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EFFECTS OF RESOURCES AND HERBIVORY ON LEAF MORPHOLOGY AND PHYSIOLOGY OF CHINESE TALLOW (*SAPIUM SEBIFERUM*) TREE SEEDLINGS

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Abstract.—Chinese tallow (*Sapium sebiferum*) is a major woody invader in a variety of ecosystems throughout the southeastern United States. This study was conducted to examine the effects of different levels of resources and herbivory on the growth and physiology of Chinese tallow leaves. Chinese tallow tree seedlings were grown outdoors in pots for fifteen weeks under experimental combinations of shade, nitrogen and simulated herbivory. All of the seedlings survived and grew vigorously under a variety of shade, nitrogen and herbivory conditions. Shade and nitrogen manipulations had the greatest effects on leaf growth and physiology. Stomatal conductance was significantly decreased by increasing levels of shade and tended to decrease with added nitrogen. Leaf area and number of new leaves were greater in shaded conditions than in full sunlight. Increased amounts of nitrogen increased average leaf area, leaf number, and leaf mass. Petiole lengths also significantly increased with higher levels of nitrogen and shade. Surprisingly, simulated herbivory did not significantly affect any of the leaf parameters measured. This study has demonstrated that Chinese tallow is capable of thriving under a number of environmental conditions and, in addition to previous research showing resistance to most native herbivores, that it is extremely tolerant of herbivory leaf damage. Combined, these factors increase the success of Chinese tallow as an invasive species and will complicate the development of an effective management strategy.

Controlling alien plant invasions is considered to be one of the greatest contemporary and future environmental challenges (Coblentz 1990; Soule 1990). The process of invasion is of central importance to ecology because the introduction of a non-native species can markedly affect community assembly dynamics and ecosystem processes (Drake & Mooney 1989; D'Antonio & Vitousek 1992; Lodge 1993; Cronk & Fuller 1995; Williamson 1996). By understanding the mechanisms underlying alien plant invasions ecologists will have gained tremendous insights into the mechanisms of succession, community assembly dynamics and ecosystem function. Moreover, they will be better equipped to assist with management strategies for a variety of imperiled ecosystems.

Invasion dynamics of Sapium sebiferum.—The alien Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) (Euphorbiaceae) - synonyms include *Croton sebifera* Linn, *Stillingia sebifera* Willd. (Roxb. 1832) and *Triadica sebifera* (L.)), is a major invader along the Gulf Coast of the

United States. It is capable of aggressively displacing native plants and forming biotically depauperate woodland thickets (Bruce et al. 1995).

Chinese tallow was originally introduced to the southeastern United States in 1772 using seeds provided by Benjamin Franklin (Bell 1966). Because it grows rapidly, has colorful fall foliage, abundant flowers, and seeds rich in oils, it has been widely planted for ornamental purposes, biomass, industrial oils, and as a nectar crop (Lieux 1975; Scheld & Cowles 1981; Rockwood et al. 1993). Research also suggests potential as a source of antibiotics, anti-viral drugs, and anti-hypertension drugs (Kane et al. 1988). Unfortunately, *Sapium* invasion seriously threatens the biotic integrity of native coastal prairies and forests, leading The Nature Conservancy to name Chinese tallow as one of the worst alien plant invaders in the United States (Flack & Furlow 1996).

The dynamics of *Sapium* invasion into coastal prairies are characterized by an initially slow 10 year increase in cover followed by a dramatic increase in *Sapium* density during the proceeding ten years. In the absence of an active management regime, a coastal prairie can be transformed into a self-replacing *Sapium* woodland within 30 years (Bruce et al. 1995). While *Sapium* invasions into upland forests and bottom-land, floodplain forests differ in the rate of increase and time of initiation, similar logistic growth increases of *Sapium* are occurring in both ecosystems (Harcombe et al. 1999).

The role of resources.—Changes in resource levels are thought to be an important cause of species replacement during succession (e.g. Connell & Slayter 1977; Bazzaz 1979; Tilman 1982; Huston & Smith 1987) and may also facilitate alien plant invasions (Dukes & Mooney 1999). Anthropogenic nitrogen additions have been shown to increase the invasibility of grasslands and temperate forests (e.g. Huenneke et al. 1990; Burke & Grime 1996; Aber et al. 1998; Bakker & Berendse 1999). Increases in nitrogen supply from atmospheric deposition (Matthews 1994; Galloway et al. 1995) may promote *Sapium* invasion. Facilitation of invasion by anthropogenically derived nitrogen additions is consistent with the recent emergence of *Sapium* as a serious problem in coastal Texas despite its previously innocuous, century-long presence in the region (Bruce et al. 1995; Bruce et al. 1997). Moreover, litter feedbacks appear to reinforce this effect. *Sapium* litter decomposes rapidly, making available nitrogen concentrations under *Sapium* trees almost double that beneath native vegetation (Cameron & Spencer 1989).

