

GROWTH OF CHINESE TALLOW TREE (*SAPIUM SEBIFERUM*) AND FOUR NATIVE TREES UNDER VARYING WATER REGIMES

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Abstract.—Abiotic stress tolerance may play a role in the invasion and spread of Chinese tallow tree (*Sapium sebiferum*). A greenhouse experiment was conducted to determine the effects of water stress on the growth of *Sapium* and four tree species native to the southeastern United States. Species identity, water treatment, and their interaction significantly influenced growth rate and mass of seedlings. No native species had as high an average growth rate as *Sapium*. Indeed, *Sapium* had a higher growth rate than every native species in every water treatment with the exception of a single native species (*Liquidambar styraciflua* L.) in the drier treatments (pulse drought, well watered). *Sapium* exhibits the potential to thrive at any point along the water gradient present in southeastern floodplain forests.

Plant species distributions often reflect abiotic conditions. Species composition may shift along a resource gradient based on efficiency of resource use at different concentrations (Tilman 1982; 1985; Huston & Smith 1987). Species distributions in some landscapes are based primarily on one resource, and in such cases analysis of the performance of species along a gradient of that resource can be useful in predicting community composition (Tilman 1987). Similarly, comparisons of the performance of an invasive species and native species along a gradient of the most limiting abiotic factor in an ecosystem may be a good predictor of the conditions in which the invasive will displace natives (Alpert et al. 2000; Sakai et al. 2001; Daehler 2003).

Invasive species often have very different ecological attributes from species in their introduced range (Bruce et al. 1997; Busch & Smith 1995). Comparisons between native and exotic congeners (Schierenbeck et al. 1994; Mack 1996; Gerlach & Rice 2003) and between ecologically similar native and exotic species (Nijjer et al. 2002; Rogers & Siemann 2002; Daehler 2003; Siemann & Rogers 2003a) have produced informative results. Studies analyzing plant growth along a resource gradient can be useful for identifying traits that may lead to the competitive dominance of invasive species, as well as for predicting potential range expansions.

In southeastern floodplain forests, water is a major determinant of the distribution of tree species (e.g. Hall & Harcombe 1998; Wall & Darwin 1999; Denslow & Battaglia 2002; Ernst & Brooks 2003). The elevational heterogeneity of these systems positions different plant communities within close proximity to each other (Christensen 2000), which likely results in distribution of propagules into a wide range of moisture conditions, making seedling establishment and growth important aspects of population dynamics. Sloughs and depressions are often flooded year round, while other areas of bottomland forests experience seasonal flooding. Upland areas may never flood, and often experience seasonal droughts (Christensen 2000).

Tree species in these forests can be expected to follow different growth strategies depending on their distribution along a water gradient. Stress tolerance is important at extreme elevations where abiotic factors limit seedling growth and survival, while competitive ability is more important in less stressful environments. Stress tolerant species are expected to have relatively restricted phenotypic responses to external stimuli since survival depends on highly conservative growth strategies (Grime 1974; 1977; Campbell & Grime 1992). This is often reflected in slow growth rates and negligible increases in mass and growth rate in less stressful conditions (Grime 1974; 1977; Pigliucci 2001). Tree species adapted to more favorable conditions can be expected to maximize resource assimilation and grow rapidly, since biotic competition is often more important than in stressful environments (Grime et al. 1986).

A greenhouse experiment was conducted to determine the growth and performance of *Sapium sebiferum* (L.) Roxb. (Chinese tallow tree) and four native tree species under a range of water conditions representative of natural conditions. *Sapium* has invaded a variety of ecosystems in the southeastern United States. Even though it thrives in early successional conditions and has extremely high growth rates (Siemann & Rogers 2003a), seedlings are also shade tolerant (Jones & McLeod 1989; Rogers & Siemann 2002; 2003; but see Lin et al. 2004) and flood tolerant (Jones & Sharitz 1990; Conner et al. 1997, 2001).

It was predicted that the range of soil moisture conditions in which native tree species sustain high growth rates and mass production would be restricted. Adaptations to particular habitats were expected to cause tradeoffs between stress tolerance and other traits such that native species with the greatest growth rates in optimal conditions should be

more sensitive to extreme conditions. Because of its widespread distribution in floodplain forests and invasive nature, *Sapium* was expected to have a higher growth rate and produce more mass than all native species under all water conditions.

