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Recruitment limitation, seedling performance and persistence of exotic tree monocultures

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Abstract

Many native plant communities are replaced by exotic monocultures that may be successional stages or persistent community types. We surveyed a stand of *Sapium sebiferum* (Chinese Tallow Tree) that replaced tallgrass prairie in Texas and performed experiments with seeds and seedlings to determine the contributions of recruitment limitation and natural enemy release to allowing such a forest type to persist or to allowing native species to reduce *Sapium* dominance. The stand was dominated by *Sapium*, especially for mature trees (>99%) and annual seed input (97%) but less so for saplings (80%). Field sown *Sapium* seeds had lower germination and survival rates than *Celtis* seeds. Together with the extreme dominance of *Sapium* in seed rain this suggests that native species are currently recruitment limited in this stand by seed supply but not by germination, early growth or survival. To investigate whether *Sapium* may benefit from low herbivory or diseases, we transplanted *Sapium* and *Celtis* seedlings into the forest and manipulated foliar fungal diseases and insect herbivores with sprays. As predicted, insect herbivores caused greater damage to *Celtis* seedlings than to *Sapium* seedlings. However, suppression of insect herbivores caused significantly greater increases in survivorship of Sapium seedlings compared to *Celtis* seedlings. This suggests that herbivores in the understory of this *Sapium* forest may significantly reduce *Sapium* seedling success. Such a pattern of strong herbivore impact on seedlings growing near adult conspecifics was unexpected for this invasive species. However, even with insects and fungi suppressed, *Sapium* seedling performance was poor in this forest. Our results point towards *Sapium* as a successional species in a forest that will eventually be dominated by native trees that are currently recruitment limited but outperform *Sapium* in the understory.

Introduction

Exotic plants may form monocultures in benign environments that historically supported a diverse assemblage of native species (Mack et al. 2000). In contrast, persistent native communities that are heavily dominated by a single species typically occur in stressful conditions such as extreme temperature, salinity or hydrology (Waide et al. 1999). In such cases, the dominance of a single species is thought to reflect unusual adaptations that allow survival in the harsh abiotic conditions. In benign environments, biotic interactions are more likely to influence the occurrence and abundance of species since many species likely could endure the physical conditions. Because exotic species may have unusual interactions with other organisms, such as herbivores (Maron and Vila 2001) or microbes (Callaway et al. 2004), they may be competitively superior to native plants in their introduced environment and be able to dominate benign environments for long time periods.

Native communities dominated by a single species do occur in benign environments as temporary stage in succession. For instance, *Prunus pensylvanica* L. [Pin Cherry] dominates early secondary succession in deciduous forests in the northeastern US (Marks 1974). In this case, an unusually persistent seed bank allows this species to become extremely abundant following disturbance. More generally, forest succession is often thought to progress from species that are good colonizers to those with low light compensation points (Walters and Reich 1996) or low mortality in low light conditions (Kitajima 1994). Exotic monocultures may be similar to temporarily abundant native species in that the high abundance of the exotic species reflects its superior performance during some potentially narrow window of time in the past and not any superiority in the current conditions (Davis et al. 2000; Davis and Pelsor 2001; Lugo 2004). However, if the exotic species has an advantage in a broad range of conditions, the exotic monoculture may be a new community type that is stable over ecological time periods (Klötzli and Grootjans 2001; Rosenzweig 2001).

Recruitment limitation hypothesis

The abundance of a plant species in a local community reflects both the magnitude of seed input and its success within the local conditions (Nathan and Muller-Landau 2000; Turnbull et al. 2000; Hubbell 2001; Rouget and Richardson 2003). At the simplest level, a plant must contribute seeds to a local site to have a chance of being present. In fact, recent empirical work in forests (Clark et al. 1998; Hubbell et al. 1999; Le Page et al. 2000) and grasslands (Tilman 1997; Foster 2001; Smith and Knapp 2001; Foster and Tilman 2003; Seabloom et al. 2003a, b) 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; Gardescu and Marks 2004). Observations that an exotic species is locally abundant as a sapling may not mean that it is competitively superior to native species in that location. Rather, it may reflect relatively high seed input for the exotic species such as when there is a high local abundance of seed producing trees because of an advantage in some earlier stage of succession (Davis and Pelsor 2001). In this case, dominance may lessen over time as competitively superior native species increase their local seed production.

Natural Enemies Hypothesis

The Natural Enemies Hypothesis assumes exotic 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 (Lankau et al. 2004). This is widely believed to give exotic plants a competitive advantage over native plants because phenotypic plasticity allows them to allocate additional resources to growth and reproduction (e.g. Elton 1958; Levine and D'Antonio 1999; Maron and Vila 2001). Several lines of evidence support the Natural Enemies Hypothesis. First, exotic plants are often taller and more vigorous in their introduced ranges (e.g. Crawley 1987; Bazzaz 1996; but see, Thebaud and Simberloff 2001). Second, herbivore loads are often lower on exotic plants compared to natives (e.g. Schierenbeck et al. 1994; Yela and Lawton 1997). Third, some plants suffer lower losses to herbivores in their introduced ranges than in their native ranges (Memmott et al. 2000; Wolfe 2002). Finally, biological control agents are sometimes dramatically successful in controlling exotic plant species (Williamson 1996; McFayden 1998).

