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# HERBIVORY, DISEASE, RECRUITMENT LIMITATION, AND SUCCESS OF ALIEN AND NATIVE TREE SPECIES

EVAN SIEMANN[1] AND WILLIAM E. ROGERS

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

*Abstract.* The Enemies Hypothesis predicts that alien plants have a competitive advantage over native plants because they are often introduced with few herbivores or diseases. To investigate this hypothesis, we transplanted seedlings of the invasive alien tree, *Sapium sebiferum* (Chinese tallow tree) and an ecologically similar native tree, *Celtis laevigata* (hackberry), into mesic forest, floodplain forest, and coastal prairie sites in east Texas and manipulated foliar fungal diseases and insect herbivores with fungicidal and insecticidal sprays. As predicted by the Enemies Hypothesis, insect herbivores caused significantly greater damage to untreated *Celtis* seedlings than to untreated *Sapium* seedlings. However, contrary to predictions, suppression of insect herbivores caused significantly greater increases in survivorship and growth of *Sapium* seedlings compared to *Celtis* seedlings. Regressions suggested that *Sapium* seedlings compensate for damage in the first year but that this greatly increases the risk of mortality in subsequent years. Fungal diseases had no effects on seedling survival or growth. The Recruitment Limitation Hypothesis predicts that the local abundance of a species will depend more on local seed input than on competitive ability at that location. To investigate this hypothesis, we added seeds of *Celtis* and *Sapium* on and off of artificial soil disturbances at all three sites. Adding seeds increased the density of *Celtis* seedlings and sometimes *Sapium* seedlings, with soil disturbance only affecting density of *Celtis*. Together the results of these experiments suggest that the success of *Sapium* may depend on high rates of seed input into these ecosystems and high growth potential, as well as performance advantages of seedlings caused by low rates of herbivory.

*Key words: biological invasions;* Celtis laevigata; *Chinese tallow tree; Enemies Hypothesis; herbivory; plant diseases; plant pathogens; recruitment limitation;* Sapium sebiferum.

## INTRODUCTION

Invasions by alien plants are often characterized by sustained rapid rates of population growth and high rates of range expansion. Some invaders achieve extreme levels of dominance that may result in displacement of native species and changes in ecosystem characteristics (e.g., D'Antonio and Vitousek 1992, Mack et al. 2000, Pimentel et al. 2000). Superiority in local interactions, either due to innate characteristics of the invaders or changes in resource conditions and disturbance regimes that favor them, is thought to be important for the extraordinary success of these invaders (Mack et al. 2000). However, ecologists are increasingly aware that local interactions and processes operating at larger scales, including exchange among habitats, interact to determine local community composition (Hubbell 2001). Understanding the roles local and larger scale processes play in alien plant invasions will help prevent future invasions and control those that are already underway.

### *Focal species*

The alien Chinese tallow tree (*Sapium sebiferum* (L.) Roxb., Euphorbiaceae, ''*Sapium*'' hereafter) is a major invader in the southeastern United States (Bruce et al. 1997). Because it grows rapidly and has seeds rich in oils, abundant flowers, and colorful fall foliage, it has been widely planted as a biomass crop, oil crop, nectar crop, and ornamental. *Sapium* has become naturalized throughout the southeastern United States. It aggressively displaces native plants and forms monospecific stands. In coastal Texas, much of the coastal prairie and some floodplain forests have been converted to *Sapium* forests (Bruce et al. 1997).

Because *Sapium* differs from the dominant plants at our sites in many ways other than being an alien species, pairing it with an ecologically similar native species in our experiments can give a better understanding of the mechanisms of invasions (Barrett and Richardson 1986, Mack 1996, Keane and Crawley 2002). In other words, by using both *Sapium* and an appropriate native tree species in our experiments, we help minimize differences between *Sapium* and other native plants that are unrelated to their alien or native status. This is especially important in the prairie because *Sapium* is a woody plant competing with herbaceous plants. Ideally, the native and alien species would be congeners (Barrett and Richardson 1986, Mack 1996), but *Sapium sebiferum* is the only member of its genus in the Gulf Coast or Texas, and there is no native tree in the Euphorbiaceae in Texas (Hatch et al. 1990). We selected the most ecologically similar native species to *Sapium*

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[1] E-mail: siemann@rice.edu

that occurred in our sites, hackberry (*Celtis laevigata* Willd., Ulmaceae, ''*Celtis*'' hereafter).

*Celtis* is one of only two native tree species commonly found in our prairie site. Both *Sapium* and *Celtis* are insect pollinated and bird dispersed (Bush and Van Auken 1986, Bruce et al. 1997). Both tend to grow in wetter sites and both species have the potential to grow rapidly. In our floodplain forest site, 19 years of forest dynamics data (Harcombe et al. 1999) show that *Celtis* is the native tree species with sapling mortality and growth rates most similar to those of *Sapium*. By using *Celtis* in our study, we can understand more clearly what allows *Sapium* to invade and permanently displace native vegetation. The utility of our results and conclusions is independent of our choice of *Celtis*. If *Sapium*'s superiority is due to its status as a nonnative, any choice of native species should be informative. However, we do believe that *Celtis* has advantages over other choices of native species that may make these comparisons unusually productive. Although inclusion of native species in this type of experiment is recommended (Barrett and Richardson 1986, Mack 1996, Keane and Crawley 2002), ecologists have only begun to do this recently (e.g., Schierenbeck et al. 1994, Radford and Cousens 2000, Blaney and Kotanen 2001).

### *Enemies hypothesis*

The Enemies Hypothesis predicts that alien plants are usually introduced with few or none of the specialist herbivores and diseases from their native habitat and are not a preferred choice of generalist herbivores in their new habitat. This is widely believed to give alien plants a competitive advantage over native plants (e.g., Elton 1958, Groves 1989, Lodge 1993, Tilman 1999). At least three lines of empirical evidence support this hypothesis. First, alien plants are often taller and more vigorous in their introduced ranges (e.g., Crawley 1987, Bazzaz 1996 but see Thebaud and Simberloff 2001) though this may reflect postinvasion evolution (Blossey and Nötzold 1995, Siemann and Rogers 2001). Second, measurements of herbivore loads on native and alien plants have typically found higher herbivore loads on native plants (e.g., Strong et al. 1984, Schierenbeck et al. 1994, Yela and Lawton 1997). Finally, the ability of biological control agents to sometimes control alien plant species is perhaps the strongest evidence in favor of the Enemies Hypothesis (Groves 1989, Williamson 1996, McFayden 1998).

*Sapium*'s success as an invader is believed by some to be due to a low incidence of diseases and herbivores (e.g., Harcombe et al. 1999, 1993, Bruce et al. 1997). In its native range, at least 26 species of specialist insects feed on *Sapium* and it suffers from several diseases (Zhang and Lin 1994), although it is not known how important a role these pests have in its population dynamics. Insect damage is low on mature *Sapium* trees in Texas despite an apparent evolutionary shift in resource allocation from defense to growth (Siemann and Rogers 2001).

The role of pathogens in determining the structure of plant communities is comparatively poorly studied, but the work that has been done suggests that pathogens may be at least as important as herbivores in influencing plant growth, reproduction and mortality, and plant community dynamics (e.g., Burdon 1987, Dobson and Crawley 1994, Crawley 1997). The greater vigor of alien plants in their introduced range (see paragraphs above) may reflect a low incidence of disease. Biological control using fungal pathogens has had a mixture of successes and failures (Cronk and Fuller 1995), which suggests that fungal pathogens may sometimes be important in influencing plant invasions. Fungal diseases appear to be an important source of mortality for woody seedlings in east Texas forests (Streng et al. 1989). This study investigates whether lower levels of herbivory or foliar fungal diseases on *Sapium* seedlings compared to native tree species could be partly responsible for the success of *Sapium* in invading a variety of Gulf Coast ecosystems.

We planted seedlings of *Sapium* and *Celtis* into two forest sites and one prairie site in east Texas, USA, and reduced aboveground insect herbivores and foliar fungi with chemical sprays to test the following predictions of the Enemies Hypothesis: (1) In the absence of insecticide or fungicide sprays, seedlings of the native *Celtis* will experience greater insect herbivory and fungal damage, respectively, than seedlings of the alien *Sapium*. (2) Excluding insect herbivores and fungal pathogens with insecticide and fungicide, respectively, will cause larger increases in survival and growth for *Celtis* seedlings than for *Sapium* seedlings. We conducted an additional experiment with *Fagus grandifolia* Ehrh. (American beech, Fagaceae) to increase the generality of our results.

### *Recruitment limitation hypothesis*

Invasion is a balance of local and regional processes. At the simplest level, a plant must disperse seeds to a local site to have a chance of successfully establishing. In the absence of sufficient dispersal, alien plants may be unable to establish even in sites where they may have a substantial competitive advantage. It has been shown theoretically (e.g., Tilman 1994, Hurtt and Pacala 1995) that plant species that might never be expected to occur together in a local community due to strong differences in competitive ability are in fact able to coexist given appropriate trade-offs between competitive and colonization abilities. In other words, the details of dispersal among patches or sites are critical in predicting local community composition. In fact, recent empirical work in forests (Clark et al. 1998, Hubbell et al. 1999, Le Page et al. 2000) and prairies (Tilman 1997, Smith and Knapp 2001) suggests that recruitment limitation may be more important than local competitive differences in determining the diversity and composition of a given local patch. In all of these studies, low seed input was the mechanism of recruitment limitation. However, recruitment limitation could take the form of poor germination, possibly due to a lack of suitable microsites (for instance, disturbed soil patches; Grubb 1977), or poor survival at the earliest stages (Rogers and Hartnett 2001). Observations that an alien species is locally abundant may not mean that it is competitively superior to native species in that location. Rather, it may reflect relatively high seed input for the alien species, such as when a small natural area is surrounded by habitats where conditions do favor the alien species in competitive interactions (Parendes and Jones 2000, Smith and Knapp 2001).

