RICE UNIVERSITY

Restoring a Prairie: Testing Effectiveness of Chinese Tallow Tree (Sapium sebiferum) Mulch to Reduce Seedling Emergence

by

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ABSTRACT

Restoring a Prairie: Testing Effectiveness of Chinese Tallow Tree (Sapium sebiferum) Mulch to Reduce Subsequent Seedling Emergence

by

Candice Donahue

The invasive Chinese tallow tree (Sapium sebiferum) is difficult to control because of its large seed bank and ability to resprout from cut stumps. I performed laboratory and field experiments to evaluate the effectiveness of mulching live trees for restoring invaded prairies. Herbicide use was limited to manual application to cut stumps. I manipulated mulch depths and types in the field and measured soil temperatures beneath them. At depths of as little as 5 cm, Sapium mulch damped soil temperature fluctuations and reduced seedling emergence. Reduced seedling emergence was not the result of allelopathic compounds in Sapium mulch because other mulch types suppressed emergence similarly. Substantial regrowth of native vegetation occurred through the mulch. Independent manipulations of mulch depth and temperature fluctuations in a lab experiment confirmed that mulch suppressed seed germination indirectly via soil temperature effects. This prairie site can now be managed by mowing or burning.

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TABLE OF CONTENTS

eı

1. Introduction	1
2. Restoring an Invaded Prairie - Effects of Sapium sebiferum Mulch on its Own S Germination	
3. Effects of Temperature and Mulch Depth on Chinese Tallow Tree (Sapium sebi Seed Germination	, ,

LIST OF TABLES

2.1.	The effect of mulch treatment, block, and seedling addition on cumulative seedling emergence from full-interaction ANOVA on <i>Sapium</i> mulch treatments (0, 5 10, and 15 cm) only
2.2.	Means table for all mulch treatments by block and whether or not an added seedling was planted in the plot
2.3.	The effect of mulch treatment, block, and seedling addition on cumulative seedling emergence from full-interaction ANOVA on 10 cm <i>Sapium</i> mulch, hardwood mulch, and straw mulch treatments only
3.1.	Dependence of <i>Sapium</i> germination on experimental temperature and mulch depth treatments in an ANOVA

LIST OF FIGURES

2.1.	The effect of <i>Sapium</i> mulch depth on the cumulative count of new seedlings in a pl (emergence) and the number of seedlings alive at the end of the growing season	
2.2.	Diurnal soil temperature fluctuations in the field for different depths of Sapium mulch for six days in April	22
2.3.	The effect of Sapium mulch on survival of naturally occurring seedlings	24
2.4.	Mean vegetation cover per plot at the end of the growing season for each depth of Sapium mulch	25
2.5.	Percentage of added seedlings alive at 98 days in relation to the number planted for each <i>Sapium</i> mulch treatment	
3.1.	Sample of field soil temperatures recorded every 30 minutes, by mulch depth, in a field that had <i>Sapium</i> trees removed with a shredding mower in late 2002	42
3.2.	Number of <i>Sapium</i> seeds germinating in each bin for each combination of temperature treatment and mulch depth	44

Chapter 1

Introduction

The Coastal Prairie, one of seven North American grassland associations, is located in a 40 to 160 km wide band along the Gulf of Mexico from southwestern Louisiana into southern Texas. This region once included 38,000 km² of tallgrass prairie, but native tallgrass prairie is now restricted to approximately 1% of its former extent, primarily in relatively small, fragmented relicts (Smeins et al., 1992; Grace, 1998; Allain et al., 1999). Several factors led to the decline of these coastal grasslands, including conversion to cropland and other uses, overgrazing, the cessation of the historical fire regime, encroachment of woody species, and, more recently, the invasion of exotic species (Axelrod, 1985; Smeins et al., 1992; Grace, 1998).

A combination of fire, grazing by large ungulates, and a clayey, shrink-swell soil once maintained a balance between the woody species along the waterways of the Gulf Coast and the grasses on the uplands (Axelrod, 1985; Smeins et al., 1992). Under these conditions, grasses are favored over trees and shrubs and woody species are limited primarily to waterways. However, once fire is suppressed, these woody species spread outward from their refugia into the adjacent grasslands (Axelrod, 1985).

Woody encroachment is facilitated by several factors. With fire suppression, plant litter accumulates. Litter accumulation increases soil moisture and reduces the competitive advantage of drought-tolerant grasses. Also, reduction of light transmission through the litter layer lowers the photosynthetic rate of grasses and favors taller woody species (McCarron and Knapp, 2001; Heisler et al., 2003). Once woody species become

established, they shade out native grasses and forbs, reducing available flammable material and creating a positive feedback.

Historically, the major woody invader of Gulf Coast prairie was the native shrub *Baccharis halimifolia* L., which had been controlled by fire (Bruce, 1993). However, during the 1970's, the invasive exotic Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) rapidly expanded from riparian areas where it had previously been restricted, and became the first tree to successfully invade undisturbed native prairies (Bruce, 1993; Bruce et al., 1995). Because of its rapid growth and prolific reproduction (Lin et al., 1958), *Sapium* can convert a diverse native prairie into a closed canopy monospecific forest in 20-25 years (Bruce et al., 1997). *Sapium sebiferum* is perhaps the most significant current threat to native coastal prairie (Bruce et al., 1995; Jubinsky and Anderson, 1996; Grace, 1998).

The experiments described in this thesis examine one approach to the challenge of restoring invaded prairies that may allow for rapid conversion of established *Sapium* forests back into grasslands. Live trees are mulched and the mulch is left in place.

Herbicide treatment is limited to manual application to the surface of cut stumps.

The field experiment described in Chapter 2 examines the effects of *Sapium* mulch on *Sapium* seed germination, the re-emergence of native vegetation, and assesses the possibility of allelopathic effects of *Sapium* mulch. *Sapium* is known to be dependent on diurnal soil temperature fluctuations for successful germination, so a primary question was whether mulch would damp temperature fluctuations enough to suppress germination and subsequent seedling emergence.

The laboratory experiment described in Chapter 3 was designed to further test the temperature hypothesis proposed in Chapter 2. I maintained specific temperature regimes under different depths of mulch to separate the temperature effects on germination and seedling emergence from the simple physical effects of mulch layers.

While some herbicide use appears to be necessary, my results indicate that mulching live trees may be an effective initial treatment method to rapidly restore *Sapium*-invaded native prairies.

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Chapter 2

Restoring an Invaded Prairie – Effects of *Sapium sebiferum* Mulch on its Own Seed Germination

Abstract

The introduced Sapium sebiferum (Chinese tallow tree) has spread across the southeastern US and is rapidly replacing native prairies with monospecific Sapium forests. Most attempts to control Sapium are only temporarily effective because of its large seed bank and ability to resprout from cut stumps. We performed a field experiment to evaluate the effectiveness of mulching live trees to restore invaded prairies. Because Sapium seed germination is highly dependent upon diurnal soil temperature fluctuations, we predicted that Sapium mulch would damp those fluctuations and suppress seed germination. We manipulated mulch depths and types in the field and measured the soil temperatures beneath them. Diurnal soil temperature fluctuations were damped at depths of as little as 5 cm, and the Sapium mulch significantly reduced seedling emergence. Deep layers of mulch (15 cm) negatively affected seedling emergence, seedling survival and native vegetation cover. Comparisons among Sapium mulch and alternative mulch materials revealed no facilitative or negative allelopathic effects of Sapium mulch on Sapium seedling emergence, survival, or growth. Vigorous regrowth of native vegetation through 5 cm of Sapium mulch was evident by the end of the growing season. With no trees or stumps to hinder a mowing regime, and vegetative fuel levels beginning to support prescribed burning, mowing and fire can now be used to manage this prairie site.