Sapium seedlings have displayed moderate growth under low light levels and rapid growth in full sunlight (Jones & McLeod 1989; 1990). As *Sapium* invades coastal prairie, light availability to grasses and forbs decreases. A single, 15 year-old *Sapium* tree is capable of reducing light to 7% of ambient in its densest shade and casting 80% or greater shade over 30 m^2. In deep shade, *Sapium* has exhibited greater growth rates relative to other plant species (Jones & McLeod 1989; 1990). The ability to grow relatively well in a wide range of light conditions may partially explain *Sapium's* successful invasion into habitats with greatly differing light environments, like coastal prairies and bottomland hardwood forests. Furthermore, if *Sapium* seedlings have high nitrogen requirements and low light requirements, *Sapium* induced changes in the relative availability of soil resources versus light may initiate a positive feedback that further facilitates its invasion (e.g., Tilman 1988; Tilman & Pacala 1993).

Effects of herbivores.—Alien plants are usually introduced with few or none of the specialist herbivores from their native habitat. This is widely believed to give alien plants a competitive advantage over native plants (e.g., Elton 1958; Drake & Mooney 1989; Lodge 1993; Williamson 1996). Measurements of herbivore loads on native and alien plants have consistently found lower herbivore loads on aliens (e.g., Strong et al. 1984; Scierenbeck et al. 1994; Yela & Lawton 1997). Consistent with this theory is the observation that alien plants are often taller and more vigorous in their introduced than their native ranges (Guzikowa & Maycock 1986; Crawley 1987; Blossey & Notzold 1995).

Sapium's success as an invader is widely attributed to a lack of herbivores (e.g., Scheld & Cowles 1981; Jones & McCleod 1989; Harcombe et al.1993; Bruce et al.1995; Jubinsky & Anderson 1996; Bruce et al. 1997). It is generally assumed that an evolutionary tradeoff involving fitness costs exists between herbivory resistance (mechanisms that reduce the probability of defoliation) and herbivory tolerance (mechanisms that facilitate regrowth following defoliation) (Herms & Mattson 1992; Simms 1992; Mole 1994). *Sapium* is believed to be resistant to many vertebrate and invertebrate herbivores because its leaves contain numerous toxic allelochemicals that act as feeding deterrents (Russell et al. 1969; Cameron & LaPoint 1978). However, in its native range, at least 26 species of specialist insects feed on *Sapium* (cf. Zhang & Lin 1994). In the United States, the amount of leaf area *Sapium* loses to herbivory is extremely low (Scheld & Cowles 1981; Jubinsky & Anderson 1996; Bruce et al. 1997).

Predictions.—The objective of this study was to examine the manner in which the leaves of Chinese tallow respond to various levels of herbivory and resources. It was hypothesized that, while resistant to many types of herbivores in the southeastern United States, were *Sapium* to experience higher levels of herbivory it would show significant decreases in leaf growth and physiological activity. In other words, *Sapium* was predicted to lack tolerance to leaf defoliation. It was also hypothesized that these decreases in growth could be compensated for by adding nitrogen. Further, it was predicted that in the absence of herbivory, full sunlight would maximize *Sapium* growth, but decreased light availability would increase the relative growth of defoliated plants by reducing the physiological stress of high sunlight on damaged leaves. Maximum leaf growth and physiological activity was predicted to occur in full sunlight with high levels of nitrogen addition and no simulated herbivory.

Materials and Methods

Seeds of Chinese tallow were individually germinated in 100 mL "cone-tainers"™ (Stuewe & Sons, Inc., Corvallis, Oregon) in an unheated greenhouse during April-May 1999. In late May, the cone-tainers were transferred outdoors and placed beneath a 50% shade cloth for two weeks in order to "harden-off" the seedlings and minimize unnatural susceptibility to environmental variability and herbivores. Similar sized *Sapium* seedlings ($n=162$) were selected and individually transplanted into 3 gallon (7.65 liter) Stuewe Treepots™ (Stuewe & Sons, Inc., Corvallis, Oregon) during the second week of June. Approximately 3 cm of peat moss was placed in the bottom of the pots, in order to improve water retention, before they were filled with a homogenized mixture of commercially available topsoil (2/3) and organic humus and peat (1/3).