Focal species

The exotic Chinese Tallow Tree (*Sapium sebiferum* (L.) Roxb., Euphorbiaceae, '*Sapium*' hereafter, synonym *Triadica sebifera* (L.) Small) is a major invader in the southeastern US (Bruce et al. 1997). It has been widely planted because it grows rapidly and has seeds rich in oils and colorful fall foliage. *Sapium* has become naturalized throughout the southeastern US where it aggressively displaces native plants. In Coastal Texas, much of the coastal prairie has been converted to *Sapium* dominated forests. We surveyed such a forest and performed experiments with seeds and seedlings to determine the contributions of recruitment limitation and natural enemy release to allowing such a forest type to persist or to allowing native species to reduce *Sapium* dominance.

Methods

Research site

The University of Houston Coastal Center (UHCC) is located ~50 km south east of Houston. Historically, it was primarily tallgrass prairie. Some areas have been allowed to be invaded by *Sapium* while others have been protected by annual mowing. The forest that was the focus of this study appeared as grassland in a 1958 aerial photograph. Personnel at the research site indicated the most likely date of the last mowing was 1968. In a 1983 aerial photograph, the forest canopy was nearly closed. At the time we began this study in 1999, we estimated that the oldest trees in the stand were approximately 30 years old.

Survey of existing stand

We surveyed trees in a 25 m × 48 m area of the *Sapium* dominated forest. We identified and counted all the tree saplings that were between 50 and 140 cm in height (‘saplings’ hereafter). We identified and measured the diameter at breast height (140 cm) for all trees at least 140 cm in height. For the purpose of this study, we considered trees to be woody plants tall enough at maturity to potentially recruit into the canopy. Woody species of shorter stature present in the stand that were excluded by this criteria were *Ilex vomitoria* Soland. in Ait. [Yaupon Holly], *Ligustrum sinense* L. [Chinese Privet], and *Myrica cerifera* L. [Southern Wax-Myrtle]. *Juniperus virginiana* L. [Red Cedar], which we would have considered a tree species, was present in the stand but all were less than 50 cm tall. The herbaceous understory was extremely sparse.

Estimation of annual seed rain

We placed six catch buckets (each 2800 cm^2 catch area, 30 cm deep) within the 25 m × 48 m stand survey area. Each was anchored to the ground. Their tops were covered with 2.5 cm plastic mesh to exclude larger animals. This mesh was large enough to allow the seeds of each of the tree species in the stand to pass through. The bottoms of the catches had a drain hole covered by 1.6 mm mesh. This mesh was small enough to retain the seeds of every tree species in the stand except for *Ulmus americana* L. [American Elm]. Catches were placed in the forest in mid-June 2000 and removed in mid-June 2001. We periodically checked the seed catches during the year. No seeds germinated in the catches. We identified and counted all the tree seeds, regardless of their condition, when the catch buckets were brought in.

Recruitment limitation experiment

We added seeds of *Sapium* and the ecologically similar native tree species *Celtis laevigata* Willd. (Hackberry, Ulmaceae, ‘*Celtis*’ hereafter) with or without soil disturbance in a *Sapium* forest monoculture to test the following predictions of the Recruitment Limitation Hypothesis: (1) If low seed input is limiting the local abundance of native trees, experimentally added *Celtis* seeds will readily germinate, grow and survive, thereby increasing *Celtis* seedling abundance more than adding *Sapium* seeds increases *Sapium* seedling abundance. (2) If a lack of suitable microsites is limiting invasion, then seeds added on artificial soil disturbances should readily grow and survive, increasing seedling abundance.

We used a complete factorial design with 12 seed addition plots for each of two species (*Sapium* or *Celtis*). We used *Celtis* for this study and the Natural Enemies experiment (see below) since it was the most common native tree species in the stand and it exhibits ecological similarities to *Sapium* (Siemann and Rogers 2003a). Plots were randomly assigned three experimental treatments: species, time of seed addition (February or December) and artificial soil disturbance (yes or no). There were three replicates for each treatment and a total of 24 plots. The seed addition plots were in two rows immediately adjacent to the survey area. We did not put them in the survey area to help minimize interference from the seed catches.

In November and December 1998, we collected seed from *Sapium* and *Celtis* trees at UHCC. In February 1999, we constructed twelve 0.5 m diameter (0.2 m^2 area), 60 cm high 2 hardware cloth exclosures (1 cm mesh). They had tops that were kept in place until seeds were no longer visible on the soil surface in order to limit seed predation. Disturbance plots received a 20 cm diameter, 10 cm high pile of dirt excavated near the experiment. These disturbances are similar to those created by crayfish which are common in this stand. 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 cues to germinate in the 1999 growing season, we established an identical set of 12 plots at each site in December 1999. No plots had any *Celtis* or *Sapium* seedlings when they were initially established. We measured germination and mortality bimonthly until October 2002. *Celtis* and *Sapium* seeds from the same batches planted into germination flats in an unheated greenhouse had 2 year germination rates of 51.5% and 21.1%, respectively, with no differences among seeds planted at different times of the year (Siemann and Rogers 2003a).

We used ANOVA to test the dependence of the number of *Celtis* seedlings alive at the end of the experiment on species of seed added, time 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 another ANOVA using the number of *Sapium* seedlings alive at the end of the experiment as the dependent variable.

We used ANOVA to test whether the emergence rate of *Celtis* seeds in plots where they were added depended on time of addition or soil disturbance. In this analysis, we subtracted the average number of *Celtis* seedlings in plots that did not receive *Celtis* seeds from the number of *Celtis* seedlings in plots that did receive *Celtis* seeds. We performed an analogous analysis to examine *Sapium* emergence rates in *Sapium* seed addition plots.