Introduction

Grasslands are one of the most endangered ecosystems (Grace, 1998; Allain et al., 1999). Research throughout the world focuses on the effects of grassland declines on rare and endangered species, from plant species in Sweden (Lennartsson, 2002) and Canada (Schwarz and Wein, 1997), to birds in Kenya (Ndang'ang'a et al., 2002), and small mammals in Australia (Cole and Woinarski, 2000). Worldwide, grasslands have declined to a fraction of their former extent because of overgrazing, conversion to cropland and other uses, and invasion of exotic species (Gupta and Amabasht, 1979; Grace, 1998; Ndang'ang'a et al., 2002; Rosenthal, 2003).

A portion of the North American grassland, the Coastal Prairie, is located along the northwestern coast of the Gulf of Mexico. Smeins et al. (1992) identify 13 potential natural vegetation associations in the Coastal Prairie region because of its location and varieties of soil types. This diversity supports 350 to 400 species of migratory birds (Smeins et al., 1992), including the federally endangered whooping crane. Although it once covered 38,000 km², current estimates indicate that less than 1% of Coastal Prairie now remains (Smeins et al., 1992; Allain et al., 1999), and this portion is under serious threat by the invasive exotic *Sapium sebiferum*.

Focal Species

The exotic Sapium sebiferum (L.) Roxb. (Sapium hereinafter) naturalized across the southeastern United States after its introduction on the East Coast in 1772 (Bruce et al., 1997; Grace, 1998). Sapium has rapid growth and early and prolific reproduction (Jubinsky and Anderson, 1996; Bruce et al., 1997; Grace, 1998). It is tolerant of both flooding and drought (Conner, 1994; Grace, 1998) and has been shown to outperform

native species in both full sun and shade (Jones and McLeod, 1989; Rogers and Siemann, 2002; Siemann and Rogers, 2003). *Sapium* has replaced much of the remaining diverse Coastal Prairie with monospecific *Sapium* forests (Bruce et al., 1995; Grace, 1998; Rogers and Siemann, 2003).

Decomposition of *Sapium* litter in these forests occurs much faster than that of native species, resulting in at least two consequences. The chemical composition of the soil is changed and nutrient release is accelerated, compared to native prairie (Cameron and Spencer, 1989). Furthermore, loss of prairie bunchgrasses and rapid decomposition of *Sapium* litter may leave the soil bare beneath trees, reducing bioremediation of anthropogenic pollutants (Harbor et al., 1995; Liaghat and Prasher, 1996; Fajardo et al., 2001) thereby speeding flow of water and sediments to bayous and rivers.

Once Sapium becomes established, it is very difficult to eradicate. Mature trees can produce 100,000 seeds annually (Lin et al., 1958), and Sapium has been shown to establish a seed bank. Renne et al. (2001) found no difference in germination number or viability (of ungerminated seeds) between Sapium seeds buried for one or two years. In maritime evergreen forest, one of the habitats they studied, significantly more seeds germinated after the second year than after the first. In addition to the seed bank, Sapium readily resprouts vegetatively and can grow two meters in height in one season if stumps are not treated chemically (Jubinsky and Anderson, 1996; Grace, 1998). Consequently, effective restoration techniques have been elusive.

Land managers employ a variety of tools to control *Sapium*. Herbicides are applied to the bark of individual trees or are sprayed by airplane over extensive infestations, but the remaining trees (even if dead) prevent mowing, and rapid

regeneration occurs from seeds. Individual trees can be removed manually, but large-scale invasions require heavy equipment that can disturb the soil and damage the root structures of perennial vegetation. Historically, fire has been a successful woody-species management tool, but fire is only effective in the very early stages of *Sapium* invasion when the trees are less than two meters in height (Grace, 1998). It is generally recognized that various combinations of the above treatments are required for initial eradication and that subsequent management efforts must be continued long-term (Jubinsky and Anderson, 1996; Grace, 1998).

In this study, we examine a new management technique to eliminate *Sapium* trees and rapidly return invaded grasslands to a condition in which native vegetation can be restored. Furthermore, we investigate the mechanisms that may underlie the success of this technique in inhibiting germination or seedling establishment and growth.

Background

Armand Bayou Nature Center (ABNC hereinafter) is a non-profit nature center established in 1974, located 43 km southeast of Houston, Texas. Part of its mission is to protect, restore, and manage nearly 1000 ha of native habitat, including mixed hardwood forest, estuarine bayous, wetlands, and coastal tallgrass prairie. *Sapium* has invaded much of the native prairie in the absence of a control program.

In one attempt to restore part of its invaded prairie, ABNC used a combination of chemical and mechanical treatments, with aerial application of herbicide (Grazon P+D at 9.36 liters per ha) to 45 ha of closed canopy *Sapium* forest in August, 1997 and August, 1998. The apparent kill rate was substantial. The chemically treated *Sapium* trees were left standing in a five ha patch. The standing trees on 40 ha were subsequently mulched

(described in detail in the Methods section) in the summer of 2000, and the mulch was left on the ground. The mulch varied in depth up to 10-15 centimeters deep in some places (personal observation).

Informal observation revealed that the subsequent development of the unmulched and mulched areas was dramatically different. By summer 2002, *Sapium* seedlings were very dense in the unmulched area, and some of the treated trees were flowering. In contrast, native vegetation substantially covered the mulched area, *Sapium* seedlings were very few in numbers, and biomass accumulation was adequate to fuel a successful prairie burn the following winter.

The success of this restoration project contrasts with the poor results often obtained in efforts to remove *Sapium* (Jubinsky and Anderson, 1996). Therefore, understanding the mechanisms responsible for its success may improve our ability to control *Sapium* invasion along the Gulf Coast and might yield important clues for successful restoration of other habitats invaded by woody species.

Hypotheses

In this study, we investigated three mechanisms that might underlie the successful suppression of *Sapium* seedling emergence from the seed bank at ABNC—a temperature hypothesis, a seedling mortality hypothesis, and an allelopathy hypothesis.

Mulch might create temperatures incompatible with *Sapium* seed germination requirements ("temperature hypothesis"). Pioneer species such as *Sapium* are commonly dependent on diurnally fluctuating temperatures for germination. Fluctuating temperatures can signal vegetation gaps or shallow seed burial depth often critical for the establishment of colonizing species (Thompson and Grime, 1983; Fenner, 1985; Baskin

and Baskin, 1989; Ghersa et al., 1992). A mulch layer on the ground might suppress the germination of *Sapium* seeds by damping diurnal soil temperature fluctuations. To test the temperature hypothesis, we manipulated *Sapium* mulch depths in a prairie restoration site on which live *Sapium* trees had been mulched by a shredding mower, measured soil temperatures beneath the mulch layers, and collected data on naturally occurring and planted seedlings. We examined whether mulch layers reduce diurnal fluctuations in surface soil temperature and whether such a temperature effect suppresses *Sapium* seed germination and subsequent seedling emergence. According to this hypothesis, we expected plots with mulch to have fewer emerging *Sapium* seedlings than plots with the mulch removed, and we expected thicker *Sapium* mulch layers to progressively suppress germination and emergence. Because the temperature hypothesis targets germination, we predicted subsequent seedling performance would be comparable across mulch treatments.

The low abundance of *Sapium* seedlings in mulched areas may be the result of high mortality of seedlings during or after emergence from the mulch layer ("mortality hypothesis"). Seeds of various species have been shown to germinate, but then fail to emerge from below excessive soil depths (Fenner, 1985). Cool, damp soils can favor fungal pathogens that attack newly emergent seedlings in a process called damping-off. To test the mortality hypothesis, we planted *Sapium* seedlings into plots with different mulch treatments in the prairie restoration site and collected data on the added seedlings and naturally occurring seedlings. According to this hypothesis, we predicted that germination and emergence would not be affected by mulch treatments, but that survival

of seedlings would diminish with increasing mulch depth if mulch has an effect only on seedling performance.