All of the 162 potted plants were randomly assigned to a treatment in a full-factorial experimental design with three levels of shade, three levels of nitrogen addition, and three levels of simulated herbivory (27 treatment combinations by six replicates, see below). The pots were then transferred to the roof (4th floor) of the biological sciences building on the Rice University campus. The tar-shingled roof was covered with sheets of wood chipboard and evenly spaced plastic water catches were placed on the boards to hold the pots. The pots were watered daily.

Plants in the shaded treatments were placed under black polypropylene shade cloths which were erected to a height of 1.5 m. Under clear skies during the hours of solar noon, the two cloths attenuated 63%

(S1) and 88% (S2) of Photosynthetically Active Radiation, as measured with a Decagon Accupar linear PAR ceptometer (Decagon Devices, Pullman, Washington, USA). Unshaded control plants (S0) received ambient levels of sunlight. Pots were spaced far enough from each other that inter-plant shading was minimal. Nevertheless, because there may have been occasions when one plant cast a shadow upon another, as well as subtle differences in light and temperature under each shade cloth, all of the pots were periodically rotated within their respective shade treatment.

Nitrogen was added to the pots as ammonium nitrate dissolved in tap water. Plants assigned to the nitrogen fertilization treatments received either 1 gn/m^2 (N1) or 3 gn/m^2 (N2) during weeks two, six and eleven (3 g/m^2 or 9 g/m^2 total respectively) of the fifteen week experiment. Plants in the unfertilized control treatment (N0) did not receive additional nitrogen.

The most common form of leaf herbivory observed on naturally occurring *Sapium* seedlings is small holes, presumably created by chewing insects or molluscs. As a result, chewing herbivory was simulated by using a steel paper hole punch (6.3 mm diameter) to mechanically damage leaves. Realistic simulation of herbivory by mechanical means is difficult because many aspects of insect chewing cannot be accurately imitated (Hendrix 1988). However, if done carefully it is regularly assumed that this type of simulated leaf herbivory provides an adequate representation of the decreased leaf area and mass loss experienced by insect damaged tree seedlings (Hendrix 1988; Marquis 1992).

Leaf herbivory was simulated twice during the experiment. Plants assigned to the simulated herbivory treatments were initially subjected to 10% leaf removal (H1) and 20% leaf removal (H2) during week three. During week nine, plants in the H1 treatment received 60 hole punches per plant while plants in the H2 treatment received 120 hole punches. A computer program was written to randomly and independently assign the hole punches to the leaves based on the total number of leaves (and average leaf area in the first herbivory event) per plant. If possible, the midveins of leaves were not punched to prevent unintended magnification of the damage. Similarly, the new leaves near the top of each seedling were excluded from damage in order to protect the apical meristems and avoid unintentionally influencing branching dynamics (Maschinski & Whitham 1989; Marquis 1992). The fourth and fifth leaves on each plant were also left undamaged so that stomatal conductance measurements (see below) could be made on intact leaves.

Control plants with no simulated herbivory (H0) were also maintained.

To prevent uncontrolled herbivory on the tree seedlings, Esfenvalerate (tradename Asana XL, DuPont Agricultural Products, Wilmington, Delaware) was periodically sprayed on the plants and surrounding area. A separate phytotoxicity experiment was conducted and no negative effects of Esfenvalerate on the growth of *Sapium* were found.

In the 14th week of the experiment, a steady-state porometer (LI-1600M, LI-COR, Inc. Lincoln, Nebraska, USA) was used to measure leaf stomatal conductance ($mmol/m^2/s$). Measurements were made on the abaxial side of fully intact and expanded leaves near the top of each plant. The measurements were taken on a clear, calm day around the hours of solar noon. Midday stomatal conductance is a quantitatively useful estimate of plant vigor (Givnish 1986; Pearcy et al. 1989) and has successfully been used by others to measure physiological stresses (i.e., photooxidation or photoinhibition) in a variety of tree species, including *Sapium* (cf. Jones & McLeod 1989; 1990).

The number of new leaves added to each plant during the experiment was calculated by subtracting the number of leaves present at the beginning from the number present at the end. Additionally, three leaves per plant (near the top, middle and bottom) were systematically selected and the leaf area (estimated from leaf length and width) and petiole length of each leaf was measured. In the 15th week of the experiment, the leaves from each plant were harvested and dried at 60°C for a minimum of 72 hours before weighing. Although all of the tree seedlings lost leaves to senescence during the study and those subjected to simulated herbivory treatments frequently lost damaged leaves, no leaves were lost on the plants between the time the final leaf count was taken and the time of leaf harvest. Analysis of variance was used to compare the different experimental treatments and Fisher's Least Significant Difference Test was used to test for differences between the treatment means (StatView 5.0, SAS Institute, Cary, North Carolina).