METHODS

The experiment was conducted in a climate controlled greenhouse in Houston, Texas between March and August 2003. The roof and walls of the greenhouse were clear glass, and humidity was approximately 100%. *Pinus taeda* L. (loblolly pine), *Liquidambar styraciflua* L. (sweetgum), *Nyssa aquatica* L. (water tupelo), and *N. sylvatica* Marsh. var. *sylvatica* (blackgum) seeds were acquired commercially (Louisiana Forest Seed Co. Lecompte, LA). *Sapium sebiferum* seeds were collected in Texas and Georgia. In Texas, seeds were collected from many different trees at the Armand Bayou Nature Center, approximately 35 km southeast of Houston. In Georgia, seeds were collected from numerous trees on Sapelo Island, a barrier island approximately 55 km south of Savannah. Seeds of all species were germinated in topsoil in early March and transplanted into individual 11 liter plastic pots in April. Potted seedlings of each native species plus one of Texas and Georgia *Sapium* were assigned to a random position in each of twenty-four 160 liter plastic tubs (a split-plot design). Seedlings were watered daily for two weeks before initiation of the treatments.

Each tub was randomly assigned one of four watering treatments, with 6 tubs per water treatment. The treatments were: (1) Control - Pots were watered daily until water flowed out of the bottom of the pot; (2) Flooded - Pots were permanently submerged in water (1-3 cm above soil surface) for the duration of the 16-week experiment. Evaporative losses were replaced with de-ionized water to avoid salt accumulations; (3) Pulsed flood - Pots received the control water treatment for two weeks followed by flood treatment for the following two weeks. This four-week cycle was completed four times during the course of the experiment; (4) Pulsed drought - Pots received the control water treatment for the first two weeks of each four-week cycle, but received no water for the latter two weeks.

Initial stem heights, basal diameters, and leaf counts were recorded for each plant on 9 April. Stem height and number of leaves per seedling were measured weekly during the experiment. After 16 weeks, all of the plants were harvested. Roots, stems, and leaves were separated and dried at 60°C for 96 hours before dry mass was measured.

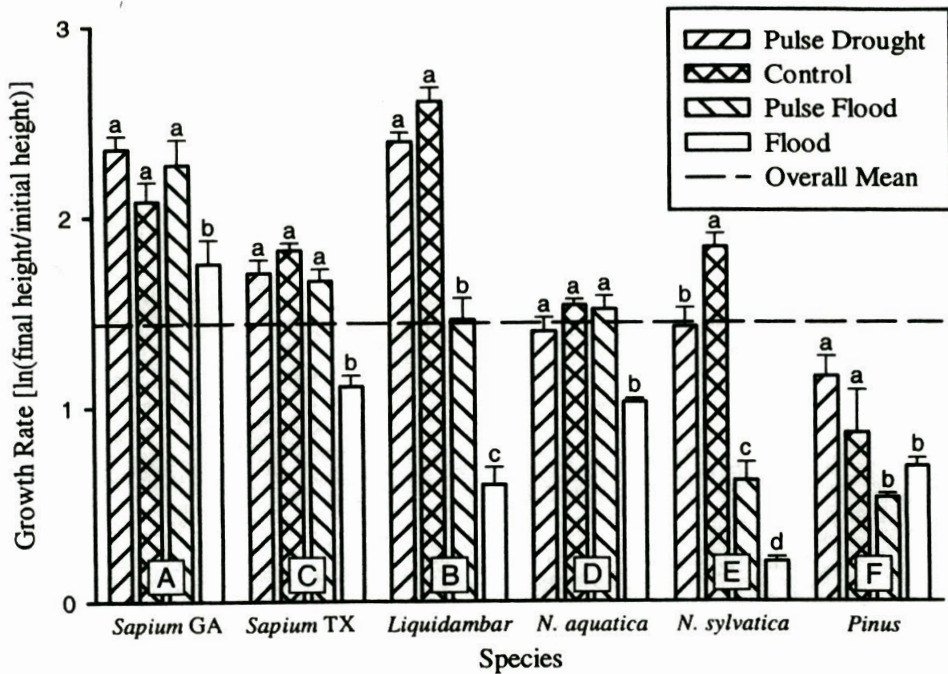


Figure 1. Dependence of the growth rate of each tree species on water treatment (mean + 1 SE). Letters indicate significantly different means ($P < 0.05$) within (lowercase) and among (uppercase) species. The mean growth rate across all species and treatments is provided as a reference.