Chemical compounds in Sapium mulch may limit germination and/or seedling survival ("allelopathy hypothesis") separately from the simple physical effects of mulch. Some plants produce compounds that inhibit growth of neighboring plants and reduce competition for resources in their immediate area. Sometimes these allelopathic compounds target different species (Hejl et al., 1993; Jose and Gillespie, 1998), but they may also prevent crowding among neighbors of the same species (Mahall and Callaway, 1992; Inderjit and Callaway, 2003). Results from previous studies of Sapium allelopathy have been mixed. Gresham and Edwards (1995) found that Sapium reduced Pinus taeda germination and seedling growth. However, other studies found that water extracts of Sapium litter improved the performance of the native grass Schizachyrium scoparium (Keay et al., 2000) and that of Sapium and Taxodium distichum (Conway et al., 2002) but had no effect on Salix nigra (Conway et al., 2002). To test the allelopathy hypothesis, we replaced the Sapium mulch with hardwood mulch and wheat straw in the prairie restoration site. According to the allelopathy hypothesis, we predicted that Sapiummulched plots would have fewer emerging seedlings than the plots with hardwood or wheat straw mulch, and that seedlings in Sapium mulch plots would have lower survivorship than those planted in alternative mulch plots.

Methods

Study site

The study site is on the eastern side of Taylor Bayou within ABNC. Average annual rainfall is 1450 mm distributed fairly evenly throughout the year (National Weather Station [NWS] station 410257). Soils are Midland silty clay loam, nearly level, poorly drained, and acidic. Surface runoff and permeability are both very low, with high available water capacity (Anonymous, 1976). On September 3, 2003, after approximately 10 cm of rain, water depths up to 14 cm were measured in experimental plots.

Historically, the area was tallgrass prairie, but it has become heavily invaded by Sapium. Within the experimental area, average Sapium density prior to stand removal ranged from 0.20 trees/m² in the east to 2.18 trees/m² in the west, as measured by the point-quarter technique. However, basal area of individual trees decreased from east to west, from an average of 972 cm² in the east block to 50 cm² in the west block. The percentage of the canopy that was open averaged 18.78% (range 14.23%-31.19%), as analyzed with Gap Light Analyzer (Version 2.0, Institute of Ecosystem Studies, Millbrook, New York, USA) with photos taken with a Nikon Coolpix 900 digital camera (Nikon, Tokyo, Japan) and FC-E8 fisheye lens. Under the Sapium canopy, wetland species such as Rynchospora spp. dominated the herbaceous vegetation. Dicanthelium oligosanthes Shult., Muhlenbergia capillaris (Lam.) Trin., Axonopus affinis Chase, Croton capitatus Michx., Rubus spp., and Myrica cerifera L. were present, as well as climax prairie grass species such as Schizachyrium scoparium (Michx.) Nash, Paspalum plicatulum Michx., and Panicum virgatum L.

During the last week of September 2002, slightly less than one ha of *Sapium* forest was mulched by a machine commonly called a "seppi." Specifically, it is a Kershaw 1200 with a Bullhog 120 shredding mower, a four-wheel drive articulating machine driven by a 225 HP engine, riding on high flotation rubber tires. The seppi can shred trees up to 50 cm in diameter to within 5 cm of the ground surface (Ecological Stability, Inc., Seabrook, Texas), discharging the mulch under the machine. Stumps were individually treated with herbicide (Garlon 4 from Dow Chemical mixed with a JBL oil surfactant) to reduce resprouting.

Experimental design

Because of observed differences in *Sapium* density across the experimental area, we used a randomized block design with three blocks. Each block consisted of eighty 1 m x 1 m plots with 1 m alleys. Within each block, plots were randomly assigned one of six mulch treatments: 0, 5, 10, or 15 cm *Sapium* mulch; 5 cm hardwood mulch; or 6 cm straw mulch. For the 0 cm *Sapium* mulch treatment, we removed the *Sapium* mulch by hand so that bare soil was exposed. *Sapium* mulch layers of 5 cm were used to evaluate the potential effectiveness of the expected average depth of mulch to be obtained at this particular site based on previous observations. The 10 and 15 cm *Sapium* mulch layers represented two additional depths that can reasonably be expected from mulching a dense stand of *Sapium*. In the hardwood mulch treatment, the existing *Sapium* mulch was removed and replaced with a 5 cm layer of hardwood mulch (commercial bag of 2 cubic feet). Although this 5 cm depth was similar in maximum depth to the 5 cm layer of *Sapium*, its mass and ground coverage was more similar to the 10 cm *Sapium* layer because of the uniform texture of commercial mulch. Therefore, the 10 cm *Sapium*

mulch depth was used for comparison to the alternative mulch treatments in the allelopathy tests. For the straw mulch treatment, the existing *Sapium* mulch was removed and replaced with a layer of wheat straw 6 cm thick, or an average of 1850 grams (three "pats" of a commercial square bale of straw). The straw was anchored into place with long staples. Heavy rains and surface water flow in September and October 2003 moved mulch from some plots, but it was replaced in November when the water receded.

The 8 x 10 design, with 80 plots per block, was not evenly divisible by the six treatments so treatments were not equally represented. Since the 5 cm *Sapium* mulch layer was the anticipated naturally occurring depth, we chose that treatment for additional replication. Therefore, there were 12 plots per block for five treatments (total of 36 each) and 20 plots per block for the 5 cm *Sapium* mulch treatment (total of 60).

HOBO Outdoor/Industrial 4-Channel External thermocoupler units (Onset Computer Corporation, Pocasset, Massachusetts) were used to compare diurnal soil temperature fluctuations among the mulch treatments. Probes were inserted into the soil in the center of a plot until the upper end of the metal probe was level with the soil surface. Since each thermocoupler unit only had four probes but each block had six mulch treatments, two units were placed in each block and the randomization of probe placement among mulch treatments was done across all three blocks. Therefore, temperature was recorded in four plots of each mulch treatment (for a total of 24 measurements) but not an equal number per treatment in each block. Temperatures were recorded once every 30 min from mid-February until the end of August.

Seedling addition

In November and December 2002, we collected seed from *Sapium* trees at Taylor Bayou and other locations in Galveston County. In late February 2003, seeds were planted into flats of commercial topsoil in an unheated greenhouse with open vent flaps. Seeds began to germinate in March, approximately the same time they began to germinate in the field. As soon as a seed germinated, it was transferred to a 115-ml Conetainer (Stuewe and Son, Corvallis, Oregon) filled with soil from the Taylor Bayou site. The Conetainers were placed in racks that were then placed in bins filled with water to slightly above the drain holes. Seedlings were grown in the greenhouse until they had secondary leaves, then grown outside under a 50% shade cloth so they could "harden off."

The assignment of mulch treatments was separately randomized in the last four rows of each block; therefore, all six mulch treatments were uniformly represented in this section of the total block. One seedling per plot was planted in these southernmost four rows of each block, for a total of 96 seedlings (4 rows x 8 columns per block x 3 blocks).

Seedlings were transplanted into the field May 14. The soil core containing a seedling was placed in a hole the size of the core in the center of each plot from which mulch had been moved aside. Planting did not otherwise disrupt soil structure or roots. We measured the height (mean 112 mm, range 83-161 mm) and number of leaves (mean 5.4, range 4-8) on each seedling at the time of planting. Since this was during a record dry, hot period, we watered the seedlings with one liter of water at the time of planting and every three to four days thereafter until June 2, when it began to rain regularly.