We used ANOVA to test whether the survival of *Celtis* seedlings until the end of the growing season in which they germinated depended on time of addition or soil disturbance in plots that received *Celtis* seeds. Some *Celtis* seedlings in these plots were likely from naturally occurring seeds since there were a small number of *Celtis* seedlings that grew in plots where no *Celtis* seeds were added. We performed another ANOVA for *Sapium* survival until the end of the growing season in which they germinated.

Natural enemies experiment

We planted seedlings of *Sapium* and *Celtis* and reduced aboveground insect herbivores and foliar fungi with chemical sprays to test the following predictions of the Natural 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 exotic *Sapium*. (2) Excluding insect herbivores and fungal pathogens will cause larger increases in survival and growth for *Celtis* seedlings than for *Sapium* seedlings.

We used a complete factorial design with 60 seedlings of each species (*Sapium* or *Celtis*) randomly assigned to two experimental treatments: insecticide (yes or no) and fungicide (yes or no) with 15 replicates for each treatment combination. We have used these methods before in natural areas where *Sapium* is in the early stages of invasion to elucidate the mechanisms of invasion (Siemann and Rogers 2003a).

In January 1999, *Sapium* and *Celtis* seeds were planted into flats in an unheated greenhouse with open vent flaps (Nijjer et al. 2002). 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 Container (Stuewe and Sons, Oregon, USA) 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 field.

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 on April 20, 1999. Seedlings were planted along five parallel transects (24 seedlings per transect) with 2 m between seedlings along a transect and 6.25 m between transects. The transects delineated the 25 × 48 m surveyed stand. The experiment ran for 903 days.

Insect herbivores were excluded by spraying seedlings with esfenvalerate (trade name: Asana XL, Du Pont Agricultural Products, Wilmington, DE), a broad spectrum synthetic pyrethroid insecticide, at approximately 3 week intervals during the growing season. Plants not receiving insecticide were sprayed with an equivalent amount of water. Although it 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, Du Pont Agricultural Products, Wilm ington, DE) at approximately three week intervals during the growing season. Non-fungicide 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. Neither esfenvalerate nor mancozeb is toxic to *Sapium* or *Celtis* seedlings even at twice the rate we applied it in the field either alone or in combination (Siemann and Rogers 2003a; Siemann et al. 2004).

We measured the height and number of leaves on each seedling before transplanting. No seedlings had any significant pest 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) and average insect or fungal damage per leaf. Leaf damage (herbivore or fungal) was assessed as the average percent of area damaged per leaf. We surveyed leaves for chewing, gall, miner and borer damage. We visually surveyed seedlings for the presence of insect herbivores. All seedlings were visited the same number of times and were handled similar amounts. After 903 days, we measured seedling heights, clipped seedlings at ground level, dried them and weighed them.

We used repeated-measures ANOVAs with a three level time variable to test whether insect chewing damage depended on our treatments (Statview 5.0, SAS Institute Inc. for all ANOVAs). 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. 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. In these and all other ANOVAs we checked whether the data met the assumptions of ANOVA, such as normality and constant variance. All types of damage data other than chewing were absent (galling and mining) or too sparse (foliar fungi – five seedlings) for statistical analysis. We used ANOVA to test whether the number of times we observed insect herbivores on a plant depended on our treatments.

We used survival analysis to examine the dependence of survival time on our treatments. We fit survival time data with an exponential model in a parametric survival analysis (Statview 5.0, SAS Inc.). We handled our experimental treatments as categorical covariates and used likelihood-ratio tests to determine whether survival time depended on our experimental treatments alone and in combination. We performed a second set of survival analyses using the Kaplan–Meier model in a non-parametric survival analysis and used Mantel–Cox tests to examine whether survival time depended on our experimental treatments (main effects only). We obtained the same results using the parametric and non-parametric methods of survival analysis.

We used ANOVA to test whether the final aboveground mass of seedlings depended on our treatments. Since no *Sapium* seedlings survived to the end of the experiment, this analysis was for *Celtis* seedlings only with insecticide and fungicide as predictors. Masses were log transformed to meet the assumption of normality. Seedlings that did not survive to the end of the experiment were treated as missing values in order to get an estimate of insecticide and fungicide effects on growth separately from those on survival.

For *Sapium* seedlings, we used an alternative analysis to examine the effects of insecticide and fungicide on seedling growth. We used ANOVA to test whether the first year instantaneous growth rate ($g = \ln$[starting height/end of first growing season height]/182 days) depended on our spray treatments. Seedlings that did not survive to the end of the first growing season were treated as missing values in order to examine effects on growth separately of those on survival.

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 dusk using a Nikon Coolpix 900 digital camera with an FC-E8 fisheye lens (Nikon, Tokyo, Japan). We used Gap Light Analyzer 2.0 (http://www.ecostudies.org/gla/) to calculate Global Site Factor (overall percent of total light that reached the seedling over the growing season). We used single species regressions to examine whether survival time, height growth rate (first growing season) or final mass (*Celtis* only) depended on global site factor.

Results

Survey of existing stand

In total there were 70 tree saplings of five species (*Sapium sebiferum*, *Celtis laevigata*, *Cornus foemina* Mill.[English Dogwood], *Ulmus americana*, and *Quercus nigra* L. [Water 10 Oak]) in the survey area (Figure 1, left of dotted line). There were 756 trees of five species (same species as saplings) that were at least 140 cm tall (Figure 1, right of dotted line). Total stand basal area was 29.41 m^2/ha. *Sapium* represented 83% of the saplings, 95% of the trees, and 98% of the stand basal area. There were 473 seeds of two tree species in the six seed traps (*Sapium* = 457, *Celtis* = 16).