All statistical analyses were conducted in SAS Version 8 (SAS Institute 1999). ANOVAs were performed using PROC MIXED to analyze the effects of species identity (split-plot factor), water treatment (whole-plot factor) and their interaction (split-plot factor) on growth rate, total biomass, and mass allocation. Stem growth rate was measured as \ln (final height/initial height). Total mass was log transformed for analyses. Proportion of total mass allocated to root, stem, and leaf tissues were measured as organ mass/total mass. Fisher's Least Significant Difference (LSD) was used for means contrasts among treatments.

RESULTS

Stem growth rate depended on species ($F_{5,100} = 124.5$; $P < 0.0001$), water treatment ($F_{3,20} = 99.1$; $P < 0.0001$), and their interaction ($F_{3,100} = 18.3$; $P < 0.0001$; Fig. 1). Georgia *Sapium* grew most rapidly, followed by *Liquidambar*, Texas *Sapium*, *N. aquatica*, *N. sylvatica*, and *Pinus* (Fig. 1). Georgia *Sapium* varied the least in growth across water treatments (1.34-fold difference between treatment in which it grew fastest and the one in which it grew slowest), followed closely by *N. aquatica* (1.49-fold) and Texas *Sapium* (1.65-fold), then *Pinus* (2.17-fold), *Liquidambar* (4.34-fold), and *N. sylvatica* (9.00-fold).

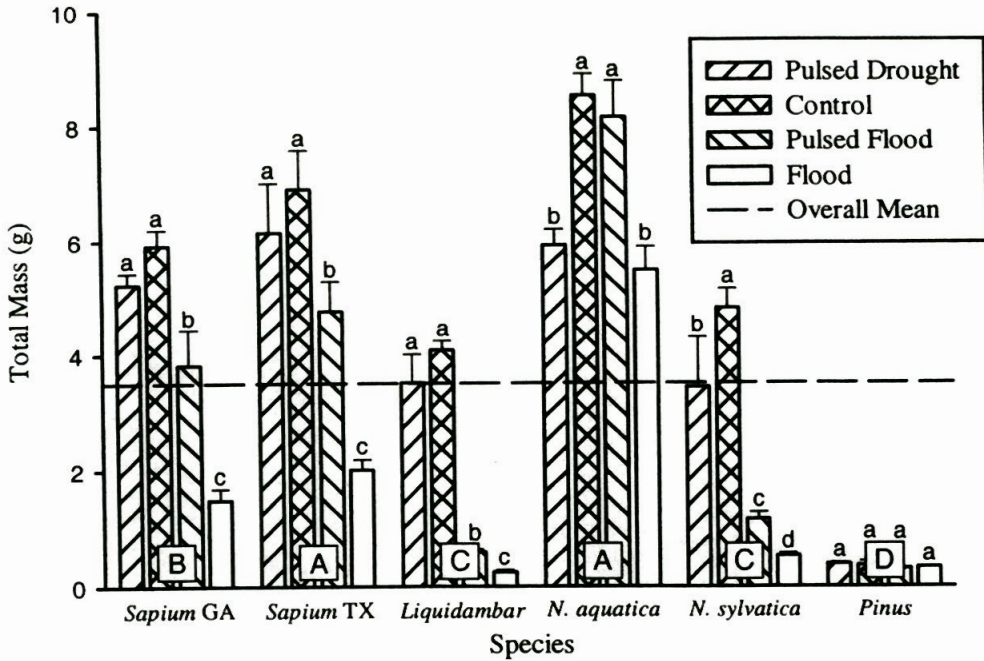


Figure 2. Dependence of total mass of each species on water treatment (mean +1 SE). Letters indicate significantly different means ($P < 0.05$) within (lowercase) and among (uppercase) species. The mean total mass across all species and treatments is provided as a reference.

Total mass depended on species ($F_{5,100} = 893.8; P < 0.0001$; Fig. 2), water treatments ($F_{3,20} = 117.7; P < 0.0001$), and their interaction ($F_{3,100} = 24.2; P < 0.0001$; Fig. 2). *Nyssa aquatica* and Texas *Sapium* had the highest total mass (Fig. 2), but *N. aquatica* seedlings were on average between two and four times as tall as the other species at the beginning of the experiment, which likely contributed to the high final mass (Fig. 3). In a split-plot design these differences in starting sizes are difficult to account for with covariates. Texas *Sapium* had a slightly larger final mass than Georgia *Sapium*, but this can also be reconciled by initial heights (Fig. 3). *Liquidambar* and *N. sylvatica* were both significantly lower than Georgia *Sapium* but were similar with respect to each other. All species but *Pinus* exhibited significant reductions in total mass in response to permanent flooding (Fig. 2).