Seedlings that died within the first two weeks were presumed to have died from transplant shock and were replaced. Nine were replaced on May 21. No additional replacements were made. The displaced mulch material was redistributed around the seedlings once it was determined they had survived transplanting.

Data collection and analysis

Sapium seedlings were first noted in the field on March 19. Approximately every two weeks through September 19, we counted all Sapium seedlings within a half-meter area in the center of each plot. Once a month, we measured the heights of the Sapium seedlings. On June 13, if more than 10 seedlings were in a plot, 10 were haphazardly selected and permanently marked with colored paper clips. Thereafter, a maximum of 10 seedling heights was measured in each plot. In total, seedlings were counted 13 times and measured six times. Vegetation cover was estimated once a month as the percentage of the half-meter area covered by vegetation other than Sapium. We evaluated survival of planted seedlings 98 days after the initial planting.

The full-interaction ANOVAs described below include mulch treatment, block, and seedling addition as factors. The seedling addition factor includes the effects of the location of these plots in the southern end of each block, the effects of mulch disturbance when the seedling was planted, and the effects of supplemental watering after the seedling was planted.

We used a full-interaction ANOVA to test whether seedling emergence (cumulative emergent seedlings in plots over the term of the experiment) or number of seedlings alive at the end of the growing season (final count) differed among bare soil and the three different depths of *Sapium* mulch (0 cm mulch and 5, 10, and 15 cm *Sapium*

mulch). We used a separate ANOVA to test whether seedling emergence and final count varied among the 10 cm *Sapium* mulch layer and the alternative hardwood or straw mulch. Seedling counts were square root transformed to achieve normality and backtransformed for graphical presentation. Fisher's PLSD revealed significant differences among categories within individual factors.

The survival percentage of naturally occurring seedlings was calculated by dividing final count of seedlings by cumulative emergence. A full-interaction ANOVA was used to test the effects of *Sapium* mulch treatment (0, 5, 10, and 15 cm *Sapium* mulch), block, and seedling addition on the survival of naturally occurring seedlings. A separate ANOVA was used to test whether survival varied among the 10 cm *Sapium* mulch layer and the alternative hardwood or straw mulch.

We tested the effects of *Sapium* mulch treatment (0, 5, 10, and 15 cm *Sapium* mulch), block, and seedling addition on the average heights of seedlings measured in each plot with a full-interaction ANOVA. Heights were log-transformed to achieve normality. We used another full-interaction ANOVA to determine if average seedling height varied among the 10 cm *Sapium* mulch depth and the two alternative mulch treatments.

Vegetation cover was square root transformed to achieve normality and was evaluated with a full-interaction ANOVA for dependence on *Sapium* mulch treatment (0, 5, 10, and 15 cm *Sapium* mulch), block, and seedling addition.

Separate correlation Z tests were used to determine if final seedling count or average heights were correlated with vegetation cover. Regression was then used to determine the relationship between average seedling height and vegetation cover.

Effects of initial height, *Sapium* mulch treatment, and alternative mulch treatment on added seedling survival were evaluated with separate logistic regressions. As a post hoc test, we used logistic regression to test the effects of only 0, 5, and 10 cm *Sapium* mulch on added seedling survival (eliminating the 15 cm *Sapium* mulch depth).

All statistical tests were performed with Statview 5.0 (SAS Institute Inc., Cary, NC, USA)

Results

Seedling emergence (cumulative emergent seedlings in plots over the term of the experiment) depended significantly on *Sapium* mulch treatment (0 cm > 5 cm > 10 cm \ge 15 cm), block (east > west only), seedling addition (yes > no), and the interactions of all of these variables (Table 2.1, Table 2.2, Fig. 2.1). Results were similar for final seedling counts. The significant mulch \times block interaction reflects a high number of seedlings in the 0 cm mulch in the east block. The mulch \times seedling term results from the large impact on seedling emergence in 0 cm mulch plots that received an added seedling. A large positive effect of seedling addition in plots in the drier east block, especially in the 0 cm mulch plots, likely contributed to the significance of the block \times seedling as well as the third level interaction terms.

The pattern of highest seeding emergence in 0 cm to lowest in 10 and 15 cm

Sapium mulch (Fig. 2.1) matches the pattern of the greatest diurnal temperature

fluctuations under 0 cm mulch to lowest under 10 and 15 cm mulch in the field (Fig. 2.2).

There was no difference in seedling emergence among 10 cm *Sapium* mulch and alternative mulch treatments (Table 2.3). Results for final seedling counts were similar.

Sapium mulch treatment had a significant effect on the survival of naturally occurring seedlings (Fig. 2.3, $F_{3,118} = 9.9$, P < 0.0001). Survival was significantly higher in 5 cm of mulch than in 0 cm (P < 0.05). Survival in the 10 cm mulch did not differ from that in 5 cm (P = 0.40) nor 0 cm (P = 0.26). Survival was significantly lower in 15 cm of mulch compared to all other depths (highest P < 0.01). There was no difference in survival of naturally occurring seedlings among 10 cm Sapium and alternative mulches ($F_{2.68} = 0.5$, P = 0.60).

No difference in final seedling height was found among *Sapium* mulch depths (0, 5, 10, and 15 cm, $F_{3,107} = 1.0$, P = 0.41) nor among the alternative mulch treatments (10 cm *Sapium*, hardwood, and straw, $F_{2,63} = 2.1$, P = 0.13). Seedlings in the west block were shorter than in the other blocks among the *Sapium* mulch depths ($F_{2,107} = 5.2$, P < 0.01).

Table 2.1. The effect of mulch treatment (Trmt), block (Blk), and seedling addition (Sdlg) on cumulative seedling emergence. "Seedling addition" factor includes location in the southern end of the blocks, disturbance of the mulch layer at planting time, and supplemental watering. Values are from full-interaction ANOVA on *Sapium* mulch treatments (0, 5, 10, and 15 cm) only. (Overall model $F_{23,144} = 7.2$, P < 0.0001, $r^2 = 0.53$)

Factor	df	SS	F-Value	P-Value
Trmt	3	160.4	20.2	< 0.0001
Blk	2	35.8	6.8	< 0.01
Sdlg	1	15.2	5.7	< 0.05
Trmt * Blk	6	82.3	5.2	< 0.0001
Trmt * Sdlg	3	24.2	3.0	< 0.05
Blk * Sdlg	2	36.8	6.9	< 0.01
Trmt * Blk * Sdlg	6	83.5	5.3	< 0.0001
Residual	144	381.8		

Table 2.2. Means table for all mulch treatments (0, 5, 10, and 15 cm *Sapium*, HW = hardwood, ST = straw) by block (E = east, M = middle, W = west) and whether or not an added seedling was planted in the plot. Means are the square root transformed means of cumulative seedling emergence or final seedling count per plot. "Added seedling" factor includes location in the southern end of the blocks, disturbance of the mulch layer at planting time, and supplemental watering.