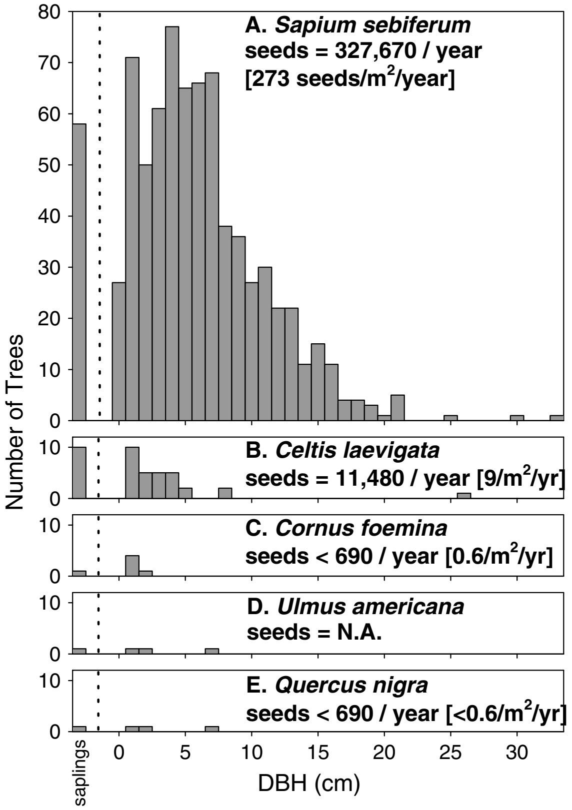

Figure 1. The number of trees by size category within a 25 × 48 m area of a *Sapium* dominated forest. Saplings (left of dotted line) are trees between 50 and 140 cm high. Seed input is shown as the number in the survey area as well as the average number per square meter. The values for *C. foemina* and *Q. nigra* represent the limit of detection.

Recruitment limitation experiment

Adding *Celtis* seeds increased the number of *Celtis* seedlings in a plot after four growing seasons ($F_{1,16} = 204.2$, $P < 0.0001$; Figure 2). The number of *Celtis* seedlings was higher for plots with seeds added in February ($F_{1,16} = 14.0$, $P < 0.0001$) but was independent of soil disturbance ($P = 0.87$) and interaction terms. *Celtis* emergence rates were higher for plots with seeds added in February (47%) than for those with seeds added in December (21%; $F_{1,8} = 27.3$,

$P < 0.001$). Soil disturbance did not affect emergence alone ($P = 0.20$) or in interaction with time of addition ($P = 0.29$). *Celtis* single growing season survival rates were independent of all treatments (mean 53%; timing $P = 0.76$; disturbance $P = 0.97$; interaction $P = 0.54$).

Adding *Sapium* seeds did not increase the number of *Sapium* seedlings present after four growing seasons ($F_{1,16} = 1.1$, $P = 0.31$; Figure 2). The number of *Sapium* seedlings was independent of time of seed addition ($P = 0.61$), soil disturbance ($P = 0.61$) and interaction terms. *Sapium* emergence and single growing season survival rates were independent of all treatments (emergence: average 4.3%, timing $P = 0.61$, disturbance $P = 0.61$, interaction $P = 0.28$; survival: average 19%, timing $P = 0.68$, disturbance $P = 0.43$, interaction $P = 0.83$).

Natural enemies experiment

Chewing damage was higher on *Celtis* seedlings than on *Sapium* seedlings ($F_{1,55} = 4.1$, $P < 0.05$; Figure 3). The amount of damage on seedlings decreased each year ($F_{2,110} = 18.0$, $P < 0.0001$). Damage was lower on insecticide treated seedlings ($F_{1,55} = 17.6$, $P < 0.0001$) with the reduction being larger in earlier years of the experiment when damage was higher on control seedlings ($F_{2,110} = 6.1$, $P < 0.01$). Chewing damage was independent of fungicide sprays ($P = 0.57$) and there were no significant interactions among any treatment terms. Other than insecticide, no factor's effect depended on growing season. The number of times we observed insect herbivores on a seedling was higher for *Celtis* than for *Sapium* (*Celtis* 0.28 times per seedling, *Sapium* 0.017 times per seedling, $F_{1,112} = 19.1$, $P < 0.0001$) but independent of insecticide ($P = 0.31$) and fungicide ($P = 0.31$) treatments. The majority of herbivore observations (90% of occurrences) were wooly aphids on *Celtis* seedlings in the final month of the experiment.