We added seeds of *Sapium* and *Celtis* into three forest and prairie sites in east Texas, USA, with or without artificial soil disturbances to test the following predictions of the Recruitment Limitation Hypothesis: (1) If low seed input is limiting local abundance, experimentally added *Sapium* or *Celtis* seeds will readily germinate, grow, and survive, thereby increasing seedling abundance. (2) If a lack of suitable microsites is limiting invasion, then seeds added on artificial soil disturbances should readily grow and survive, thereby increasing seedling abundance.

## METHODS

### *Study sites*

*Coastal prairie*.—The University of Houston Coastal Center (UHCC) is located ~50 km southeast of Houston. Historically, the UHCC was largely tallgrass prairie. Some areas have been allowed to be invaded by *Sapium*, while others have been protected by annual mowing. The annually mowed coastal grassland areas are dominated by grasses (75% of biomass), with *Schizachyrium scoparium* (Michx.) Nash as the main species (Harcombe et al. 1993). Forbs and woody plants comprise ~18% of the plant cover (main species: *Solidago canadensis* L. and *Liatris pycnostachya* Michx.). Mowing was stopped in the area of our prairie experiments for the duration of this study. Average annual precipitation is 1070 mm (National Weather Station [NWS] station 20026043).

*Mesic forest*.—Wier Woods is located 160 km east of Houston. The closed canopy of tall trees (25–40 m) is dominated by *Pinus taeda* L., *Quercus nigra* L., *Fagus grandifolia*, and *Magnolia grandiflora* L., and *Q. alba* L. Dominant saplings (in descending order) include: *F. grandifolia*, *Q. laurifolia*, *Q. alba*, *Q. nigra*, and *Sapium sebiferum* (Harcombe et al. 1999). Average annual precipitation is 1410 mm (NWS station 30000098).

*Floodplain forest*.—Neches Bottom is a bottomland hardwood forest unit in the Big Thicket National Preserve. The Neches River floodplain at this location is ~8 km wide, with a main channel and a large system of smaller channels. We set up our experiment on the flats where *Liquidambar styraciflua* L., *Quercus michauxii* Nutt., and *Q. nigra* dominate the overstory. Dominant saplings (in descending order) include: *Sapium sebiferum*, *L. styraciflua*, and *Carpinus caroliniana* Walt. (Harcombe et al. 1999). Average annual precipitation is 1420 mm (NWS station 20024669). During times of high water, our seedlings were partially or entirely submerged. The average seedling had at least its stem base submerged for 35 days (range 14 to 61). The maximum water depth a seedling experienced ranged from 20 to 52 cm (mean 35 cm).

### *Experimental design—seedling experiment*

We used a randomized-block design (site = block) with 60 seedlings of each species (*Sapium sebiferum* or *Celtis laevigata*) at each of the three sites in east Texas described above (coastal prairie, mesic forest, floodplain forest). The seedlings were randomly assigned to two experimental treatments: insecticide (yes or no) and fungicide (yes or no). There were 15 replicates for each treatment and a total of 360 seedlings. In the forest sites, seedlings were planted along four parallel transects (30 seedlings per transect) with 1 m between seedlings along a transect and 2 m between transects. At the prairie site, the seedlings were centered in 1 × 1 m plots with 1-m alleys (30 seedlings per row). Within each block (site), seedlings were randomly assigned to a location and randomly assigned a treatment combination.

### *Seedlings*

In November and December 1998, we collected seed from *Sapium* and *Celtis* trees at UHCC. In January, seeds were planted into flats in an unheated greenhouse with open vent flaps. Seeds began to germinate in March, which is approximately the time the first seedlings appeared in the field. As soon as a seed germinated, it was transferred to a Conetainer (Stuewe and Sons, Corvallis, Oregon) filled with 1 cm of peat moss and 12 cm of commercially available topsoil. We used topsoil so seedlings would be uniform in size and condition when they were transplanted to the study sites. Seedlings were grown in the greenhouse until they had secondary leaves, then grown outside under a 50% shade cloth so they could ''harden off.'' Seedlings were transplanted into the field in the last weeks of April 1999. In the coastal prairie, soils were very dry at the time of transplanting so seedlings were lightly watered twice during the week after planting. The experiment ran for ~900 days at each site.

### *Seedling experiment—spray treatments*

Insect herbivores were excluded by spraying seedlings with esfenvalerate (trade name: Asana XL, DuPont Agricultural Products, Wilmington, Delaware), a broad-spectrum synthetic pyrethroid insecticide, at approximately three-week intervals during the growing season. Plants not receiving insecticide were sprayed with an equivalent amount of water. Although the insecticide kills phytophagous insects quickly, it has comparatively low toxicity to predators and parasites. The amount of nitrogen added by spraying this chemical was several orders of magnitude lower than background rates of nitrification (Cameron and Spencer 1989).

Fungal pathogens were excluded from seedlings by sprayings of mancozeb (trade name: Dithane, DuPont Agricultural Products, Wilmington, Delaware) at approximately three-week intervals during the growing season. Nonfungicide plants received an equal amount of water. Mancozeb is effective at controlling a broad spectrum of foliar fungal diseases but quickly breaks down in the soil, surface water, and ground water and so does not control soil fungi (Edwards et al. 1991). The amount of nitrogen added by this spray treatment was also negligible.

### *Phytotoxicity tests*

We performed an experiment to test for phytotoxic effects of sprays on our seedlings. Pots were filled with topsoil, and then assigned treatments: plant species (*Sapium* seedling, *Celtis* seedling, or 0.5 g of field-collected *Schizachyrium* seed), insecticide (none, field rate, or double field rate), and fungicide (none, field rate, or double field rate). These plants were grown outside on the Rice University campus under 50% shade cloth and watered regularly. Plants were destructively harvested after 15 weeks, roots washed gently from the soil and dry masses (root, shoot, leaves) were determined. We used ANOVA (SAS 1999) to test whether final mass or the proportion of mass aboveground was affected by sprays.

An apparently larger release from herbivory for *Sapium* could be caused by stronger suppression of *Celtis* growth relative to *Sapium* growth by toxic effects of insecticides or by stimulation of *Sapium* relative to *Celtis* (Brown et al. 1987). However, final mass of plants in our tests was independent of sprays (insecticide $P = 0.98$, fungicide $P = 0.62$) and all interaction terms. Proportion of mass aboveground almost depended on insecticide sprays ($F_{2,82} = 2.5$, $P = 0.09$), but not on fungicide ($P = 0.58$) or interaction terms. The proportions of mass aboveground of seedlings sprayed with water vs. insecticide were 53% and 54% for *Sapium*, 55% and 61% for *Celtis*, and 59% and 59% for *Schizachyrium*, respectively. Estimates of increased growth from reduction of insect herbivory based on only aboveground measurements would tend to slightly overestimate the release for *Celtis* compared to that for *Sapium* if they were biased by phytotoxic effects.

### *Seedling measurements*

We measured the height and number of leaves on each seedling before transplanting. No seedlings had any significant damage at the time of transplant. We collected the following seedling data approximately monthly in the first growing season and bimonthly in the second and third growing seasons, which lasted from mid-March to mid-October: survival (simply whether the seedling was alive or dead), number of leaves on the seedling, average insect or fungal damage per leaf, visual counts of numbers and types of invertebrate herbivores present on seedlings (typically family-level identifications, though some were to order and some were to species) and whether a seedling had been browsed by vertebrates. Leaf damage (herbivore or fungal) was assessed as the average percentage of area damaged per leaf. We surveyed leaves for chewing, sucking, gall, miner, and borer damage. Three times during each growing season (April, July, October) we also measured seedling height. In total, we collected data on seedlings 24 times. All seedlings were visited the same number of times and were handled similar amounts. After approximately 900 days, we clipped seedlings at ground level, separated leaves from stems, dried them, and weighed them.

We estimated light available to seedlings. In the prairie, we used an ACCUPAR linear PAR ceptometer (Decagon, Pullman, Washington) with an external sensor (LICOR, Lincoln, Nebraska) to measure light availability at the tops of seedlings. We took measurements twice during each growing season (June and August) at midday on cloud-free days. We estimated light availability as the average of the six measured values of light transmittance, TAU (PAR at seedling top/above-canopy PAR × 100). In the two forest sites, we used hemispherical canopy photographs to estimate growing season light availability. Photos were taken above seedling locations in the middle of the third growing season at a height of 50 cm at dawn or dusk using a Nikon Coolpix 900 digital camera (Nikon, Tokyo, Japan) with an FC-E8 fisheye lens. We used Gap Light Analyzer 2.0 (available online)[2] to calculate Global Site Factor (overall percentage of total light that reached the seedling over the growing season). Global site factor and TAU are roughly equivalent light indexes for prairies and forests.