		Mean ± 1 SE					
		Square 1	oot emergence	Square root	Square root final sdlg count		
Mulch	Block	No Sdlg	Added Sdlg	No Sdlg	Added Sdlg		
0 cm	E	3.0 ± 0.3	9.7 ± 2.0	2.4 ± 0.3	8.6 ± 1.9		
0 cm	M	2.2 ± 0.7	2.6 ± 1.2	1.7 ± 0.6	2.3 ± 1.0		
0 cm	W	3.7 ± 1.1	2.4 ± 0.3	2.9 ± 1.0	1.8 ± 0.3		
5 cm	E	2.9 ± 0.4	3.3 ± 0.5	2.5 ± 0.4	3.1 ± 0.4		
5 cm	M	3.2 ± 0.5	2.9 ± 0.6	2.6 ± 0.5	2.6 ± 0.6		
5 cm	W	2.4 ± 0.3	2.2 ± 0.4	2.2 ± 0.3	1.9 ± 0.3		
10 cm	E	1.3 ± 0.4	1.6 ± 0.6	1.1 ± 0.3	1.5 ± 0.6		
10 cm	M	2.1 ± 0.5	1.5 ± 0.2	1.8 ± 0.5	1.3 ± 0.2		
10 cm	W	0.5 ± 0.2	2.5 ± 0.9	0.3 ± 0.2	2.0 ± 1.0		
15 cm	E	1.0 ± 0.3	1.6 ± 0.5	0.5 ± 0.2	1.1 ± 0.5		
15 cm	M	1.6 ± 0.6	1.3 ± 0.1	1.2 ± 0.4	0.7 ± 0.3		
15 cm	W	1.0 ± 0.4	0.8 ± 0.4	0.7 ± 0.3	0.5 ± 0.3		
HW	E	1.4 ± 0.4	2.2 ± 0.9	1.3 ± 0.3	1.9 ± 0.9		
HW	M	2.3 ± 0.6	2.7 ± 0.6	1.9 ± 0.6	2.5 ± 0.5		
HW	W	2.2 ± 0.5	2.3 ± 0.4	2.0 ± 0.5	2.0 ± 0.4		
ST	E	1.3 ± 0.7	1.7 ± 0.5	1.2 ± 0.6	1.3 ± 0.5		
ST	M	2.6 ± 0.7	1.6 ± 0.6	2.1 ± 0.5	1.5 ± 0.6		
ST	W	0.8 ± 0.3	1.6 ± 0.4	0.7 ± 0.3	1.2 ± 0.3		

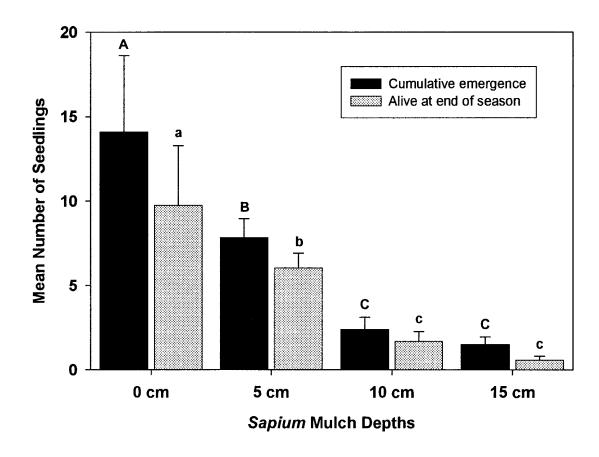


Fig. 2.1. The effect of *Sapium* mulch depth on the cumulative count of new seedlings in a plot (emergence) and on the number of seedlings alive at the end of the growing season. Error bars indicate + 1 SE. Different letters indicate means that were significantly different in Fisher's PLSD means contrasts for emergence (capital letters) or seedlings alive at the end of the season (lower case letters).

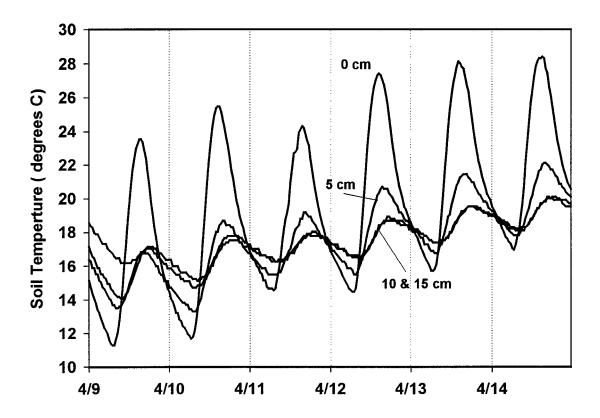


Fig. 2.2. Diurnal soil temperature fluctuations in the field for different depths of *Sapium* mulch for six days in April. *Sapium* mulch depths are indicated on the graphs.

Table 2.3. The effect of mulch treatment (Trmt), block (Blk), and seedling addition (Sdlg) on cumulative seedling emergence. "Seedling addition" factor includes location in the southern end of the blocks, disturbance of the mulch layer at planting time, and supplemental watering. Values are from full-interaction ANOVA on 10 cm *Sapium* mulch, hardwood mulch, and straw mulch treatments only. (Overall model $F_{17,90} = 1.3$, P = 0.22, $r^2 = 0.20$)

Factor	df	SS	F-Value	P-Value
Trmt	2	8.8	2.5	0.09
Blk	2	6.3	1.8	0.18
Sdlg	1	3.1	1.8	0.19
Trmt * Blk	4	2.1	0.3	0.88
Trmt * Sdlg	2	1.1	0.3	0.73
Blk * Sdlg	2	9.2	2.6	0.08
Trmt * Blk * Sdlg	4	8.0	1.1	0.35
Residual	90	158.7		

Sapium mulch depth significantly affected vegetation cover (Fig. 2.4, $F_{3,144}$ = 46.7, P < 0.0001) with vegetation cover in 0 cm > 5 cm > 10 cm ≥ 15 cm. Vegetation cover was reduced by seedling addition ($F_{1,144}$ = 6.2, P < 0.05). There was no correlation between final vegetation cover and final seedling count in the Sapium mulch plots (P = 0.11). Sapium seedling height was positively correlated with vegetation cover in the Sapium mulch treatment (0, 5, 10, 15 cm mulch) plots ($R^2 = 0.03$, P < 0.05).

The probability of an added seedling's survival was not dependent on its initial height when planted ($\chi^2 = 0.5$, 1 d.f., P = 0.47), but survival was affected by *Sapium* mulch depth. The odds of survival were lower at greater mulch depths (Fig. 2.5, $\chi^2 = 9.5$, 3 d.f., P < 0.05); however, there was no effect of *Sapium* mulch treatment when the 15 cm *Sapium* mulch depth was not included ($\chi^2 = 0.4$, 2 d.f., P = 0.83). Survival of added seedlings did not vary among 10 cm *Sapium* mulch and the alternative mulch treatments ($\chi^2 = 0.5$, 2 d.f., P = 0.77).

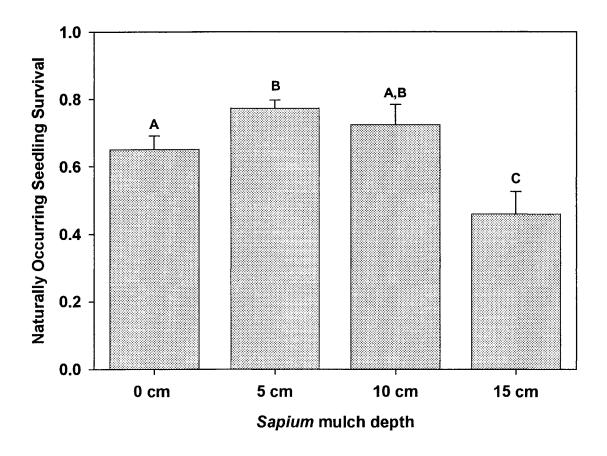


Fig. 2.3. The effect of *Sapium* mulch on survival of naturally occurring seedlings. Survival was calculated as the proportion of seedlings alive at the end of the growing season in relation to the cumulative emergence of new seedlings per plot. Error bars indicate + 1 SE. Different letters indicate means that were significantly different in Fisher's PLSD means contrasts.