Survival was higher for *Celtis* than for *Sapium* (χ^2(1df) = 32.5, $P < 0.0001$; Figure 4) but did not depend on insecticide (χ^2(1df) = 1.0, $P = 0.32$) or fungicide sprays (χ^2(1df) = 1.3, $P = 0.34$). Survival depended on species*insecticide (χ^2(1df) = 31.7, $P < 0.0001$), species*fungicide (χ^2(2df) = 31.8, $P < 0.0001$), and species* insecticide*fungicide (χ^2(3df) = 32.3, $P < 0.0001$), but not insecticide*fungicide ($P = 0.31$). These significant higher-order terms, together with no significant main effects of sprays, indicate sprays only influenced the survival of a single species. Visual inspection of survival curves and examination of estimated half-lives suggest that *Sapium* was the

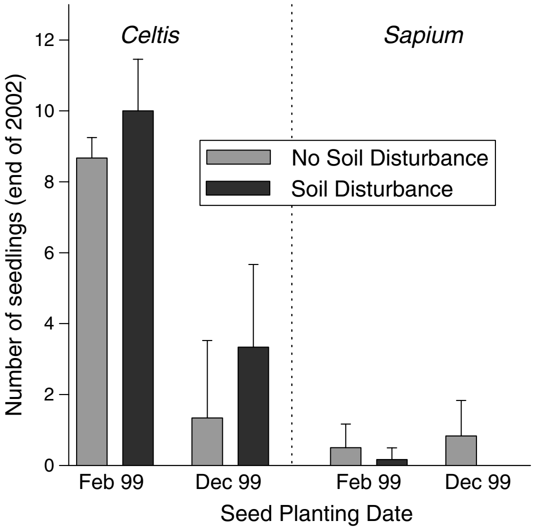

Figure 2. The number of seedlings alive at the end of the 2002 growing season for plots that received either 50 *Celtis* or *Sapium* seeds. The numbers of seedlings have had background rates of seedling emergence subtracted from them (*Celtis* 1.3 per plot, *Sapium* 0.17 per plot).

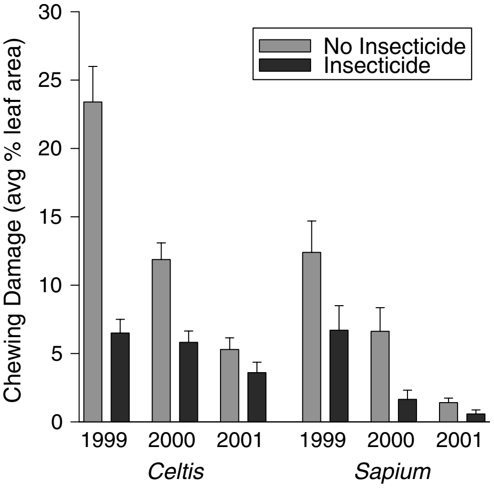

Figure 3. Herbivore damage. Effect of seedling species and insecticide sprays on the average amount of insect chewing damage during three growing seasons. Means + 1s.e.

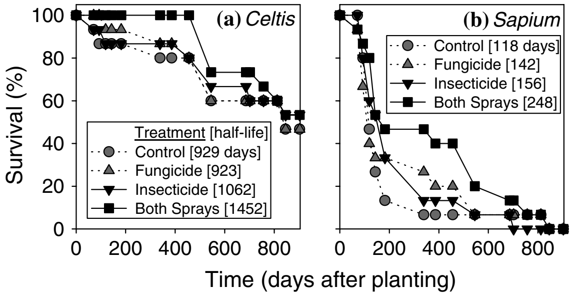

Figure 4. Seedling survival. Percent of seedlings surviving during the course of the experiment within each treatment for each species. Symbols represent a date on which survival was checked. Time is the number of days after planting (April 20, 1999).

species more responsive to each spray alone and in combination (Figure 3). Excluding values for *Celtis* seedlings still alive at the end of the experiment (i.e. right censored datapoints) did not change the significance of any terms.

Insecticide treated *Celtis* seedlings were larger (147.9 ± 1.62 g) than those that were not treated with insecticide (85.1 ± 1.9 g; $F_{1,26} = 6.4$, $P < 0.05$). *Celtis* seedling mass was independent of fungicide treatment ($P = 0.51$) and the interaction of sprays ($P = 0.48$).

Insecticide treated *Sapium* seedlings grew faster in the first growing season (15.38×10^{-4}/day) than those that were not treated with insecticide (5.77×10^{-4}/day; $F_{1,50} = 6.9$, $P = 0.01$). First year growth rate was independent of fungicide treatment ($P = 0.63$) and the interaction of sprays ($P = 0.53$).

Global site factor (GSF) was independent of all treatments (average 19.2 ± 2.5). GSF did not affect survival time of either species (*Celtis* $P = 0.40$; *Sapium* $P = 0.36$), first year height growth rate for *Celtis* ($P = 0.35$) or final mass for *Celtis* ($P = 0.43$). GSF did not predict any of these variables when spray treatments were included as covariates in multiple regressions (as dummy variables with values of 0 and 1) or when *Celtis* survival time data were censored to exclude seedlings alive at the end of the experiment. First year height growth rate for *Sapium* increased with GSF ($g = -8.42 \times 10^{-4} + 1.04 \times 10^{-4} * \mathrm{GSF}$, $P \leq 0.05$, $r = 0.28$). Overall *Sapium*'s first growing season growth (average 12.1×10^{-4}/day) was twenty times as high as *Celtis*' growth (average 0.6×10^{-4}/day). Growth rates through the end of the second growing season were similar to those in the first year (*Sapium* 11.0×10^{-4}/day; *Celtis* 0.5×10^{-4}/day).