Proportion of total mass allocated to roots depended on species identity ($F_{5,100} = 81.4; P < 0.0001$) but not on water treatment ($F_{3,20} = 1.2; P = 0.35$) or their interaction ($F_{3,100} = 1.8; P = 0.10$). Proportional leaf mass depended significantly on both species identity ($F_{5,100} = 198.6; P < 0.0001$) and water treatment ($F_{3,20} = 5.54; P < 0.01$) but not on their interaction ($F_{3,100} = 0.46; P = 0.94$). Stem mass proportion

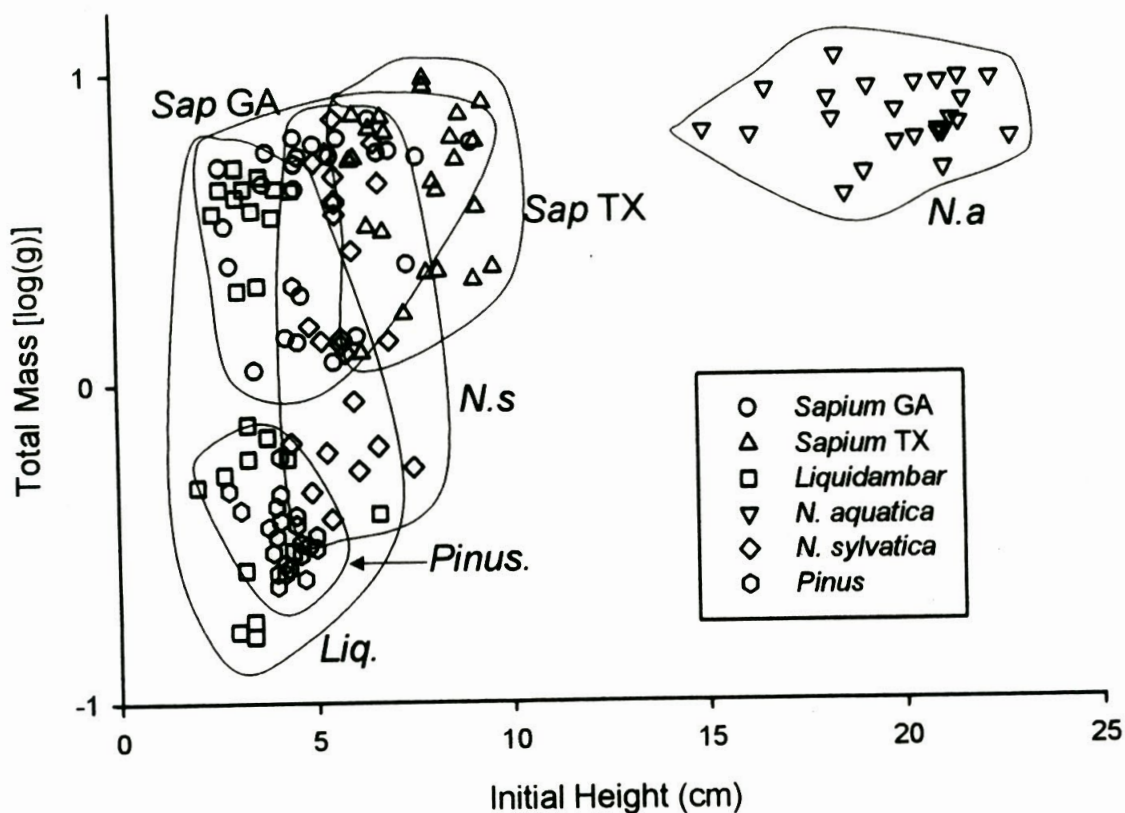


Figure 3. Initial height at planting versus log (total mass) for each species.

was significantly affected by species identity ($F_{5,100} = 349.2$; $P < 0.0001$) and the interaction between species identity and water treatment ($F_{3,100} = 15.1$; $P < 0.0001$), but not water treatment alone ($F_{3,20} = 0.7$; $P = 0.54$). *Sapium* seedlings allocated approximately 30% of mass to leaves, 30% to stems and about 40% to roots. *Nyssa aquatica* had a root to shoot ratio similar to *Sapium*, but allocated markedly less mass to leaves. *Liquidambar* and *N. sylvatica* were similar to each other in their stem versus leaf allocation ratios, but *N. sylvatica* had the highest root to shoot ratio of any species, while *Liquidambar* allocated a relatively low amount of mass belowground. *Pinus* had the lowest root to shoot and stem to leaf ratios (Table 1).