We used measuring tapes and a line level to measure elevation of seedling bases at the floodplain forest site relative to a common elevation marker. Repeated observations of the depth of water at the elevation marker at different river levels along with daily gauge data (see USGS data)[3] allowed us to estimate the number of days a seedling had at least its base submerged and the maximum water depth a seedling experienced. Visible water lines on seedlings confirmed the depth estimates from the elevation method.

### *Seedling experiment—analyses*

We used repeated-measures ANOVAs with a three-level time variable to test whether insect chewing dam-

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[2] URL: 〈www.ecostudies.org/gla/〉

[3] URL: 〈http://tx.waterdata.usgs.gov/nwis/uv?08041000〉

age or vertebrate browsing depended on our treatments (see SAS 1998 [Statview 5.0] for all ANOVAs and means contrasts unless otherwise indicated). We used the average of all the readings during a growing season to give one data point per seedling per growing season. For seedlings that died during the season, we used the average amount of damage before death for that season's value. For vertebrate browsing, we used a three-level time variable with a dichotomous response variable. If a seedling had been browsed by vertebrates at some point during a growing season it was given a value of one, and if it had not been browsed it was given a value of zero. We realize that this is not an ideal way to analyze this type of data, because it can predict values below 0 or above 1, but we are not aware of any straightforward way to perform a repeated-measures logistic regression with categorical predictors and their interactions. To check whether this analysis could have given misleading results, we also performed a noninteractive logistic regression (SAS 1998) with a categorical response variable for whether a seedling had been browsed at all during the experiment and found the same main effects to be significant as in the repeated measures ANOVA (at the same level of significance). In both the insect and vertebrate ANOVAs, there were missing values for seedlings that were dead before the second and/or third growing seasons began. This caused unbalanced numbers of data points for the time term and some time by treatment interaction terms in the models. In this and all other ANOVAs we used a full interaction model, and we also checked whether the data met the assumptions of ANOVA, such as normality and constant variance. In this and all other ANOVAs we used Fishers LSD (very sensitive test) and Tukey-Kramer (very robust test) posthoc comparisons to test for differences in means among sites in analyses in which site was a significant predictor. In all cases both contrast tests gave identical results at the $P < 0.05$ level.

We used logistical regression for each species to test whether seedling survival to the end of the experiment depended on our treatments. We used a repeated-measures ANOVA with a three-level time variable to test whether seedling height depended on our treatments. We used the heights at the end of each of the three growing seasons as the response variable. For seedlings that died before the end of the first growing season, there were missing values that caused unbalanced numbers of data points for the time term and some treatment and time by treatment interaction terms in the model. For seedlings that lived until the end of the first growing season but that died before the end of the second and/or third growing seasons there were missing values that caused unbalanced numbers of data points for the time term and some time by treatment interaction terms. We used ANOVA to test whether the final aboveground mass of seedlings depended on our treatments. We assigned values of zero to dead seedlings so this ANOVA was balanced.

Because an ANOVA with a categorical predictor for insecticide is a crude tool to examine the relationship between damage and individual plant performance, we performed regressions to examine effects of damage on survival and the growth of surviving plants. We performed a logistic regression (SAS 1998 for all logistic regressions) to test whether survival to end of the first growing season (a dichotomous response variable) depended on species (two dummy variables: the first was equal to one if *Sapium*, zero if *Celtis*; the other variable was zero if *Sapium*, one if *Celtis*) and average chewing damage a plant experienced in the first year (two variables that were the product of each of the dummy variables and chewing damage). This most general type of regression model fits independent intercepts (intercept log likelihoods in logistic regression) and coefficients for each species (''model 1'' in Weisberg 1985). An analogous ordinary least squares (OLS) multiple regression (ARC v. 1.03, available from Statistics Department, University of Minnesota, used for all OLS regressions) tested whether the change in height of surviving plants in the first year depended on chewing damage for each species. We performed a second pair of regressions to test whether survival (logistic regression) and change in height (OLS regression) in the second year depended on the average damage in the first and second years in general regression models. These regressions allowed us to start to tease apart the immediate effects of damage and the delayed effects of damage in the previous year (Root 1996). In the third pair of regressions, we tested whether survival and change in height in the third year depended on damage in the first, second, or third years in general regression models. For all OLS regressions, we examined component-plus-residual plots to check whether data needed to be transformed to achieve linearity (Cook and Weisberg 1994). For all OLS regressions, we tested whether there was significant lack of fit using a model-free estimate of residual variance (Weisberg 1985), where a significant result indicates a model is inadequate to explain the data.

In order to investigate factors besides herbivory and fungal damage that may have influenced survival or growth of seedlings, we performed several regressions. For the prairie site we tested whether survival time or log (mass) depended on species (two dummy variables) and light (average TAU) in the general ''model 1'' structure (i.e., predictors were *Sapium* dummy, *Celtis* dummy, *Sapium* dummy × TAU, *Celtis* dummy × TAU). For the mesic and floodplain forest sites we performed two analogous regressions but substituted Global Site Factor for TAU. Finally, for the floodplain forest site, we performed one additional pair of regressions in which we substituted number of days a seedling was at least partially submerged for Global Site Factor.

### Fagus *experiment*

As a check on whether using a native tree species other than *Celtis* might have given different results, we performed an additional experiment at the mesic forest site in 2000–2001. In March 1999, we located 24 newly germinated, naturally occurring *Fagus grandiflora* (American beech) seedlings at Wier Woods. The seedlings were randomly assigned two experimental treatments: insecticide (yes or no) and fungicide (yes or no) in a complete factorial design. We applied sprays and collected the same data at the same intervals for these seedlings as for those in the main seedling experiment. In October 2001, we harvested these seedlings (572-day experiment). We used repeated-measures ANOVA to test whether insect chewing damage depended on our treatments. We used logistic regression to test whether sprays affected survival. We used ANOVA to test whether the final mass of seedlings depended on our treatments. An analogous experiment was initiated at the floodplain forest site with *Carpinus caroliniana* seedlings, but was destroyed by feral hogs after only 82 days.

### *Seed addition experiment*

We used a randomized-block design (site = block) with 12 seed addition plots for each species (*Sapium sebiferum* or *Celtis laevigata*) at each of the three sites in east Texas described above (coastal prairie, mesic forest, floodplain forest). The plots were randomly assigned two experimental treatments: year of seed addition (1999 or 2000) and artificial soil disturbance (no soil disturbance or 20 cm diameter soil disturbance). There were three replicates for each treatment and a total of 72 plots. In the prairie site, the plots were in a single row with 1 m between plots. In the forest sites, the plots were laid out in a 4 × 6 plot grid with 1 m between plots. At each site, the seed addition plots were adjacent to the seedling experiment plots.

In February 1999, we constructed twelve 0.5 m diameter, 60 cm high hardware cloth exclosures (1-cm mesh) at each site. They had tops that were kept in place until seeds were no longer visible on the soil surface in order to limit seed predation. The disturbance plots received a 20 cm diameter, 10 cm high pile of dirt excavated near the experiment. We put 50 *Sapium* seeds or 50 *Celtis* seeds into each exclosure. Keeping the species separate allowed us to estimate background numbers of emerging seedlings. In case seeds lacked the proper environmental cues to germinate in 1999, we established an identical set of 12 plots at each site in 2000. We measured germination and mortality at least monthly until October 2001. No plots had any *Celtis* or *Sapium* seedlings when they were set up.

We planted seeds from the same batches as the field experiments in flats in fall 1999 (2160 *Sapium* seeds and 1080 *Celtis* seeds) and spring 2000 (2160 *Sapium* seeds). We left the flats in a greenhouse until September 2001. In winter, the greenhouse was unheated and vent flaps were always fully open. In the summer, it was temperature controlled to keep the temperature below 38°C. We recorded and removed germinated seeds at least biweekly and kept trays watered. We stirred the soil once a month. Germination rates did not differ for spring and fall sets of *Sapium* seeds, so we pooled all the *Sapium* data. We standardized the germination rates for each species in the field experiment by dividing by its greenhouse germination rate (*Celtis* 51.5%; *Sapium* 21.1%).

We tested the dependence of total number of *Celtis* germinants on site, species of seed added, year of seed addition, and soil disturbance. In performing the analysis this way, we used the *Sapium* addition plots as de facto controls for background *Celtis* seedling emergence. We performed three other ANOVAs using the number of *Sapium* germinants, the number of *Celtis* seedlings alive at the end of the experiment, and the number of *Sapium* seedlings alive at the end of the experiment as the dependent variables.

## RESULTS

### *Damage*

Chewing damage depended significantly on site (forests > prairie), species (*Celtis* > *Sapium*), insecticide (control > spray), site × species, site × insecticide, and species × insecticide (Table 1, Fig. 1A). These interaction terms with insecticide reflect similar low damage levels on all sprayed plants, regardless of species or site. The site × species term indicates that damage at some sites is particularly high on just one of the two species. Fungal damage was very low (average = 0.05% of leaf area) and independent of all treatments (lowest $P$ value = 0.08). It was rare to observe herbivores on plants (on average 0.1 insect herbivore per plant per growing season). There was a nonsignificant trend ($P = 0.2$) for fewer herbivores to be found on insecticide-sprayed seedlings. Herbivores observed on seedlings included: Acrididae (Orthoptera), Alydidae (Hemiptera sensu lato), Aphididae (Hemiptera), Cicadellidae (Hemiptera), Cercopidae (Hemiptera), Chrysomelidae (Coleoptera), Coccoidea (Hemiptera), Miridae (Hemiptera), Coreidae (Hemiptera), Fulgoroidea (Hemiptera), Lasiocampidae (Lepidoptera), Tettigoniidae (Orthoptera), several Lepidoptera that could not be visually identified beyond order, and two snails. We observed only two instances of leaf mining (both were control *Celtis* in floodplain forest) and only four instances of damage from sucking insects on plants without sucking insects present. We did not run statistical analyses on these sparse data for rarely observed types of damage. *Celtis* seedlings were more frequently browsed than *Sapium* seedlings, especially in the first growing season (Table 1, Fig. 1B).