RESULTS

At the onset of the experiment, there was an average of 11.1 ± 0.13 leaves per *Sapium* seedling. All of the tree seedlings survived for the entire experiment. The shade and nitrogen manipulations had the greatest effects on leaf growth and physiology. Stomatal conductance was significantly decreased by increasing shade levels (Fig. 1a, $F_{2,135}=45.6$, $P<0.0001$). There was also a trend for stomatal conductance to decrease with increasing amounts of nitrogen addition (Fig. 1b, $F_{2,135}=2.6$, $P=0.0815$) and the means separation test for the N0 and N2 treatments

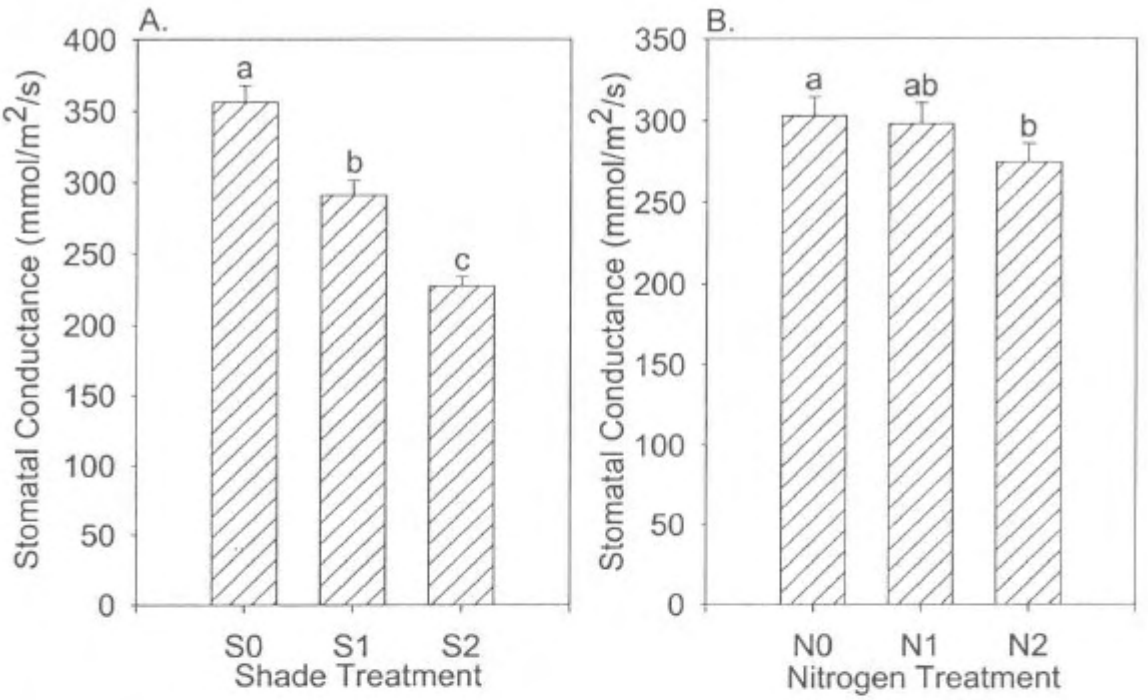

Figure 1. Stomatal conductance (means ± 1 SE) of *Sapium* leaves at (a) three levels of shade (S0 = 100% sunlight, S1 = 37% sunlight, S2 = 12% sunlight) and (b) three levels of nitrogen (N0 = 0 g/m^2, N1 = 3 g/m^2, N2 = 9 g/m^2). Bars with different letters indicate significance at $P \leq 0.05$.

was significant (Fig. 1b, $P=0.0359$). Average leaf area was also affected by shade treatment. *Sapium* leaf area significantly increased with increased shade (Fig. 2a, $F_{2,135}=104.1$, $P<0.0001$). The number of leaves added to each plant during the experiment was also higher in the shaded treatments than in full sunlight (Fig. 3a, $F_{2,135}=7.46$, $P=0.0008$). Additionally, increased amounts of nitrogen significantly increased leaf area (Fig.2b, $F_{2,135}=7.76$, $P=0.0006$), leaf number (Fig. 3b, $F_{2,135}=10.21$, $P<0.0001$), and individual leaf mass (Fig. 4, $F_{2,135}=7.97$, $P=0.0005$). The combined effect of shade and nitrogen on petiole lengths was the only significant interaction observed. Petiole lengths were significantly increased by increasing amounts of nitrogen and shade (Fig.5, $F_{4,135}=3.54$, $P=0.0089$). The simulated leaf herbivory treatments did not significantly affect any of the *Sapium* leaf measurements.

