; $P = 0.046$

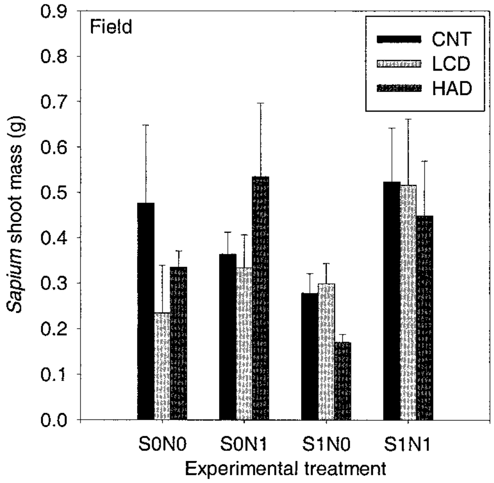

Fig. 4. Mean *Sapium* shoot mass (+1 SE) for field-experiment seedlings ($N = 48$) grown in full-factorial combinations of shade, nitrogen, and simulated leaf herbivory.

cally significant effects on *Sapium* height or diameter growth rates, new leaves added, average leaf surface area, or any measure of shoot or root mass. *Sapium* fully compensated for both types of simulated leaf herbivory in all conditions.

Previous studies have shown *Sapium* is able to tolerate different levels of chronic leaf herbivory when grown without competition for resources (Rogers et al., 2000; Rogers and Siemann, 2002). However, we predicted that *Sapium* would not be able to fully compensate for lost leaf tissue while concurrently competing with native vegetation for limited resources, particularly if defoliation was severe (e.g., Coley, Bryant, and Chapin, 1985; Maschinski and Whitham, 1989; Louda, Keeler, and Holt, 1990). This was not the case. Rather, these experiments revealed that *Sapium* is remarkably tolerant of intense defoliation levels and able to fully compensate for lost leaf mass under a variety of resource levels in competitive conditions. The morphological plasticity of *Sapium* is exhibited in the greenhouse study, where root : shoot mass was significantly affected by a nitrogen and herbivory interaction. In these conditions, *Sapium* invested more mass in roots in the absence of herbivory, but defoliation shifted allocation toward rebuilding lost leaf mass with added soil nitrogen. Regardless of its effect on allocation patterns, defoliation did not negatively impact *Sapium* growth in any resource condition.

In a previous study, Siemann and Rogers (2001) demonstrated that the increased competitive ability and invasive success of introduced *Sapium* is likely due to a genetically determined reallocation away from costly anti-herbivore defenses toward increased rapid growth and reproduction. In other words, in a relatively brief period *Sapium* has evolved from an herbivore-resistant into a rapidly growing, herbivore-tolerant tree. Further, because it does not have an appreciable herbivore load like other herbivore-tolerant native plants, it is not experiencing the typical trade-off between these strategies (Herms and Mattson, 1992). Other researchers have suggested that an isolated population of introduced plants may lose adaptations to herbivory over time (Blossey and Nötzold, 1995; Daehler and Strong, 1997; Mack et al., 2000; Willis, Memmott, and Forrester, 2000; Mooney and Cleland, 2001). This explanation for the success of *Sapium* as an exotic invader remains consistent with our current results and suggests that the ability to thrive in a variety of environmental conditions, low herbivory damage, and rapid compensatory regrowth are all likely to contribute to *Sapium*'s invasion of the endangered coastal prairie ecosystem and will complicate the development of a management strategy for controlling this aggressive invader.

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