### *Survival and growth*

The odds of survival to the end of the experiment depended significantly on site for each species (prairie >

TABLE 1. The effect of site, seedling species, insecticide sprays, and fungicide sprays on insect chewing damage, mammal browsing, and height of seedlings in the first, second, and third growing seasons (full-interaction, repeated-measures ANOVAs), and aboveground mass of seedlings at the end of the third growing season (full-interaction ANOVA).

| | | Chewing | | | Browse | | | Height | | | Mass | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | df† | *F* | *P* | T | *F* | *P* | T | *F* | *P* | T | df | *F* | *P* |
| Site | 2, 170 | **13.8** | **** | **T** | 2.7 | (0.07) | | **10.4** | **** | **T** | 2, 336 | **18.7** | **** |
| Species | 1, 170 | **23.0** | **** | **T** | **11.7** | *** | **T** | **48.6** | **** | **T** | 1, 336 | 2.3 | (0.13) |
| Insecticide (I) | 1, 170 | **41.1** | **** | **T** | 0.9 | (0.36) | | **10.3** | ** | **T** | 1, 336 | **8.8** | ** |
| Fungicide (F) | 1, 170 | 0.4 | (0.51) | | 1.0 | (0.32) | | 0.7 | (0.42) | | 1, 336 | 0.3 | (0.62) |
| Site × species | 2, 170 | **3.2** | * | **T** | 1.3 | (0.28) | | 1.3 | (0.27) | | 2, 336 | 1.1 | (0.33) |
| Site × I | 2, 170 | **6.0** | ** | **T** | 0.7 | (0.52) | | 0.2 | (0.82) | | 2, 336 | **3.1** | * |
| Site × F | 2, 170 | 1.1 | (0.32) | | 0.3 | (0.77) | | 0.3 | (0.77) | | 2, 336 | 0.1 | (0.87) |
| Species × I | 1, 170 | **5.8** | * | | 0.1 | (0.80) | | **7.8** | ** | **T** | 1, 336 | **6.3** | * |
| Species × F | 1, 170 | 0.1 | (0.79) | | 0.1 | (0.80) | | 1.5 | (0.22) | | 1, 336 | 0.2 | (0.64) |
| I × F | 1, 170 | <0.1 | (0.86) | | 0.6 | (0.42) | | <0.1 | (0.92) | | 1, 336 | <0.1 | (0.91) |
| Site × species × I | 2, 170 | 1.7 | (0.19) | | <0.1 | (0.98) | | 0.2 | (0.79) | | 2, 336 | 2.1 | (0.12) |
| Site × species × F | 2, 170 | 0.7 | (0.50) | | 0.2 | (0.78) | | 0.3 | (0.78) | | 2, 336 | 0.2 | (0.80) |
| Site × I × F | 2, 170 | <0.1 | (0.99) | | 1.4 | (0.25) | | 0.3 | (0.77) | **T** | 2, 336 | <0.1 | (0.99) |
| Species × I × F | 1, 170 | 0.1 | (0.70) | | <0.1 | (0.89) | | <0.1 | (0.93) | **T** | 1, 336 | 0.1 | (0.73) |
| Site × species × I × F | 2, 170 | 0.1 | (0.89) | | 0.5 | (0.63) | | 1.0 | (0.39) | **T** | 2, 336 | 0.1 | (0.94) |
| Growing season | 2, 340 | 1.9 | (0.15) | | **9.5** | **** | | **7.5** | *** | | 2, 336 | | |

*Notes:* **T** denotes a term with a significant ($P < 0.05$) interaction with year. The significance of growing-season differences is also shown with $F$ value and significance level. Significant values are in boldface. See Figs. 1 and 3 for means.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$. $P$ values for nonsignificant terms are reported in parentheses.

† Degrees of freedom for chewing, browse, and height categories.

forests, Fig. 2). Odds of survival depended significantly on insecticide for *Sapium* (spray > control; $P < 0.0001$) but not for *Celtis* ($P = 0.10$). Fungicide did not change survival odds for either species. Height depended significantly on site (prairie > floodplain forest > mesic forest), species (*Celtis* > *Sapium*), insecticide (spray > control) and species × insecticide (Table 1, Fig. 3A). The interaction term indicates a stronger effect of insecticide sprays on *Sapium* seedlings, since sprays increased *Celtis* and *Sapium* seedling heights by 9% and 55%, respectively. Final mass depended significantly on site (prairie > forests), insecticide (spray > control), and species × insecticide (Table 1, Fig. 3B). The interaction term reflects a smaller increase in mass for *Celtis* (18%) with insecticide sprays compared to *Sapium* (431%). Recall that this analysis has zero values for dead seedlings. If dead plants are excluded, the changes in mass with insecticide sprays would be −3% for *Celtis* and +60% for *Sapium*.

### *Regressions*

Odds of survival to the end of the first growing season were independent of chewing damage for both species (*Celtis* $P = 0.40$, *Sapium* $P = 0.10$). Change in height of surviving seedlings in the first year was independent of damage for *Celtis* (height = 1.1 mm − 0.3 mm [for each 1% damage], $P = 0.45$) and *Sapium* (height = 97.8 mm − 0.6 mm [for each 1% damage], $P = 0.29$). Odds of survival from the beginning to the end of the second growing season decreased significantly with first growing season damage (*Celtis* coefficient = −0.077, $P < 0.01$, *Sapium* −0.116, $P < 0.01$) but not second growing season damage (*Celtis* $P = 0.10$, *Sapium* $P = 0.51$). These coefficients mean that the amount of damage in the first year required for the odds of death to be twice as likely as for an undamaged seedling in the second year is 9.0% for *Celtis* (ln 0.5/−0.070) and 6.0% (ln 0.5/−0.116) for *Sapium*. Change in height in the second year depended on damage in the second year for *Sapium* (−5.7 mm for each 1% damage, $P < 0.05$) but not *Celtis* ($P = 0.51$). Height change was independent of first year damage for both species (*Celtis* $P = 0.22$, *Sapium* $P = 0.81$). Odds of survival from the beginning to the end of the third growing season depended on damage in the first and second years for *Celtis* ($P < 0.05$, third year $P = 0.22$) but not for *Sapium* ($P = 0.89$, $P = 0.16$, $P = 0.33$). Height change in the third year was independent of damage for both species (*Celtis* $P > 0.61$, *Sapium* $P > 0.41$).

Light did not significantly affect survival time or mass of either species in the mesic forest (survival $P > 0.16$, mass $P > 0.51$) or floodplain forest (survival $P > 0.61$, mass $P > 0.18$). Neither survival ($P > 0.31$) nor mass ($P > 0.35$) of either species depended on time submerged in the floodplain forest. In the prairie, survival of *Sapium* seedlings increased significantly with light, while *Celtis* survival did not change with light (survival in days = *Sapium* × 375 + light × *Sapium* × 4.0; each term, $P < 0.05$; light × *Celtis*, $P = 0.12$; regression, $P < 0.0001$). Light significantly increased *Sapium* seedling growth but not that of *Celtis* seedlings [log(mass) = *Sapium* × 2.41 + light × *Sapium* × 0.01; each term, $P < 0.05$; light × *Celtis*, $P = 0.48$; regression, $P < 0.0001$]. In other words, each additional 1% of light penetration increased *Sapium* survival by 4 d and final mass by 2.3% ($1.023 = 10^{0.01}$).

### Fagus *experiment*

In the *Fagus* experiment, insecticide sprays significantly reduced chewing damage (Fig. 4, $P < 0.05$) but