Discussion

This study has reinforced the notion that the invasive capacity of Chinese tallow is partially due to a combination of its ability to thrive under a variety of environmental conditions and its immunity to regulation by herbivores.

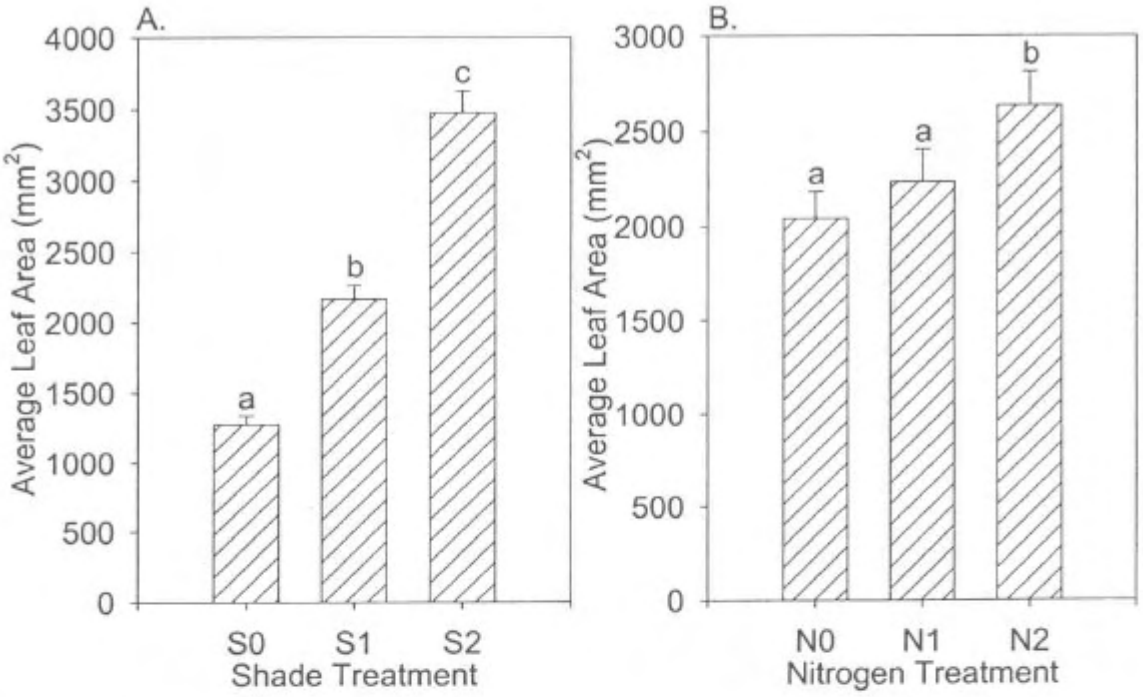

Figure 2. Average leaf area (means ± 1 SE) of *Sapium* at (a) three levels of shade (S0 = 100% sunlight, S1 = 37% sunlight, S2 = 12% sunlight) and (b) three levels of nitrogen (N0 = 0 g/m², N1 = 3 g/m², N2 = 9 g/m²). Bars with different letters indicate significance at $P \leq 0.05$.