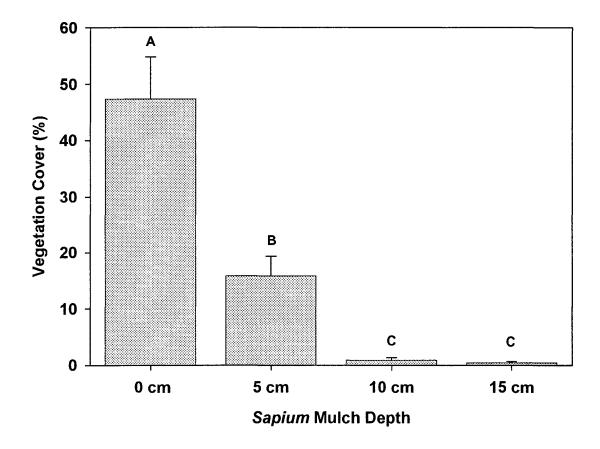


Fig. 2.4. Mean vegetation cover per plot at the end of the growing season for each depth of *Sapium* mulch. Vegetation cover was estimated as the percentage of area covered by vegetation other than *Sapium*. Error bars indicate + 1 SE. Different letters indicate means that were significantly different in Fisher's PLSD means contrasts.

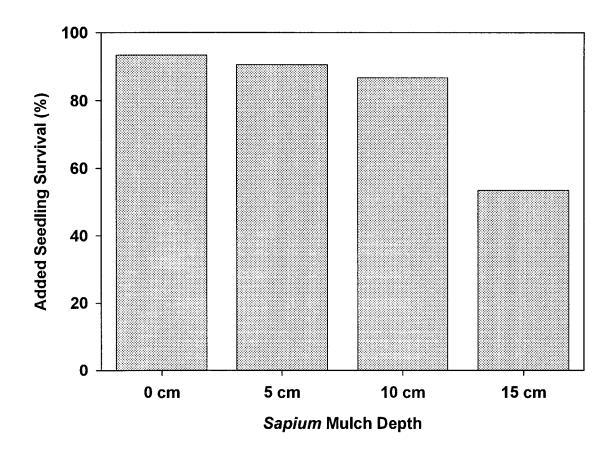


Fig. 2.5. Percentage of added seedlings alive at 98 days in relation to the number planted for each *Sapium* mulch treatment.

Discussion

Mulch effects

As little as 5 cm of *Sapium* mulch reduced *Sapium* seedling emergence compared to bare soil (Fig. 2.1). Increasing the mulch depth to 10 cm further decreased emergence, but suppression leveled off at that depth. Deeper mulch layers also suppressed native vegetation (Fig. 2.4), and the seedling mortality effects were stronger in deep mulch (Figs. 2.3, 2.5). There was no evidence for allelopathy of *Sapium* mulch on seedling emergence or seedling survival.

Sapium mulch likely suppresses Sapium seedling emergence because of temperature effects on germination. Mulch depths of 5 and 10 cm progressively damped soil surface temperature fluctuations from those evident at 0 cm mulch (Fig. 2.2), and the same pattern was seen in seedling emergence (Fig. 2.1). Neither soil temperature fluctuations nor seedling emergence differed between 10 and 15 cm of mulch (Fig. 2.1, 2.2). These results support the temperature hypothesis: Mulch layers reduced diurnal fluctuations in soil temperature, and seedling emergence was lower as mulch depth increased, until mulch depth no longer affected soil temperature fluctuations.

Consequently, the prediction of the mortality hypothesis that germination would not be affected was not supported.

Mulch depth alone is known to reduce seedling emergence. Fenner (1985) investigated the germination and emergence of two weed species sown at various depths. He found that germination declined at considerable depths, but 13% of one species and 40% of the other did germinate but were unable to emerge through the soil. To separate indirect temperature effects from possible direct effects of mulch depth on seedling

emergence, we performed a separate lab experiment in which we held soil temperature treatments constant while varying the depth of *Sapium* mulch (Chapter 3). We found seedling emergence was significantly higher among mulch treatments with high diurnal temperature fluctuations compared to mulch treatments at constant temperatures or low temperature fluctuations. However, there were no consistent differences in seedling emergence among various mulch depths within the same temperature treatment. The similar seedling emergence results in this field experiment for 10 cm and the deeper 15 cm layers of mulch, both of which had similar temperature fluctuations, support these findings.

The effects of mulch varied between naturally occurring seedlings and planted seedlings, but deep mulch decreased seedling survival in both groups (Figs. 2.3, 2.5).

Some mulch (5 cm) increased seedling survival among naturally planted seedlings (Fig. 2.3) possibly because it reduced the effects of summer drought. This pattern was probably not seen among planted seedlings because they were watered. Mulch did not affect seedling height. Therefore, neither the prediction of the temperature hypothesis that seedling performance would be comparable across mulch treatments nor the prediction of the mortality hypothesis that survival of seedlings would diminish with increasing mulch depth was strongly supported.

The poor survival of planted seedlings in the 15 cm *Sapium* mulch was likely because the 15 cm depth completely covered the seedling (average seedling height at planting was 112 mm) after it had invested significant seed resource reserves in production of true leaves. *Sapium* has a relatively large seed, especially compared to native pioneer tree species (Bonner, 1989a, b, c), and larger seeds have been shown to

increase seedling establishment in many environments (Dzwonko and Gawronski, 2002; Christie and Armesto, 2003; Grundy et al., 2003). In our lab experiment (Chapter 3) seedlings in the cotyledon stage emerged through 10 cm of mulch on long thin stems, possibly with adequate resource reserves to put on true leaves. However, the seedlings planted in this experiment had already invested seed energy reserves in true leaves before burial in the mulch. Mortality in the 15 cm mulch depth likely resulted from inability to photosynthesize and generate additional resources adequate to increase stem length above the mulch cover.

There was no difference in seedling emergence (Table 2.3) or seedling survival among *Sapium* and alternative mulch plots, and seedling height was also unaffected by *Sapium* mulch. These results indicate absence of allelopathic effects of *Sapium* mulch on *Sapium* seeds or seedlings. One study has shown negative effects of *Sapium*, and this was on a native tree species (Gresham and Edwards, 1995). Some studies have found positive effects of *Sapium* litter extracts on growth of other tree species (Conway et al., 2002) and a native grass (Keay et al., 2000). Our results differed from those of Conway et al. (2002), who found *Sapium* extracts facilitated its own germination and enhanced seedling size and mass. Possible explanations for the difference are that compounds did not leach from the mulch layers into the soil, mulch (all parts of the tree) does not contain the concentration of compounds found in the litter or fresh leaves used in the Conway et al. (2002) study, and field results may differ from lab results.

Environmental effects

Environmental factors influenced the effects of the mulch treatments. There was a gradient from larger, more mature trees in the east block to smaller trees in the west

block prior to treatment. This might have resulted in a larger seed bank in the east block, which would result in more germinating seedlings, especially in the bare soil plots where no suppression occurred. Suppression effects of mulch were the most pronounced in the east block. Because the land sloped westward toward Taylor Bayou, a moisture gradient existed from west to east in our blocks. Continued presence of standing water on the west block in the spring may have contributed to later germination of seedlings in that block and the resultant shorter height of the naturally occurring seedlings at the end of the experiment. The early part of the summer of 2003, when the added seedlings were planted and watered, was a hot dry period; the recorded rainfall for Feb-May was 62% below average (National Weather Station [NWS] station 410257). Supplemental watering did not increase seedling emergence or final seedling count in the wetter west block but did increase seedling emergence and final seedling count in the other two drier blocks, especially in 0 cm mulch, where the effects of the drought would be expected to be strongest.