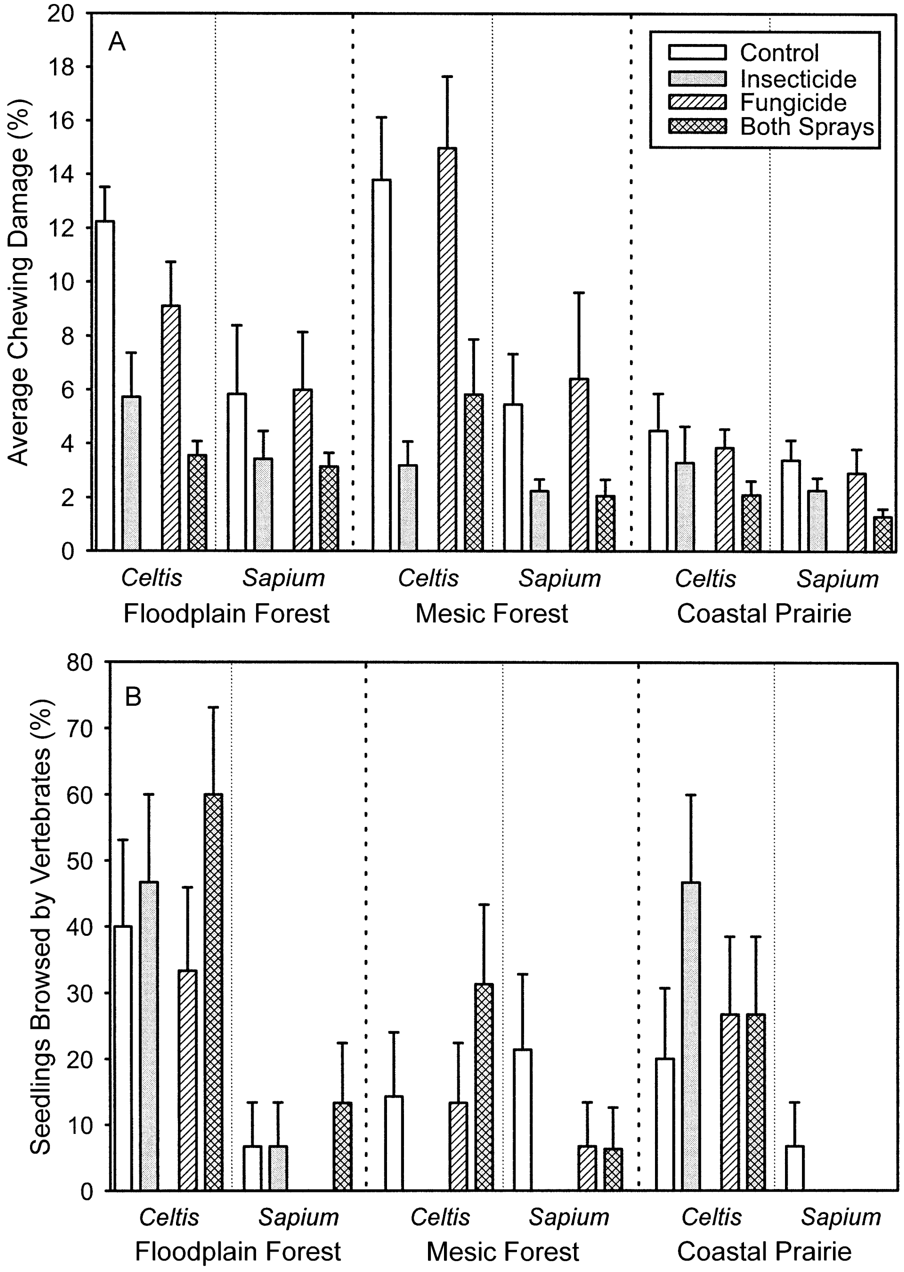

FIG. 1. Herbivore damage: the effect of site, seedling species, insecticide sprays and fungicide sprays on (A) the average amount of insect chewing damage and (B) the percentage of seedlings browsed by vertebrates over three growing seasons. Error bars indicate +1 SE.

chewing damage was independent of fungicide ($P$ = 0.88) and spray interactions ($P$ = 0.20). Chewing damage was higher in 2001 ($P < 0.05$). Survival odds and final mass were independent of insecticide (survival, $P$ = 0.57 Fig. 4; mass: spray 233 mg, no spray 242 mg, $P$ = 0.92), fungicide (survival $P$ = 0.30; mass $P$ = 0.84) and their interaction (mass $P$ = 0.22). In comparison, over three years at the mesic forest site in the seedling experiment, survival and final mass were independent of insecticide sprays for *Celtis* (survival $P$ = 0.72; mass: 133 mg vs. 112 mg vs. 75 mg, $P$ = 0.88) but depended on insecticide sprays for *Sapium* (survival: $P < 0.01$; all died vs. 340 mg, $P < 0.05$). Heights of *Fagus* seedlings were independent of insecticide sprays (Fig. 4, $P$ = 0.49).

### *Seed experiment*

The number of *Celtis* germinants depended significantly on addition of *Celtis* seed, site × disturbance, seed × year, site × seed × disturbance, and site ×

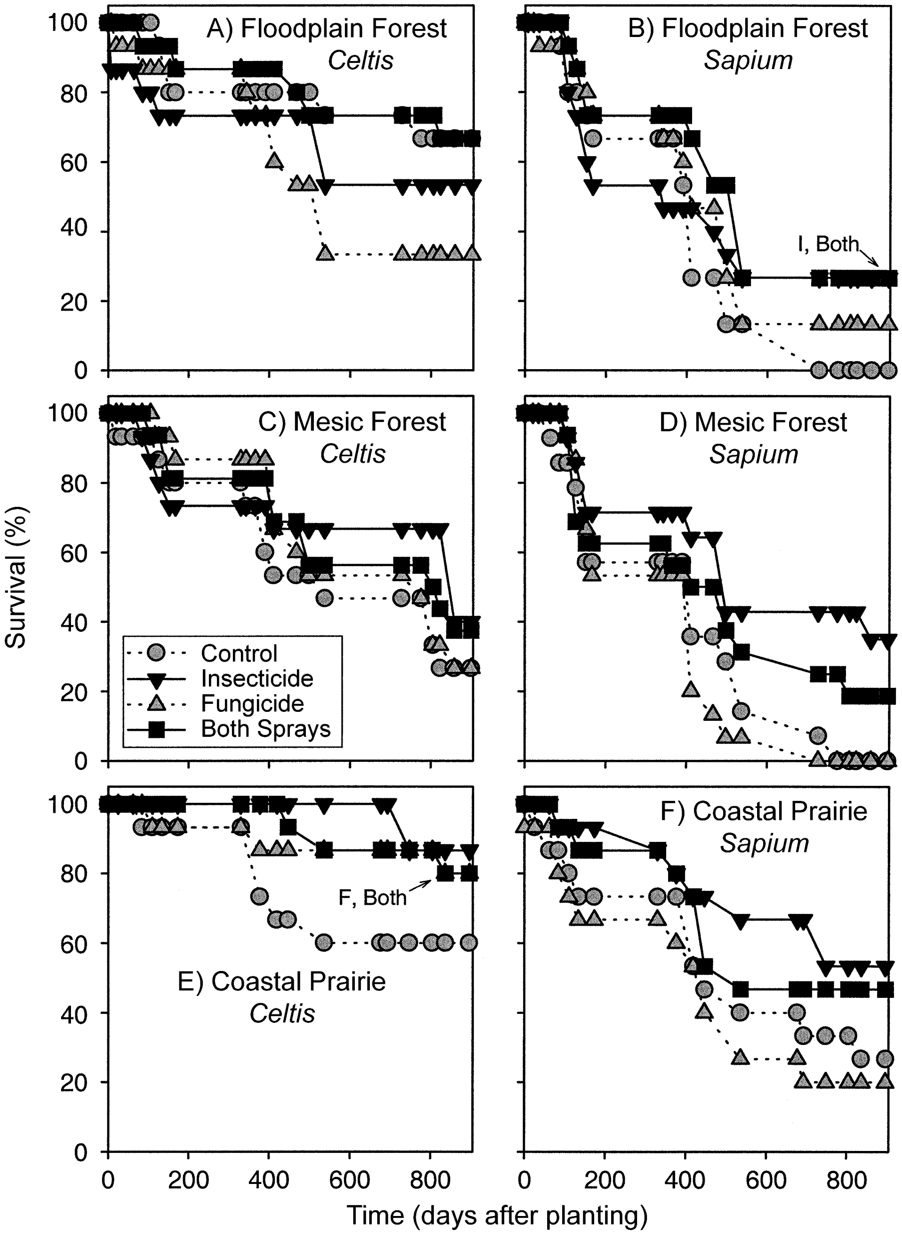

FIG. 2. Seedling survival: the percentage of seedlings surviving during the course of the experiment within each treatment for each species in each site. Symbols represent a date on which survival was checked. Time is the number of days after planting at that site. Abbreviations are: I = Insecticide, F = Fungicide, and Both = Both spray treatments.

seed × disturbance (Table 2, Fig. 5A). This large number of significant interaction terms together with few significant main effects indicates an idiosyncratic dependence of germination on our treatments. The number of surviving *Celtis* seedlings depended significantly on site (prairie > forests), addition of *Celtis* seeds, site × seed, site × year and site × seed × year (Table 2, Fig. 5B). Particularly high numbers of seedlings from prairie additions in 2000 and strong increases and decreases in seedling numbers with disturbance in the floodplain and mesic forests, respectively, were at least partly responsible for the significance of the interaction terms (Fig. 5B). The number of *Sapium* germinants and the number of surviving *Sapium* seedlings were significantly greater when *Sapium* seeds were added (Table 2, Fig. 5).