Discussion

The current numerical dominance of *Sapium* in every life stage of the forest (Figure 1) implies that *Sapium* is likely to be a major component of the next canopy of this forest but not because of superior performance as a seed (Figure 2) or seedling (Figure 4) but because of massive seed input (Figure 1). Indeed, the abundance of *Sapium* in the understory appears to reflect its extreme dominance in the canopy (Figure 1). However, this dominance is apparently a consequence of *Sapium*'s superiority in invading tallgrass prairie (Rogers and Siemann 2003; Siemann and Rogers 2003a, b) that was the original habitat at this location and is not indicative of its current regenerative ability in this forest (Davis and Pelsor 2001). Such a pattern of early woody invaders of grasslands being replaced by other trees in succession is typical of native trees though it has also been shown for some exotic trees (Lugo 2004). Others, notably *Melaleuca quinquenervia* (Cav.) Blake [Bottle brush tree] have been described as persistent monocultures (Lugo 2004) but a number of native woody species do occur in the understory of older *Melaleuca* stands (Van et al. 2000). On the whole, it seems possible that the cases of apparently persistent exotic monocultures may be similar to *Sapium* in that native species are able to invade but some factors cause this invasion to be slower than for stands of pioneer native woody plants.

Insights from the stand survey

Sapium's numerical advantage over native tree species was more pronounced in larger size classes than in smaller ones (Figure 1). This suggests that a near-monoculture *Sapium* forest, such as this first growth forest that replaced a coastal tallgrass prairie, is not a stable community type that will persist over multiple generations. The shapes of the size-frequency distributions for *Sapium* (unimodal) versus native trees (high frequencies in smaller size classes) also suggest that *Sapium* dominance may be declining (Figure 1). However, *Sapium* is currently so abundant in the understory, it may be an abundant, if not the most abundant, species in the next canopy. In order for any of the relatively rare native tree species in the understory to dominate the next canopy of the forest individually or collectively, they would need to have a disproportionately large chance of capturing gaps compared to their current density (Denslow 1987).

This could happen if the current dominance of *Sapium* in the understory (Figure 1) is transient and natives become more common before gaps occur. Relatively high mortality for *Sapium* currently present in the understory prior to gap creation could shift the understory composition towards native species in a process analogous to shifts among different native tree species in other forests (Montgomery and Chazdon 2002). Alternatively, native tree saplings may remain rare in the understory until a gap occurs but have a higher probability of capturing a gap than *Sapium* saplings once one occurs (Denslow 1987). However, long-term observational data (Lin et al. 2004) and experimental data (Jones and McCleod 1990; Rogers and Siemann 2002; Siemann and Rogers 2003a, b) show that *Sapium* has a higher growth rate than native species, especially at high light levels. Together these studies suggest that *Sapium* present at the time of gap formation will have a greater chance of capturing gaps in which they occur than native saplings will.

Recruitment limitation

The large changes in seedling species composition in response to native tree seed addition (Figure 2) support the hypothesis that *Sapium* is abundant as a sapling not because it has a high per seed or per seedling success rate but rather because native tree species are recruitment limited under the current *Sapium* dominated overstory. Such a finding of strong recruitment limitation in this forest is perhaps not surprising since the majority of seeds in the soil would likely be those of grassland species and native forests were historically restricted to riparian areas in this area. It agrees with the growing evidence in the literature that recruitment limitation plays an important role in determining community diversity and community structure (e.g. Clark et al. 1998; Foster 2001; Smith and Knapp 2001). The large spatial extent of *Sapium* invasion and the apparent paucity of native tree seeds in the soil of this site may increase the importance of recruitment limitation as it does for California grasslands invaded by exotic grasses (Seabloom et al. 2003a, b). Lugo (2004) also found that recruitment limitation appears to slow the replacement of exotic dominated primary forests by native trees. Since exotic plants that are successful invaders are often from previously absent functional groups, such as trees invading grasslands (Mack 2003), this example of *Sapium* may provide insights into the mechanisms that contribute to the persistence of a number of novel exotic dominated assemblages.

Negative feedback in Sapium forest

In this *Sapium* dominated forest, *Sapium* seedling survival was very low. This was certainly true in an absolute sense since none of our planted *Sapium* seedlings survived for three growing seasons and their 1 year survival was only 7% in control treatments that did not receive insecticide or fungicide sprays (Figure 4b). Survival of *Sapium* seedlings was also low compared to that of seedlings of the native *Celtis* we planted in this forest (47% for three growing seasons, 80% for 1 year, Figure 4a). Furthermore, *Sapium* survival was low compared to the survival of *Sapium* seedlings planted at the same time with the same protocol in other habitats (> 50%, Siemann and Rogers 2003a). Finally, the difference between *Sapium* and *Celtis* seedling survival in these habitats was smaller than the dozen-fold difference in their 1 year survival in the *Sapium* dominated forest investigated here. What mechanisms cause the poor survival of *Sapium* seedlings in *Sapium* dominated forest?

The large positive effect of insecticide and fungicide sprays on *Sapium* seedling survival suggests an unexpectedly strong role for insect herbivores and pathogenic foliar fungi in determining the surprisingly poor performance of *Sapium* seedlings in this *Sapium* dominated forest (Figure 4b). Insecticide increased the growth rate of *Sapium* seedlings more than two-fold in their first year. This increase in growth rate was larger for *Sapium* seedlings in this forest (+166%) than for *Celtis* seedlings (+114%) and was far larger than that observed with insect suppression for *Sapium* in other east Texas ecosystems in which increases in growth were less than 25% (Siemann and Rogers 2003a). Furthermore, both sprays increased survival of *Sapium* seedlings with their additive effects (Figure 4b). This indicates that foliar fungi also significantly affect *Sapium* seedling survival in this habitat. This is the only east Texas ecosystem in which suppression of foliar fungi on *Sapium* seedlings has had any effect on *Sapium* seedling survival (Siemann and Rogers 2003a). Taken together, these results suggest that pests (i.e. herbivores and pathogens) in the understory of this *Sapium* forest significantly reduce seedling success. Such a pattern of strong top-down impact on seedlings growing near adult conspecifics is typical of native trees but was unexpected for this invasive species.