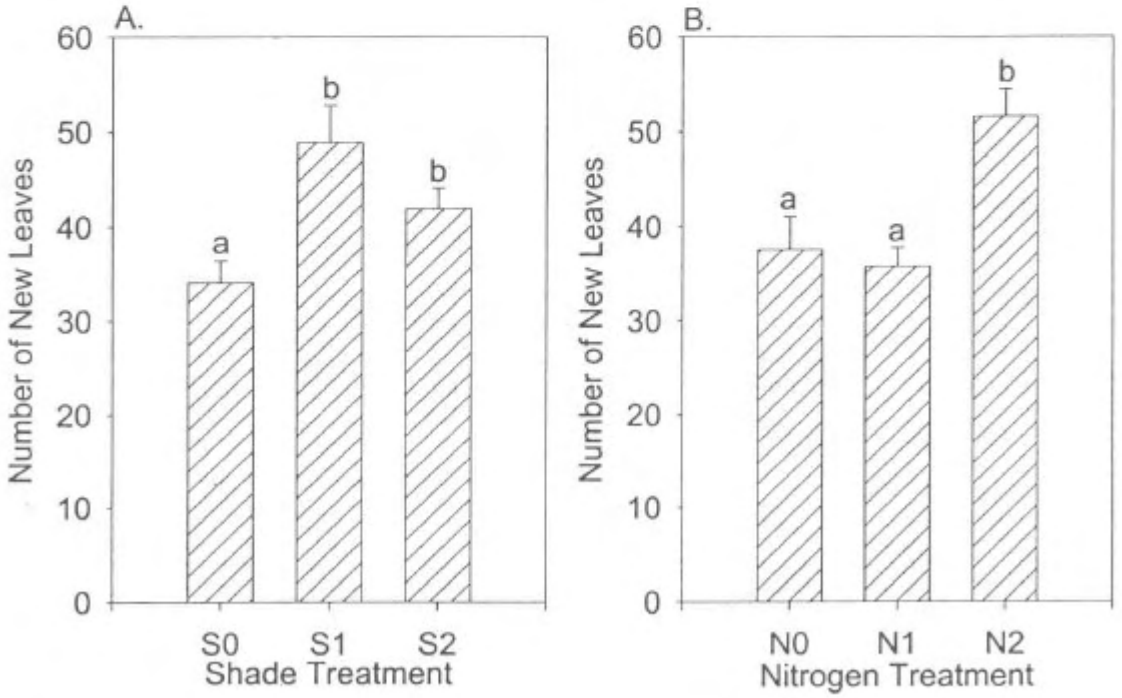

Figure 3. Change in leaf number (means ± 1 SE) of *Sapium* at (a) three levels of shade (S0 = 100% sunlight, S1 = 37% sunlight, S2 = 12% sunlight) and (b) three levels of nitrogen treatment (N0 = 0 g/m², N1 = 3 g/m², N2 = 9 g/m²). Bars with different letters indicate significance at $P < 0.05$.