## DISCUSSION

There was no experimental evidence to support the premise of the Enemies Hypothesis that low herbivory on alien seedlings is responsible for their competitive advantage over native seedlings that experience more

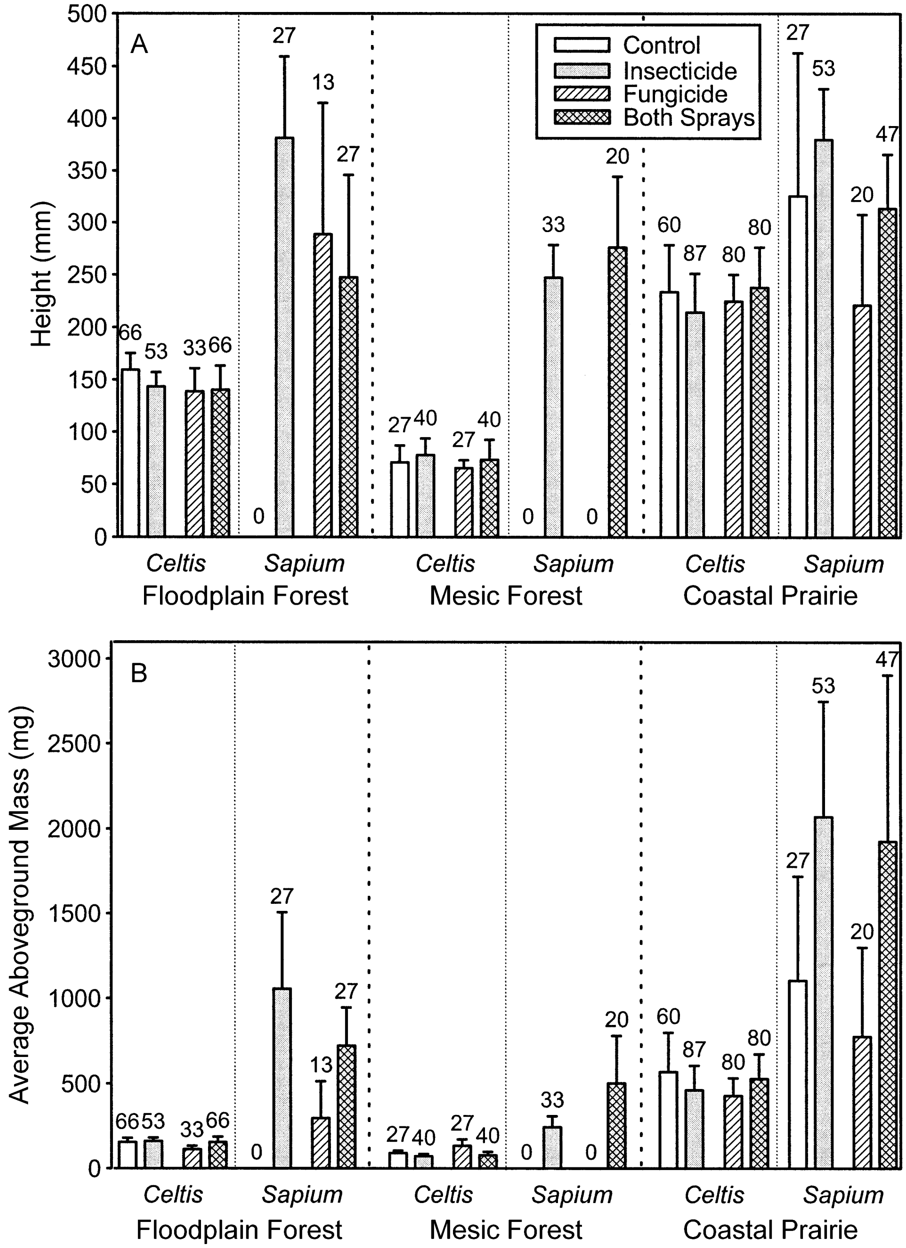

FIG. 3. Seedling size: the effect of site, seedling species, insecticide sprays, and fungicide sprays on (A) height and (B) aboveground mass after three growing seasons. Error bars indicate +1 SE. Numbers indicate the percentage of seedlings of that treatment combination alive at the end of the experiment.

herbivory. Lower rates of insect herbivory or disease on Chinese tallow tree (*Sapium sebiferum*) seedlings compared to native seedlings did not appear to be a primary cause of the invasive success of *Sapium* seedlings in prairies or forests in Texas. Insect chewing damage was lower on untreated *Sapium* seedlings than untreated native seedlings as predicted by the Enemies Hypothesis (Table 1, Fig. 1A). However, suppressing insect herbivores increased survival odds for *Sapium* seedlings only (Fig. 2), contrary to the prediction that there would be a negligible benefit for *Sapium*. Further, there were strong positive effects of insect suppression on *Sapium* seedling height and mass (Table 1, Fig. 3). These increases in height and growth with insecticide treatments were larger for *Sapium* seedlings than those of *Celtis* seedlings both in absolute and relative terms. These results suggest that lower chronic insect herbivory on *Sapium* compared to native plants is not responsible for its success in Texas.

The finding that *Sapium* has an unexpectedly large release from herbivory does not seem to depend strictly on the choice of *Celtis* as the native species in the

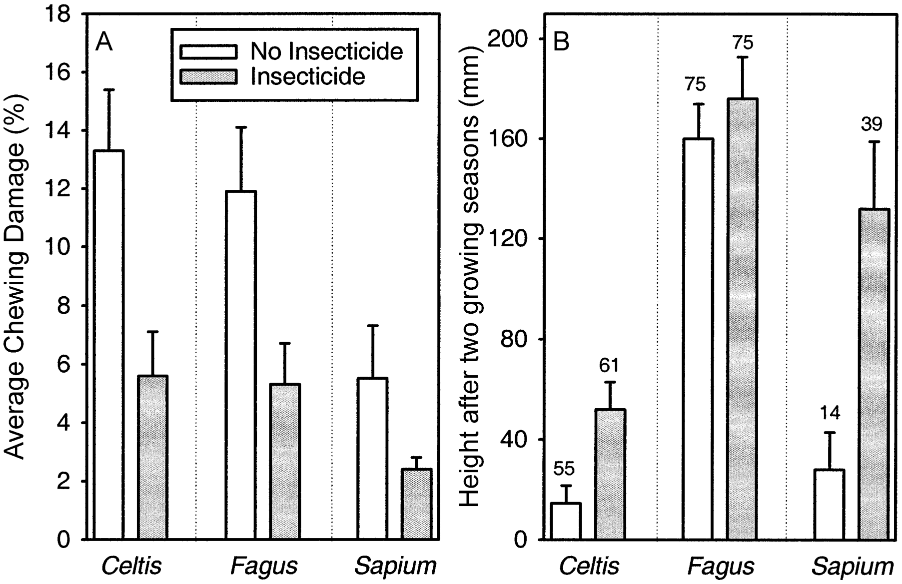

FIG. 4. *Fagus* seedling experiment and main seedling experiment at mesic forest site: the effect of insecticide sprays on (A) average amount of insect chewing damage in 2000 and 2001 and (B) average height of seedlings at the end of the second growing season. Numbers indicate the percentage of seedlings surviving to the end of the second growing season. Error bars indicate +1 SE.

experiment. In the additional experiment at the mesic forest site, *Fagus* seedlings had no significant dependence of survival, height, or mass on insecticide spray treatments, although the reductions in damage on *Fagus* seedlings were large compared to those for *Sapium* seedlings at that site (Fig. 4). The *Fagus* experiment was not started until the second year of the *Sapium* and *Celtis* seedling experiment, and naturally recruiting seedlings were used, so the results are not strictly comparable to those of the main seedling experiment. Nonetheless, the amount of damage was higher on *Fagus* seedlings than *Sapium* seedlings at that site, and the response to herbivore suppression was weaker for *Fagus* seedlings than for *Sapium* seedlings (Fig. 4). This is the same qualitative response to insect suppression on *Celtis* and *Sapium* seedlings at that site after two years (Fig. 4) and in the main seedling experiment across all three sites after three years (Figs. 1–3). At least for the mesic forest site, the same conclusions about the relative strengths of *Sapium* and native tree seedling responses to insect suppression likely would have been obtained using a different native species than *Celtis*.

The large difference between insecticide-treated and untreated *Sapium* masses in the balanced analysis using zero values for dead plants (Table 1) reflected differences in mortality (more than threefold, Fig. 2) more than differences in the sizes of surviving plants (1.5-fold, Fig. 3). In regressions, insect chewing damage to *Sapium* seedlings in the first year did not change growth or mortality in that year; *Sapium* seedlings were able to compensate for the damage they experienced. The negative consequences of insect chewing damage a *Sapium* seedling experienced in the first growing season were not apparent until the growing season after the damage occurred. Damage in the first growing season increased mortality in the second growing season in a multiple regression. These results agree with the finding that *Sapium* seedlings are able to compensate for simulated herbivore damage in the short term (Rogers et al. 2000, Rogers and Siemann 2002) but suggest that this compensation leaves them vulnerable to some future stress. In the multiple regression, the lack of a significant effect of the amount of insect chewing damage in the second year on survival in the second year is some evidence against repeated chewing damage on weakened plants being the cause of the delayed mortality. However, it is possible that increased vulnerability to other forms of herbivory, such as belowground herbivory, which we did not manipulate or measure, may have been a factor (Crawley 1997). Another possibility is that aboveground compensation by *Sapium* seedlings reduced root mass, which left them more susceptible to abiotic stresses (Maschinski and Whitham 1989, Bazzaz 1996, Crawley 1997). Indeed, in some resource conditions, *Sapium* reduces root growth, but maintains aboveground mass, in response to simulated leaf damage in pot experiments (Rogers and Siemann 2002). Because delayed mortality of this magnitude occurred at levels of damage that would typically be considered ecologically unimportant (Crawley 1997), this result merits further investigation in future studies.