Comparisons to Sapium in other ecosystems

It is unlikely that low light levels were the cause of the *Sapium* seedlings' slow growth or low survival in this forest compared to native dominated forest types that are invaded by *Sapium* (Siemann and Rogers 2003a). Light levels were higher, on average, in this *Sapium* dominated forest than in floodplain or mesic forest where *Sapium* readily invades (Siemann and Rogers 2003a). Light levels in coastal prairie, however, were much higher than in any of the forest sites (Siemann and Rogers 2003a, b) even in the first growing season before *Sapium* seedlings began to overtop the herbaceous vegetation. Therefore, differences in growth and survival between prairie and *Sapium* forest, especially in later years, may be due to differences in light availability.

Low soil nutrient levels in the *Sapium* forest do not seem to explain the low survival and growth of *Sapium* seedlings either. The coastal prairie and *Sapium* forest sites are immediately adjacent to each other and compared to coastal prairie at this site, *Sapium* forest has higher soil concentrations of phosphorus, pottasium, nitrogen, zinc, manganese and iron (Cameron and Spencer 1989). The floodplain forest site has soil nitrate levels (Hall 1993) that are comparable to those in the *Sapium* dominated forest (Cameron and Spencer 1989) and lower soil phosphorus (Hall 1993) than the *Sapium* forest (Cameron and Spencer 1989). Bioassays using *Liquidambar styraciflua* L. [sweetgum] and *Acer rubrum* L. [red maple] seedling growth in soil collected from the floodplain forest site and the mesic forest site showed both species grew slower in the mesic forest soil (Knox et al. 1995). Serial nutrient additions indicated that the mesic forest soil had lower nitrogen and phosphorus availability compared to the floodplain forest soil (Knox et al. 1995). In short, the *Sapium* forest seems to have soil fertility comparable to or higher than each of the native ecosystems. Low levels of soil resources are not a likely explanation for the poor performance of *Sapium* seedlings in the *Sapium* dominated forest.

There are other explanations for the poor performance of *Sapium* seedlings in the *Sapium* dominated forest even with insect herbivores and foliar pathogens suppressed but there is little evidence to evaluate most of these. For instance, allelochemicals could be responsible for the poor performance of *Sapium* seedlings but there is no evidence in the literature of an allelopathic effect of *Sapium* on its own seedlings (Conway et al. 2002). Alternatively, it is possible that the poor performance of *Sapium* seedlings in the understory of the *Sapium* dominated forest represents a negative feedback via the soil biota (Reynolds et al. 2003). This would be unprecedented for an introduced plant since feedbacks via soil biota tend to be negative for native plants and have only been shown to be positive for introduced plants (Klironomos 2002; Reinhart et al. 2003; Callaway et al. 2004; Packer and Clay 2004). Further investigations that show the cause of negative relationship between adult *Sapium* density and *Sapium* recruitment success have the potential to give insights into the factors that accelerate or constrain invasions. Indeed, there is a positive relationship between the presence of pioneer *Sapium* trees and *Sapium* seedling recruitment success in the early stages of invasion in prairie which is mediated through changes in resource availability (Siemann and Rogers 2003b).

Conclusions

Our experiments suggest that recruitment limitation and natural enemies interact to determine the persistence of a *Sapium* dominated forest. The apparent strong impact of natural enemies on *Sapium* seedlings creates an opportunity for native tree seedlings in the understory of this forest. However, the current low seed input by native tree species limits their ability to increase their abundances despite this advantage in seedling performance. If native trees increase their seed input in this stand, however, the strong effect of natural enemies on *Sapium* seedlings may become more important in determining the abundance of *Sapium*. Understanding the conditions under which there is a positive or negative feedback between current invasion extent and future invasion intensity is critical for management of invasive plant species now and in the future.

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References

Bazzaz FA (1996) Plants in a Changing Environment, Cambridge University Press, NY

Bruce KA, Cameron GN, Harcombe PA and Jubinsky G (1997) Introduction, impact on native habitats, and management of a woody invader, the Chinese Tallow Tree, *Sapium sebiferum* (L.) Roxb. Natural Areas Journal 17: 255–260

Callaway RM, Thelen GC, Rodriguez A and Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731–733

Cameron GN and Spencer SR (1989) Rapid leaf decay and nutrient release in a Chinese tallow forest. Oecologia 80: 222–228

Clark JS, Macklin E and Wood L (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecological Monographs 68: 213–235

Conway WC, Smith LM and Bergan JF (2002) Potential allelopathic interference by the exotic Chinese tallow tree (*Sapium sebiferum*). American Midland Naturalist 148: 43–53

Crawley MJ (1987) What makes a community invasible? In: Gray AJ, Crawley MJ and Edwards PJ (eds) Colonization, Succession and Stability, pp 429–453. Blackwell Scientific Publications, Oxford

Davis MA, Grime JP and Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528–534

Davis MA and Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4: 421–428

Denslow JS (1987) Tropical rain-forest gaps and tree species-diversity. Annual Review of Ecology and Systematics 18: 431–451

Edwards IR, Ferry DG and Temple WA (1991) Fungicides and related compounds. In: Hayes WJ and Laws ER (eds) Handbook of Pesticide Toxicology, pp 1409–1470 Academic Press, NY