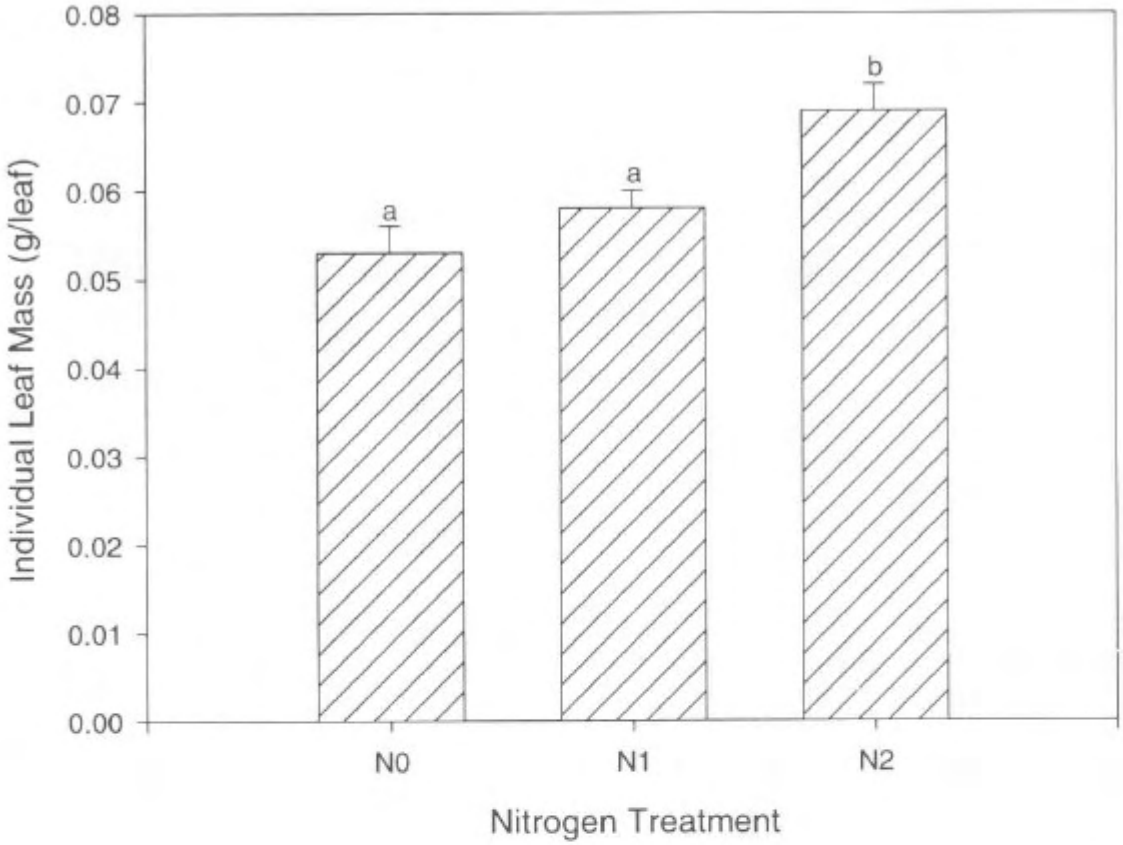

Figure 4. Individual leaf mass (means ± 1 SE) of *Sapium* at three levels of nitrogen. (N0 = 0 g/m^2, N1 = 3 g/m^2, N2 = 9 g/m^2). Bars with different letters indicate significance at $P \leq 0.05$.

Shade intolerant tree species typically have high growth rates in full sunlight and grow significantly slower in deep shade, while shade tolerant tree species grow only slightly faster in high rather than low light (Loach 1970; Connell & Slayter 1977; Bazzaz 1979; Pearcy & Sims 1994). These generalizations, however, do not apply to *Sapium*. Similar to the findings of others (Jones & McLeod 1989; 1990), this experiment has shown that *Sapium* is capable of growing vigorously under a variety of light levels and its leaves exhibit considerable physiological and morphological variability based on environmental conditions.

Sapium leaves appear to exhibit a great deal of physiological plasticity which likely promotes maximum growth under various light conditions (Jones & McLeod 1989; 1990). Assuming that the stomatal conductance of *Sapium* is correlated with transpiration (Givnish 1986), the decreased levels of stomatal conductance observed with increased shade are reasonably explained by physiological adaptations that enable *Sapium* to maintain a high water-use efficiency under low light conditions (Fig 1a