The effects of insects on *Sapium* growth and survival were variable across the three sites. At some sites, such as the floodplain forest, larger amounts of insect damage (Fig. 1A) had smaller effects on survival (Fig. 2),

TABLE 2. The effect of site, seed addition, sowing year, and soil disturbance on germination rate and number of surviving seedlings of each species at the end of the experiment.

| | | *Celtis* | | | | *Sapium* | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Germinants | | Seedlings | | Germinants | | Seedlings | |
| Variable | df | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| Site | 2, 48 | 1.3 | (0.27) | **8.3** | *** | 0.2 | (0.85) | 1.5 | (0.24) |
| Seed addition | 1, 48 | **99.2** | **** | **41.0** | **** | **7.4** | ** | **4.9** | * |
| Year | 1, 48 | 3.1 | (0.09) | 3.6 | (0.06) | 1.5 | (0.23) | 2.8 | (0.1) |
| Disturbance | 1, 48 | 2.5 | (0.12) | 0.1 | (0.77) | 2.3 | (0.14) | 0.3 | (0.58) |
| Site × seed | 2, 48 | 1.7 | (0.20) | **8.3** | *** | 0.6 | (0.55) | 1.5 | (0.24) |
| Site × year | 2, 48 | 1.6 | (0.22) | **7.3** | *** | 2.3 | (0.11) | 1.6 | (0.21) |
| Site × disturbance | 2, 48 | **6.8** | ** | 2.5 | (0.10) | 0.3 | (0.75) | 0.1 | (0.93) |
| Seed × year | 1, 48 | **4.2** | * | 3.6 | (0.06) | 0.4 | (0.55) | 2.8 | (0.1) |
| Seed × disturbance | 1, 48 | 0.5 | (0.50) | 0.1 | (0.77) | 0.8 | (0.37) | 0.3 | (0.58) |
| Year × disturbance | 1, 48 | 0.1 | (0.82) | 1.0 | (0.31) | 0.4 | (0.55) | <0.1 | (0.99) |
| Site × seed × year | 2, 48 | 0.5 | (0.62) | **7.3** | *** | 2.1 | (0.14) | 1.6 | (0.21) |
| Site × seed × disturbance | 2, 48 | **6.1** | * | 2.5 | (0.10) | 0.2 | (0.82) | 0.1 | (0.93) |
| Site × year × disturbance | 2, 48 | 2.4 | (0.1) | 0.3 | (0.77) | 0.6 | (0.57) | 0.2 | (0.79) |
| Seed × year × disturbance | 1, 48 | <0.1 | (0.94) | 1.0 | (0.31) | 0.4 | (0.55) | <0.1 | (0.99) |
| Site × seed × year × disturbance | 2, 48 | **3.4** | * | 0.3 | (0.77) | 1.4 | (0.26) | 0.2 | (0.79) |

*Notes:* *F* values and significance levels are shown from full-interaction ANOVAs. *P* value for nonsignificant terms are reported in parentheses. See Fig. 5 for means.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

height (Fig. 3A), and mass (Fig. 3B) of *Sapium* seedlings, but at other sites, such as the mesic forest, lower levels of herbivory (Fig. 1A) had much larger impacts on *Sapium* seedlings (Table 1, Figs. 2, 3). The interaction of insecticide sprays and site had a significant effect on mass (Table 1). It has been shown in other systems that site suitability (i.e., soil, moisture, light) interacts with herbivory to determine plant success (Maschinski and Whitham 1989). *Sapium* has a large potential to compensate from insect damage in ideal conditions, but in less suitable sites, small amounts of herbivory may have large impacts on *Sapium* performance and invasion success. In general, the ability of a plant to compensate for damage may be limited in more stressful, low-resource or highly competitive environments (Maschinski and Whitham 1989). For instance, Meiners et al. (2000) showed that insect herbivore suppression had a much stronger effect on tree seedling survival in old fields in a drought year than in a year with normal precipitation. At one extreme, insect suppression experiments have established that insect herbivores may sometimes exclude plants from otherwise suitable habitats (Louda and Rodman 1996). In the prairie, it appears that modest amounts of damage (Fig. 1A) greatly reduce the intensity of *Sapium* invasion (Fig. 3A) because reduction in insect damage from 2.1% to 1.1% of leaf area increased survival time by six months and doubled the masses of surviving seedlings. In the floodplain forest where *Sapium* is also invading aggressively, it suffers much higher levels of insect chewing damage (9.2%), but insect suppression (reduced to 3.4%) had little effect on its growth or survival. The extremely rapid growth rate of *Sapium* in this habitat suggests that it may have a large ability to compensate for damage in those conditions. This is consistent with a gradient of habitat suitability in which insect herbivores have a strong effect on a plant's success at less suitable sites and a negligible effect at the other extreme (Louda and Rodman 1996).

Regressions helped to identify environmental factors not under experimental control that may have influenced seedling success. *Sapium* seedlings appeared to be limited by light availability in the prairie. *Sapium* seedlings in the prairie site that received more light grew faster and survived longer. This suggests that there may be a more vulnerable period when *Sapium* is below the herbaceous canopy and growth is slow and mortality is high (Carson and Root 1999). Once *Sapium* overtops the herbaceous canopy, or when it germinates in a microsite with high light, it may grow extremely rapidly and experience much lower mortality. Soil moisture may also change with light. *Celtis* showed no relationship to light availability in the prairie. In the comparatively more homogeneous forest understories (coefficient of variation: coastal prairie site = 0.367, mesic forest site = 0.129, floodplain forest site = 0.105), there was no effect of light on the survival or growth of either seedling species. Although flooding is often an important agent of mortality for plants in bottomland hardwood forests (Streng et al. 1989, Jones et al. 1994), *Sapium* and *Celtis* seedling survival and growth were independent of depth and duration of flooding in the relatively level area of the experiment.

Observational data show that *Sapium* is more than an order of magnitude more abundant in our coastal prairie site than *Celtis*, the next most abundant native tree species (Bruce 1993). Observational data also show that it is the most abundant and fastest growing sapling in our floodplain forest site (Harcombe et al. 1999). It is reasonable to expect that removing enemies would close the gap in success between *Sapium* and native species. Instead, the results of our ANOVAs and

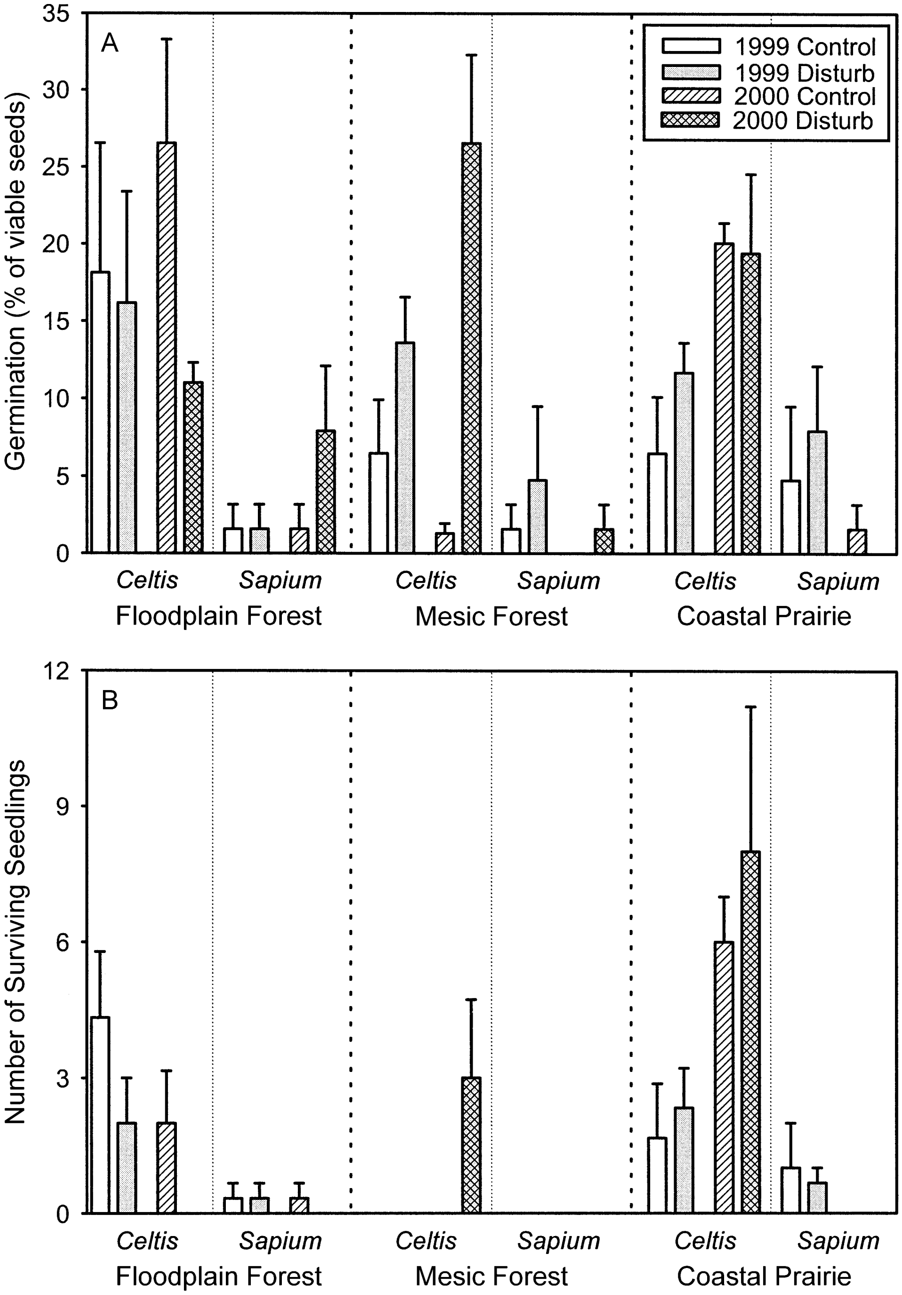

FIG. 5. Germination and survival in the seed experiment: dependence of (A) seed germination rates (standardized by greenhouse germination rates) from 1999 to 2001 and (B) number of seedlings alive at the end of the experiment on site, species planted, year seeds were planted, and soil disturbance. There were no *Celtis* seedlings in *Sapium* seed addition plots or vice versa. Error bars indicate +1 SE.

regressions indicate this would increase the disparity instead. Assuming that our control seedling data, averaged across all sites, are representative of current natural conditions, 100 *Celtis* seedlings would result in 52 seedlings with an average aboveground mass of 302 mg three years later. One hundred *Sapium* seedlings would result in 10 seedlings with an average aboveground mass of 815 mg. The results of the ANOVAs with insecticide can be used to generate an extremely conservative estimate of performance with no insect chewing damage. *Celtis* would have an additional 1 surviving seedling with survivors no larger on average, while *Sapium* would have an additional 24 surviving seedlings with survivors 471 mg larger on average (i.e., 34 seedlings, 1286 mg). These results raise two questions: How is *Sapium* such a successful invader even though its survival on a per seedling basis is not particularly high? How is it that *Sapium* is able to simultaneously have a growth rate far higher than any native tree species and still have impressive increases in growth and survival when insect herbivores are removed?