Elton CS (1958) The Ecology of Invasion by Plants and Animals, Chapman and Hall, London

Foster BL (2001) Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4: 530–535

Foster BL and Tilman D (2003) Seed limitation and the regulation of community structure in oak savanna grassland. Journal of Ecology 91: 999–1007

Gardescu S and Marks PL (2004) Colonization of old fields by trees vs. shrubs: seed dispersal and seedling establishment. Journal of the Torrey Botanical Society 131: 53–68

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52: 107–145

Hall RBW (1993) Sapling growth and recruitment as affected by flooding and canopy gap formation in a river floodplain forest in southeast Texas. PhD thesis. Rice University, Houston, TX

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ and de Lau SL (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283: 554–557

Hubbell SP (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ

Jones RH and McCleod KW (1990) Growth and photosynthetic responses to a range of light environments in Chinese Tallowtree and Carolina Ash seedlings. Forest Science 36: 851–862

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98: 419–428

Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417: 67–70

Knox RG, Harcombe PA and Elsik IS (1995) Contrasting patterns of resource limitation in tree seedlings across a gradient in soil texture. Canadian Journal of Forest Research 25: 1583–1594

Lankau RA, Rogers WE and Siemann E (2004) Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. Ecological Entomology 29: 66–75

LePage PT, Canham CD, Coates KD and Bartemucci P (2000) Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. Canadian Journal of Forest Research 30: 415–427

Levine J and D'Antonio CD (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15–26

Lin J, Harcombe PA, Fulton MR and Hall RW (2004) Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas. Oecologia 139: 399–407

Lugo AE (2004) The outcome of alien tree invasions in Puerto Rico. Frontiers in Ecology and the Environment 2: 265–273

Mack RN (2003) Phylogenetic constraint, absent life forms, and preadapted alien plants: a prescription for biological invasions. International Journal of Plant Sciences 164: S185–S196

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M and Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710

Marks PL (1974) The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs 44: 73–88

Maron JL and Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95: 361–373

McFayden REC (1998) Biological control of weeds. Annual Review of Entomology 43: 369–393

Memmott J, Fowler AC, Paynter Q, Sheppard AW and Syrett P (2000) The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. Acta Oecologia 21: 11 213–222

Montgomery RA and Chazdon RL (2002) Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. Oecologia 131: 165–174

Nathan R and Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. TREE 15: 278–285

Nijjer S, Lankau RA, Rogers WE and Siemann E (2002) Effects of temperature and light on Chinese tallow (*Sapium sebiferum*) and Texas sugarberry (*Celtis laevigata*) seed germination. Texas Journal of Science 54: 63–68

Packer A and Clay K (2004) Development of negative feedback during successive growth cycles of black cherry. Proceedings of the Royal Society of London Series B 271: 317–324

Reinhart KO, Packer A, Van der Putten WH and Clay K (2003) Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. Ecology Letters 6: 1046–1050

Reynolds HL, Packer A, Bever JD and Clay K (2003) Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology 84: 2281–2291

Rogers WE and Hartnett DC (2001) Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. American Journal of Botany 88: 1634–1642

Rogers WE and Siemann E (2002) Effects of simulated herbivory and resource availability on native and invasive exotic tree seedlings. Basic and Applied Ecology 3: 297–307

Rogers WE and Siemann E (2003) Effects of simulated herbivory and resources on Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasion of native coastal prairie. American Journal of Botany 90: 243–249

Rosenzweig ML (2001) The four questions: what does the introduction of exotic species do to diversity? Evolutionary Ecology Research 3: 361–367

Rouget M and Richardson DM (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. American Naturalist 162: 713–724

Schierenbeck KA, Mack RN and Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. Ecology 75: 1661–1672

Seabloom EW, Borer ET, Boucher VL, Burton RS, Cottingham KL, Goldwasser L, Gram WK, Kendall BE and Micheli F (2003a) Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications 13: 575–592

Seabloom EW, Harpole WS, Reichman OJ and Tilman D (2003b) Invasion, competitive dominance, and resource use by exotic and native California grassland species. PNAS 100: 13384–13389

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

Siemann E and Rogers WE (2003b) Changes in resources under pioneer trees may facilitate tree invasions of grasslands. Journal of Ecology 91: 923–931

Siemann E, Carson WP, Rogers WE and Weisser WW (2004) Reducing herbivory using insecticides. In: Weisser WW and Siemann E (eds) Insects and Ecosystem Function, pp 329–355. Springer-Verlag, Berlin

Smith MD and Knapp AK (2001) Size of the local species pool determines invasibility of a C-4-dominated grassland. Oikos 92: 55–61

Thebaud C and Simberloff D (2001) Are plants really larger in their introduced ranges? American Naturalist 157: 231–236

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78: 81–92

Turnbull LA, Crawley MJ and Rees M (2000) Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88: 225–238

Van TK, Rayachhetry MB and Center TD (2000) Estimating above-ground biomass of *Melaleuca quinquenervia* in Florida, USA. Journal of Aquatic Plant Management 38: 62–67

Vitousek PM and Walker LR (1989). Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59: 247–265

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP and Parmenter R (1999) The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257–300

Walters MB and Reich PB (1996) Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. Ecology 77: 841–853

Williamson M (1996) Biological Invasions. Chapman & Hall, London

Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. American Naturalist 160: 705–711

Yela JL and Lawton JH (1997) Insect herbivore loads on native and introduced plants; a preliminary study. Entomologia Experimentalis et Applicata 85: 275–79