DISCUSSION

The results of this experiment suggest that *Sapium* has characteristics of both stress tolerant and rapidly growing species without experiencing the same magnitudes of tradeoffs between these characteristics as are evident for the native tree species in this study. *Sapium* had high growth rates across all water treatments and experienced only modest

Table 1. Proportion of total mass allocated to root, stem, and leaf parts by species.

Species	% Total Mass		
	Root	Stem	Leaf
<i>Sapium</i> GA	39	31	30
<i>Sapium</i> TX	42	28	30
<i>Liquidambar</i>	31	27	42
<i>Nyssa aquatica</i>	37	45	18
<i>Nyssa sylvatica</i>	44	21	35
<i>Pinus</i>	26	16	58

reductions in growth in response to water stress (Figs. 1, 2). *Sapium*'s stress tolerance appears to extend across the entire experimental water gradient. Within this range of tolerance, *Sapium*'s growth rate was always high relative to most native species. The only species that grew faster than *Sapium* was *Liquidambar* in drier treatments, and it was a very poor performer in the flood treatment (Fig. 1).

While *Sapium* may not be able to out perform *N. aquatica* in permanently flooded conditions if differences in initial seedling sizes observed here are typical of field conditions (Fig. 2), *Sapium* seedlings may still survive to reproductive maturity due to relatively low competition in such stressful environments (Ernst & Brooks 2002). The high leaf-to-stem mass ratio of *Sapium* relative to *N. aquatica* also indicates that *Sapium* may be able to survive in very wet areas with dense canopies in which *N. aquatica* may not be able to capture enough light to grow well (Jones & Sharitz 1990). *Sapium* should also be able to exist in the middle-to-high moisture range of *Liquidambar* and *N. sylvatica*. In areas that are highly favorable for either of the natives, *Sapium*'s shade tolerance (Rogers & Siemann 2002; 2003) and ability to reproduce as a sub-canopy species may favor its presence. The performance of *Sapium* in areas with drier moisture regimes was not tested in this study, but it has been shown to be much less successful in dry uplands that support *Liquidambar* and *N. sylvatica* (Hall & Harcombe 1998; Harcombe et al. 2002; Lin et al. 2004).

Sapium also exhibited positive traits similar to *Liquidambar* and *N. sylvatica*. High growth rates in non-flood treatments (Fig. 1) and high leaf-to-stem ratios (Table 1) of these two natives are indicative of seedlings adapted to relatively nutrient-rich, disturbed areas (Grime 1974; 1977). *Nyssa sylvatica* had high root : shoot ratios (Table 1) and relatively greater mass production in flood treatments (Fig. 2) indicating that seedlings of this species may survive periods of flooding and grow

rapidly when floodwaters subside (Grime et al. 1986). *Liquidambar* performed as a more typical gap species, allocating more resources to stem growth rate in a relatively narrow range of dry to moist soils (Fig. 1, Table 1). *Sapium* exhibited growth traits that were characteristic of these two native species including high root to shoot ratios, intermediate leaf to stem ratios, and high growth rates (Table 1).