### *Recruitment limitation*

Local abundance may be set by the magnitude of local seed supply with seedling success acting as an additional, subsequent filter (De Steven 1991, Eriksson and Ehrlén 1992, Levine 2000, Mazia et al. 2001). At one extreme, with strict limitation of seedling success by density-dependent factors, experimentally adding seeds may not increase the density of seedlings (Shaw and Antonovics 1986, Mazia et al. 2001). At the other extreme, without strong density dependence in the seedling stage, adding seeds may increase the density of seedlings. In the seed addition experiment, adding seeds increased the density of *Celtis* and *Sapium* seedlings (Table 2, Fig. 5). A cautious conclusion from our data is that *Sapium* invasion would be more intense with greater seed input and less intense with lower seed input.

Adding seeds of *Sapium* into forests in South Carolina increases the density of seedlings at the end of a single growing season (Renne et al. 2001). The three-year emergence rate in our experimental seed additions was more than an order of magnitude lower than that in a single growing season in South Carolina, but the first-year survival rate of South Carolina germinants across sites (53%) was similar to average survival for a single growing season here (46%). The emergence rates are both adjusted for viability of the source seeds. In the South Carolina study, seeds were buried and then litter and vegetation were removed, which may have contributed to the higher germination rates. Because *Sapium* seeds are largely dispersed by birds, water, and gravity (Bruce et al. 1997) and may not often be buried in litter- and vegetation-free areas, their emergence rates likely are an estimate for ideal germination conditions. Buried *Sapium* seeds have double the germination rate of surface-sown seeds in the greenhouse (Renne et al. 2001). Our results suggest that emergence rates may often be substantially lower than this ideal estimate.

Our three study sites appear to differ in the relative contributions of seed supply and seedling survival in determining local abundance of *Sapium* and *Celtis*. In the mesic forest, germination was slightly lower for both species than at the other two sites, but the survival of germinated seedlings at this site was extremely low (Table 2, Fig. 5). The complete loss of all *Sapium* germinants at this site (Fig. 5B) together with the death of all noninsecticide treated *Sapium* seedlings in the other experiment at the site (Figs. 2, 3) suggests the demography of *Sapium* in mesic forests is strongly influenced by seedling mortality.

For the prairie and floodplain forest sites, adding seeds of either species was an effective way to increase the density of seedlings up to three years later (Fig. 5B). These increases in seedling density for *Sapium* and *Celtis* suggest that it may be common for the local abundances of tree species in these habitats to be recruitment limited to some extent. Differences in seed input are at least as important as measures of per seedling success in explaining the relative abundances of tree seedlings invading Piedmont old fields (De Steven 1991), the understory composition of Appalachian forests (Clark et al. 1998), and sapling species composition in gaps in Neotropical forests (Hubbell et al. 1999). The mechanisms that allow *Sapium* to introduce an unusually large amount of seed into our study sites include a high abundance in the surrounding landscape, a low incidence of seed parasitism and/or predation, and an unusually rapid maturity and heavy seed production (Bruce et al. 1997, Grace 1998).

The relatively higher germination of *Celtis* vs. *Sapium* at all three sites agrees well with published accounts of their germination requirements. *Celtis* and *Sapium* have been shown to have the greatest germination rates in oscillating temperature conditions, but only *Celtis* had any appreciable germination in constant cold or warm temperatures (Nijjer et al. 2002). This is consistent with *Sapium* being the type of species best adapted to germinate in disturbed conditions and the observation that *Sapium* is especially abundant in treefall gaps (Harcombe et al. 1999). Large-scale disturbances may facilitate *Sapium* invasion from seed. However, the availability of proper microsites for germination does not seem to limit the ability of *Sapium* to recruit from seed. Germination and survival of *Sapium* was independent of small scale soil disturbance (Table 2, Fig. 5). The apparently stronger recruitment limitation for natives compared to *Sapium* may allow *Sapium* invasions to be managed by adding native seeds species or by reducing *Sapium* seed input.

### *Why does* Sapium *grow so rapidly?*

Genotypes of *Sapium* from Texas, such as were used in these experiments, have been shown to have significantly higher growth rates, earlier and greater seed production, but lower foliar tannin concentrations than genotypes from Asia (Siemann and Rogers 2001). The Evolution of Increased Competitive Ability hypothesis (Blossey and Nötzold 1995), which postulates an evolutionary mechanism for reallocation of resources from defense to growth in response to low herbivory, is consistent with these patterns for native and invasive genotypes of *Sapium*. In this scenario, there is little increase in the rate of herbivory on alien plants with lower allocation to defense, whereas for native plants, herbivory is expected to increase strongly as defenses decrease. The discrepancy in growth rates between alien and native plants arises from this combination of low herbivory and low defense that native plants are unable to achieve.

### *Fungicide effects*

Fungal damage and impacts were minor for seedlings of both species regardless of site or treatment. If fungal diseases have larger impacts on native species such as *Celtis* than on *Sapium* that we did not detect, they might be damping-off diseases that infect seedlings at an earlier stage than the seedlings we planted (Streng et al. 1989). It is also possible that diseases occurring at high levels in occasional years could have larger impacts on woody seedling survival and growth, especially in wetter years. Regardless, the greater survival and growth of *Sapium* compared to *Celtis* in this study (Table 2, Figs. 1–3) could not be explained by foliar fungal diseases.

### *Caveats*

Our results for the role of enemies in *Sapium* invasion are not definitive. There are at least four ways that herbivory on seedlings could still influence *Sapium*'s invasion success:

1) The greater impacts of chronic insect herbivory we observed on *Sapium* compared to *Celtis* (Table 2, Figs. 2, 3) could be offset if native species such as *Celtis*, but not alien species such as *Sapium*, suffer from periodic outbreaks of specialist herbivores that cause high levels of damage (Louda et al. 1990, Root 1996). During this study, we observed three severe outbreaks of *Malacosoma disstria* Hübner (Lasiocampidae: forest tent caterpillar) and one of *Datana* sp. (Notodontidae: walnut caterpillar) at the floodplain forest site and one of *Fagiphagus imbricator* (Fitch) (Aphididae: beech blight aphid) at the mesic forest site. Some native tree species such as *Liquidambar styraciflua* were completely defoliated at least once every year of our study, while *Sapium* never suffered any damage from any of these insect outbreaks.

2) Browsing mammals attacked almost a third of our *Celtis* seedlings, but rarely attacked *Sapium* seedlings (Fig. 1B). Vertebrate browsing has been shown to be a major limiting factor for tree recruitment in old fields (especially rodents [De Steven 1991, Manson et al. 2001]), and forests (especially ungulates [Crawley 1997]). Although regressions using observational data suggest that browsing does not have a large enough effect on native seedlings to explain the difference between natives and *Sapium*, experimental manipulations of browsing would strengthen this conclusion.

3) Herbivores may serve as vectors for diseases that may impact seedling vigor or survival (Crawley 1987).

4) Finally, we did not test whether a paucity of insect herbivores or fungal pathogens on *Sapium* may be impacting its success in other life stages besides the seedling stage. Seed parasites and underground herbivores may also significantly reduce the success of native species, which could provide an advantage to *Sapium* if it does not suffer comparable levels of seed loss or belowground herbivory. In China, insect herbivores (primarily Lepidoptera and Coleoptera) feed on the roots, parasitize the seeds (Lepidoptera), bore in the wood (Coleoptera), suck fluids (Hemiptera), in addition to a robust folivorous herbivore guild (chiefly Coleoptera, Orthoptera, Lepidoptera) (Zhang and Lin 1994).

### *Summary and conclusions*

Lower levels of insect herbivory or fungal diseases on *Sapium* seedlings relative to native species in its introduced range do not seem to be key factors influencing its invasive ability. *Sapium* seedlings had far greater growth rates and final mass than *Celtis* even when insects and fungi were experimentally excluded from both species. Although native insect herbivores feed on *Sapium* seedlings at a sufficient rate to impact its survival and growth in mesic forests, herbivory levels are too low to have as much impact on *Sapium* seedling success in coastal prairie and floodplain forests where it is most aggressively invading. In those habitats, the intensity of invasion appears to depend on rates of seed input as well as density-dependent factors that affect seedlings.

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