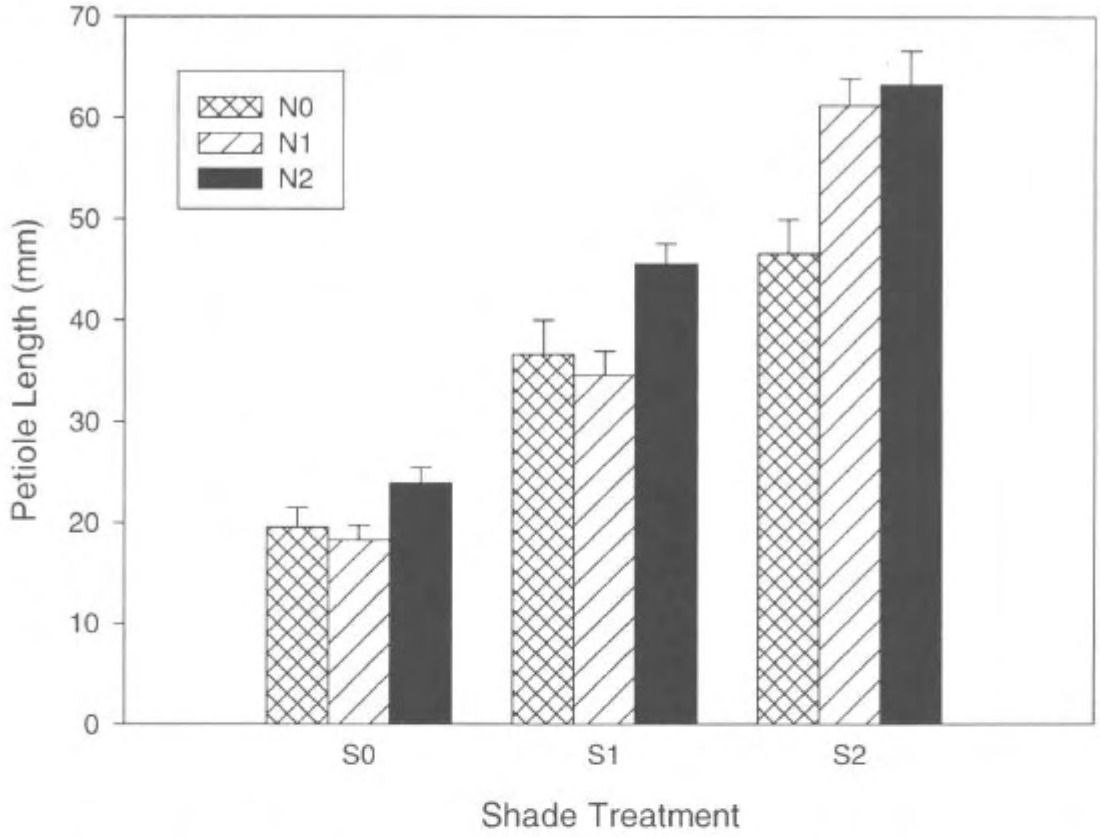

Figure 5. Petiole length of *Sapium* leaves for the interaction of three levels each of shade (S0 = 100% sunlight, S1 = 37% sunlight, S2 = 12% sunlight) and nitrogen (N0 = 0 g/m^2, N1 = 3 g/m^2, N2 = 9 g/m^2).

this study; Jones & McLeod 1990). Likewise, the high midday stomatal conductance measures in full sunlight indicate that the plants maintained high levels of physiological activity (Fig. 1a). However, contrary to the predictions of this study and the findings of others (Jones & McLeod 1989; 1990), the growth of *Sapium* leaves was not maximized by increased sunlight in the absence of herbivory (Figs. 2-3, 5). This result is puzzling, but may potentially be explained by periods of photoinhibition or photooxidation induced by temperature and water stresses (Givnish 1986; Pearcy & Sims 1994), although the high levels of stomatal conductance observed in full sunlight and the fact that the tree seedlings were watered daily weaken this interpretation.

The number of new leaves per plant was greater in the shaded compared to the unshaded treatments (Fig. 3a). Jones & McLeod (1990) found the opposite. In their study, leaf numbers increased on *Sapium* trees exposed to higher light levels. However, similar to the findings of Jones & McLeod (1990), the surface area, but not necessarily the mass, of individual *Sapium* leaves was larger in shade relative to leaves grown in full sunlight (Fig. 2a). Large, thin leaves, commonly referred to as "shade leaves", are a common adaptation for maximizing carbon gain in

low light conditions (Loach 1970; Bazzaz 1979; Pearcy & Sims 1994; Givnish 1986).

Sapium seedlings responded strongly to increased nutrient levels as predicted (Scheld & Cowles 1981; Cameron & Spencer 1989). Increased nitrogen reduced stomatal conductance and may reflect increased water-use and nutrient-use efficiencies (Fig. 1b). Leaf area, leaf number and leaf mass increased with nitrogen additions (Figs. 2b, 3b, 4b). Correspondingly, petiole lengths also increased with increasing shade and nitrogen (Fig 5).

Surprisingly, simulated herbivory did not significantly affect any of the parameters measured for this study. Leaf morphology and physiology appeared unaffected by the high levels of mechanical leaf damage inflicted upon *Sapium* seedlings. It is possible that stomatal conductance responded to the simulated herbivory immediately after the damage, but the plants quickly compensated and no effect was observed by the time the measurements were made.

In addition to previous evidence that *Sapium* is resistant to many North American herbivores, these results seem to indicate it is also remarkably tolerant of leaf damage and is capable of rapid morphological and physiological compensation to herbivory. Numerous examples of compensatory growth can be cited (McNaughton 1983; Maschinski & Whitham 1989; Vail 1992; but see Belsky et al. 1993), but these findings are typically reserved for plants that are adapted to regular defoliation by herbivores. An evolutionary trade-off involving fitness costs is frequently inferred between the mechanisms that produce resistance to herbivory and the mechanisms that promote tolerance of herbivore defoliation (Herms & Mattson 1992, Simms 1992; Mole 1994). The absence of herbivores feeding on *Sapium* in its introduced range combined with its tolerance of moderate and high levels of mechanical leaf damage suggest that *Sapium* is a "herbivore tolerant" plant that is currently reaping the benefits of a "herbivore resistant" plant without the associated costs. Further, in view of *Sapium's* tolerance to high levels of mechanical leaf damage, these results caution that the effectiveness of possible bio-control management options be thoroughly evaluated prior to implementation (Jubinsky & Anderson 1996; McFayden 1998; McEnvoy & Coombs 1999). It is unclear at this time whether its spread could be controlled by higher herbivore loads in a natural setting.

The considerable morphological and physiological plasticity of *Sapium* leaves demonstrated in this study likely contributes to the competitive

success and invasive potential of Chinese tallow in a variety of ecosystems throughout the southeastern United States. The ability to thrive under a variety of environmental conditions coupled with a high herbivory tolerance and current lack of an appreciable herbivore load makes for an extremely successful species and will complicate the development of a management strategy for controlling this aggressive invader.

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