Vegetation cover

Deep mulch suppressed native vegetation (Fig. 2.4), limiting its possible interference with *Sapium* seedling success. Many experiments have demonstrated negative effects of herbaceous vegetation on the establishment and growth of tree seedlings (Zutter et al., 1986; De Steven, 1991). Seedlings compete for light, soil moisture, and nutrients, but seedlings of larger-seeded species, such as *Sapium*, are generally more successful at surviving in such competitive conditions (Burke and Grime, 1996; Jakobsson and Eriksson, 2000; Coomes and Grubb, 2003; Rogers and Siemann, 2003). This is usually explained by a larger reserve of seed resources to allocate to

survival after the commitment to seedling structure (Westoby et al., 1996). Sapium's large seed size probably contributed to the lack of a negative correlation between vegetation cover and final seedling count in the experimental plots. Additionally, vegetation cover was minimal in early spring when seedlings began to emerge and did not reach significant coverage until June, about the time maximum seedling counts had already been reached.

Vegetation cover did not decrease average *Sapium* seedling height, possibly for two reasons. First, the rapid decomposition of *Sapium* leaves is known to increase nitrogen concentrations in the soil (Cameron and Spencer, 1989), and Siemann and Rogers (2003) demonstrated that nitrogen additions to plots of *Sapium* seedlings in prairie vegetation increased *Sapium* growth without affecting the growth of the native vegetation. Therefore, the recent presence of a *Sapium* forest on the experimental site would be expected to have elevated nitrogen concentrations in the soil and favor the *Sapium* seedlings over the background vegetation. Second, competition for light would be expected to stimulate a plant to grow taller, and *Sapium* height growth rate has been shown to increase in shade compared to ambient sunlight (Rogers and Siemann, 2002).

Conclusions and implications

This experiment demonstrated that mulching live *Sapium* trees in an invaded prairie can be a rapid restoration technique. The forest stand in this experiment was not as dense as the one originally successfully restored at ABNC. However, the average mulch depth throughout this restoration site was approximately 5 cm (personal observation), and this depth was sufficient to significantly reduce the number of *Sapium*

seedlings emerging in the experimental plots. This would suggest that success of this technique is not limited to mature, closed-canopy *Sapium* forests but is also effective in earlier stages of invasion. Adequate mulch material was obtained from this stand to significantly suppress seedling emergence, while allowing for substantial return of native vegetation within one growing season.

Modern native prairie management involves mimicking the historic forces of grazing and fire that shaped prairies over time (Singh and Joshi, 1979; Axelrod, 1985; Smeins et al., 1992). Mowing often replaces grazing, and this technique facilitates mowing by removing all of the *Sapium* present, including the stumps. A successful prairie burn depends on adequate fine fuels to carry the fire, and the mulching technique allowed rapid regeneration of these fuels at this site. The final heights of the *Sapium* seedlings that did emerge in the experimental plots are below that which fire has been shown to kill (Grace, 1998). Mowing and fire can now be used to manage this prairie site.

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Chapter 3

Effects of Temperature and Mulch Depth on Chinese Tallow Tree (Sapium sebiferum) Seed Germination

Abstract

Shredding mowers can be used in prairie and savannah restoration to quickly eliminate trees, such as the invasive Chinese tallow tree (Sapium sebiferum), and leave a layer of mulch on the ground. Sapium has shown highest germination rates in fluctuating daily temperatures, and mulch has been shown to damp those fluctuations in the field. A lab study was conducted to separate direct effects of mulch depth per se and indirect effects via changes in soil temperatures on Sapium seed germination. Sapium seeds were exposed to different combinations of mulch depth and temperature oscillations. Sapium seeds showed highest germination in large temperature oscillation treatments regardless of the depth of the mulch. Seedlings were able to emerge through mulch up to 10 cm deep, the maximum used in this study. While herbicide use appears to be necessary because of resprouting from stumps, this study indicates that mulching Sapium trees shows promise as a restoration tool by removing existing trees as well as by reducing Sapium regeneration from seed through the indirect effects of mulch on seed germination. The lower subsequent seedling numbers might reduce the frequency and intensity of future herbicide treatments.

Introduction

Native ecosystems are currently being invaded by exotic species that have the ability to dominate those ecosystems and alter their function in the landscape. The invasive Chinese tallow tree (Sapium sebiferum (L.) Roxb.), Euphorbiaceae, was introduced to the United States from Asia in 1772 and has spread across the southeastern states (Barrilleaux & Grace 2000; Bruce et al. 1997). Grasslands have always been subject to woody encroachment, but the great seed output, bird dispersal, rapid growth, and adaptation to wide environmental conditions of Sapium (Renne & Gauthreaux 2000; Rogers et al. 2000; Siemann and Rogers 2003a) have allowed it to become the most serious threat to endangered prairies along the upper coast of the Gulf of Mexico (Grace 1998). Once Sapium becomes established, it shades out the native herbaceous vegetation and forms a monospecific forest (Bruce et al. 1997; Siemann & Rogers 2003b). This also displaces native animal species, such as several federally endangered grassland birds (Herkert et al. 2003; Perkins et al. 2003). The loss of prairie bunchgrasses and rapid decomposition of Sapium litter (Cameron & Spencer 1989) leave the soil bare beneath the trees; such a condition may reduce bioremediation of anthropogenic pollutants and speed the flow of water and sediments to rivers (Fajardo et al. 2001; Harbor et al. 1995; Liaghat & Prasher 1996).

Sapium invasion is not limited to prairies. A 20-yr forest dynamic study (Harcombe et al. 1999) revealed that Sapium had increased dramatically in the Neches Bottom Unit of the Big Thicket National Preserve between 1981 and 1995. Among small saplings, Sapium growth was three times the median of all species studied during that period, and among large saplings, Sapium growth significantly exceeded that of all other

species. In another study of the area, Hall and Harcombe (1998) documented an interaction of shade tolerance and flood tolerance among the species present. For example, species often were found in higher light conditions than would be expected from their known tolerance for shade, apparently having to make environmental tradeoffs to survive both stresses of shade and flooding. Since *Sapium* is known to perform well in shade (Jones & McLeod 1989; Rogers 2002) and withstand flooding (Conner 1994; Grace 1998), it may become a serious threat to native tree species in the Big Thicket.

Effective control for *Sapium* has been elusive, and a great percentage of coastal prairie has been displaced by this exotic species. A promising new technique for prairie restoration uses shredding mowers to mulch stands of *Sapium*. This method employs a large shredding mower to chip entire trees at ground level. Herbicide is manually applied to the cut surface of the stumps to reduce resprouting. For restoration to be successful, *Sapium* regeneration needs to be controlled while simultaneously promoting native prairie plant regeneration. Mulch from *Sapium* trees may contribute to successful prairie restoration by limiting *Sapium* regeneration from seed. However, mulch depths necessary for suppression of *Sapium* seed germination and the mechanisms that contribute to suppression are not known.

Armand Bayou Nature Center, located 44 km southeast of Houston, Texas, has twice mulched *Sapium* trees on invaded prairie with a shredding mower, once in summer of 2000 and again in fall 2002/spring 2003. In the 2000 restoration, the stand was more mature and resulting mulch depths ranged up to 15 cm. In the younger stand mulched in 2002/2003, average mulch depths were approximately 5 cm. The subsequent emergence

of *Sapium* seedlings in the area mulched in 2000 appeared lower than in the area where *Sapium* trees were killed with herbicide and left standing (C. Donahue, personal observation).