The potential gradient distributions of native seedlings in this experiment corresponded relatively well with observed distributions of mature trees. *Nyssa aquatica* was clearly the most tolerant of both flood treatments. Mature *N. aquatica* trees often coexist with *Taxodium distichum* (L.) Rich. as the dominant species in anoxic bottomlands (Marks & Harcombe 1981; Visser & Sasser 1995). *Nyssa sylvatica* seedlings can likely survive periodic flooding while taking advantage of intermittent dry periods, as well as thrive in moist areas. Distribution of mature individuals of this species also covers a wide range of moisture conditions, including areas with seasonal flooding and drought (Keeland et al. 1997). *Liquidambar* performed best in moist to dry conditions, which does appear to deviate slightly from the observed distribution of mature trees. *Liquidambar* is primarily a floodplain species (Marks & Harcombe 1981; Denslow & Battaglia 2002; Ernst & Brooks 2003), but the drought treatment in this experiment was not severe enough to simulate upland conditions. Therefore, dry conditions in this experiment are similar to more elevated areas within a floodplain. Light may also play an important role in the distributions of *Liquidambar* and *N. sylvatica*. Their strategy of maximizing shoot growth in this study is an adaptation consistent with these species being shade intolerant (Hall & Harcombe 1998; Lin et al. 2004). The high variability of total mass and mass allocation under varying water regimes also indicates that these species maximize growth under relatively specific, favorable conditions. *Pinus* was more flood tolerant in this study than was expected (Kozlowski 1997) and was relatively incongruous with respect to distribution of mature trees. Light availability is another important predictor of *Pinus* distribution in nature, which may explain this discrepancy (Harcombe et al. 2002). The apparent flood tolerance may also be a reflection of the fine-grained soils used in this study, which may have stunted the growth of seedlings in all water treatments.

It is not clear what mechanism would contribute to the superior performance of the invasive species observed in this study. One possibility is that *Sapium* possesses novel physiological or biochemical traits as a result of taxonomic novelty or an evolutionary history in a different

biotic province or under different selection pressures (Tilman 1999). This possibility cannot be discounted. *Sapium* is unusual in that it is the only tree in the southeastern U.S. that is a member of the Euphorbiaceae. In addition, *Sapium* is the only plant from Asia in this study, and it is possible that in general Asian trees would outperform North American trees in this type of experiment. Finally, *Sapium* has a long history of being cultivated in Asia for its oil rich seeds, and was originally introduced to the U.S. as an agricultural crop (Bruce et al. 1997). The traits observed here could be the result of artificial selection prior to introduction to North America. There are, however, proximate ecological factors that contribute to the success of invasive plants that may have relevance to the results of this experiment.

Low herbivore loads in the introduced range is one of the factors that is widely believed to contribute to the greater vigor of exotic plants (Keane & Crawley 2002), and has been shown to contribute to *Sapium*'s success (Rogers & Siemann 2002; Siemann & Rogers 2003a). One way in which plants may benefit from low herbivore loads is by a plastic phenotypic response to low losses to herbivores in which additional resources are used for growth (Elton 1958). In this greenhouse study, however, there was negligible damage to any plants, either natives or *Sapium*, so this is unlikely to be the cause of *Sapium*'s unusual combination of high growth rates and high flood tolerance observed here. In fact, *Liquidambar*, the only species that was able to outperform *Sapium* in this study, sometimes suffers extremely high herbivore damage in natural settings (Siemann & Rogers 2003a) which would only strengthen the conclusion that *Sapium* has an unusual combination of growth and tolerance to stress.

Release from herbivory may also affect plant performance by directional selection on plant defense and growth (Blossey & Nötzold 1995). *Sapium*'s high level of vigor in a wide range of conditions may be due to genetic responses to low herbivory resulting in reallocation of resources from defense to faster growth (Siemann & Rogers 2001, 2003b) and perhaps also to phenotypic plasticity (Bazzaz et al. 1987, Alpert et al. 2000). If this is true, the tradeoff between growth rates and stress tolerance examined in this study may be applicable to plant responses under varying conditions of other resources and other forms of stress. Comparisons of the results of a greenhouse study such as this and natural distributions may give insights into the role of other factors, such as herbivory, in determining plant distributions.

This study adds further support to the importance of stress tolerance in the invasion of southeastern floodplain forests by *Sapium*. The two primary determinants of species distribution in these forests are light and water (Hall & Harcombe 1998). Other studies have demonstrated *Sapium*'s ability to grow in a variety of light levels (Jones & McLeod 1989; Rogers & Siemann 2002; 2003; Siemann & Rogers 2003c). In accordance with other studies on soil moisture regimes (Jones & Sharitz 1990; Barrilleaux & Grace 2000; Conner et al. 2001), this experiment confirms that *Sapium* can perform well under a wide range of water conditions. Regardless of the mechanism, *Sapium* is able to exhibit traits of both rapidly growing and stress tolerant species, which may allow it to spread into bottomlands with anoxic soils as well as into seasonally dry areas of floodplain forests. Perhaps more importantly, this study demonstrates the ability of an introduced species to minimize tradeoffs that substantially affect the performance and growth strategies of native species.

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