The mulch layer might have reduced germination by limiting day/night variation in surface soil temperatures. Experimental studies have shown highly variable germination rates for *Sapium*, depending on the geographic source of the seeds (Cameron et al. 2000) and the germination protocols. Conway et al. (2000) only achieved 0-10% gemination on filter paper in petri dishes under an oscillating light and temperature regime, but Cameron et al. (2000) and Renne et al. (2001) achieved 26% and 22.5% gemination rates, respectively, for seeds planted in soil in greenhouses under natural temperatures and light. Seeds under these conditions would be expected to experience natural daily fluctuations in soil temperatures. In another study, highest germination rates were obtained for seeds planted in soil under experimentally controlled fluctuating daily temperatures (Nijjer et al. 2002).

The objective of this lab study was to separate direct effects of mulch *per se* and indirect effects *via* changes in soil temperatures on *Sapium* seed germination by maintaining constant temperature regimes under varying mulch depths. If direct effects of mulch on seed germination are the primary cause of lower germination rates, then germination should decrease as mulch depth increases for all temperature treatments. However, if indirect effects *via* changes in soil temperatures are more important, germination should be greatest in high oscillating temperatures regardless of the mulch depth.

Methods

Seeds of *Sapium* were collected from trees at the University of Houston Coastal Center in Galveston County, Texas, from August to September, 2002 and stored at room temperature. On July 16, 2003, 50 seeds were planted in each of 48 plastic bins (16 by 30 by 10 cm deep) on a 2.5 cm layer of commercially available topsoil and covered with another 2.5 cm layer of topsoil. Bins were randomly assigned to a temperature treatment (high oscillation, low oscillation, warm, and cool) and a mulch treatment (bare soil, 5 cm *Sapium* mulch, and 10 cm *Sapium* mulch) in a full-factorial design. Temperature treatments were chosen based on field soil temperatures measured during spring 2003 in the field that was mulched in late 2002 (Fig. 3.1). Bins were in a temperature controlled room (21° C) without windows or artificial light for the duration of the experiment. *Sapium* germination is independent of light conditions (Nijjer et al. 2002).

Electric roof de-icing cables (EASYHEAT, New Carlisle, IN) laid in the bottoms of the bins raised the soil temperatures. Cables passed once through low-oscillation bins and twice through high-oscillation and warm bins. Oscillation treatments were warmed for 16 hours and allowed to return to room temperature over eight hours. The high oscillation temperature maximum was 33° C, and the low oscillation temperature maximum was 27° C. The warm treatment was a constant 33° C, and the cool treatment was constant room temperature (21° C).

Fresh *Sapium* mulch was collected from a recently mulched *Sapium* restoration area at Armand Bayou Nature Center. Mulch was spread evenly across the soil in the 5 cm and 10 cm mulch treatment bins. Plastic baffles were used to support the mulch layer at the edges of the 10 cm treatment bins. Because the 0 cm and 5 cm mulch treatments lost more heat to the air than the 10 cm mulch treatment and did not maintain the desired

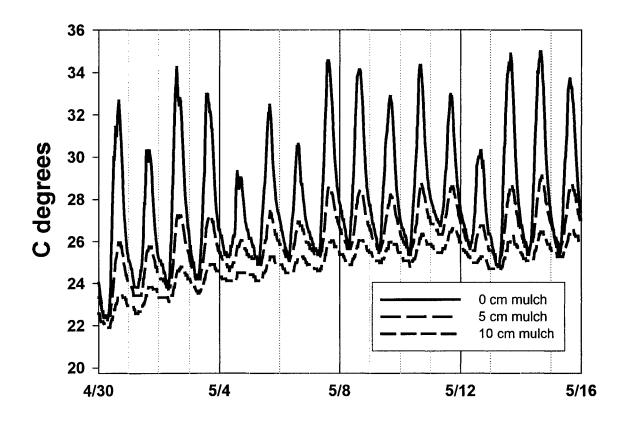


Figure 3.1. Sample of field soil temperatures recorded every 30 minutes, by mulch depth, in a field that had *Sapium* trees removed with a shredding mower in late 2002. Vertical bars indicate midnight on successive days.

soil temperatures, heavy-duty plastic sheeting was cut slightly larger than each bin and laid over the tops of the bins for these two treatments. The plastic was neither sealed to the bins nor in contact with the soil or mulch layers.

All treatments were thoroughly watered three times each week until water drained from the bins, and newly germinated seeds were counted and removed from the bins during these periods. The experiment was conducted for 125 days, but no seeds germinated after 110 days.

ANOVA was used to compare the different experimental treatments and Fisher's PLSD tests were used for post-hoc means contrasts (Statview 5.0, SAS Institute, 1998, Cary, North Carolina). Data were checked for normality and square root transformed to meet the assumptions of ANOVA. Data were back-transformed for presentation.

Results

Temperature treatment and mulch depth treatment, but not their interaction, had significant effects on seed germination; however, temperature alone explained 87% of the variation in germination (Table 3.1). All pairwise comparisons among temperature treatments were significantly different (*P* ranging from <0.0001 to 0.0152) with the greatest germination in the high oscillation (217 germinants from 600 seeds total) followed by low oscillation (34 germinants), warm (18 germinants) and cool (1 germinant) treatments (Fig. 3.2). The only significant difference among mulch treatments was the lower germination rate under 5 cm of mulch compared to bare soil (Fig. 3.2).

Table 3.1. Dependence of *Sapium* germination on experimental temperature and mulch depth treatments in an ANOVA.

Factor	df	SS	F-Value P -Value
Temperature	3	112.2	123.5 < .0001
Mulch Depth	2	2.0	3.4 0.05
Temp * Mulch	6	3.5	1.9 0.11
Error	36	10.9	

Discussion

Germination success for *Sapium* clearly depends on daily fluctuations in temperature, and the amplitude of the fluctuation is critical, as evidenced by the magnitude of the difference between germinants in the high-oscillation treatment and the low-oscillation treatment (Fig. 3.2). Pioneer species and wetland species commonly use diurnal temperature fluctuations as an indicator of canopy gaps (Fenner 1985; Baskin & Baskin 1989), proximity to the soil surface (Thompson & Grime 1983; Ghersa et al.

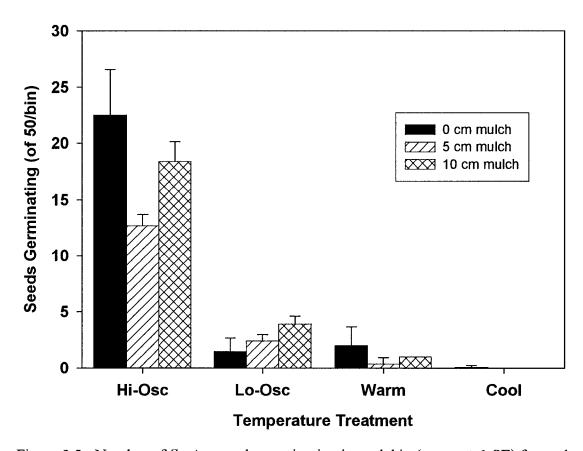


Figure 3.2. Number of *Sapium* seeds germinating in each bin (means + 1 SE) for each combination of temperature treatment (Hi-Osc = 21-33° C, Lo-Osc = 21-27° C, Warm = constant 33° C, Cool = constant ambient 21° C) and mulch depth (0 cm, 5 cm, 10 cm).

1992), or recession of standing water (Fenner 1985). These environmental conditions are often critical to subsequent seedling success (Thompson & Grime 1983; Fenner 1985; Vleeshouwers et al. 1995).

Several studies of invasive species have shown dependence on temperature fluctuations for successful germination (Ghersa et al. 1992; Lonsdale 1993; Young & Clements 2001). Also, several threatening invasives are woody invaders of wetland areas, including *Sapium* (Davis et al. 1946; Bruce et al. 1997), *Schinus terebenthifolius* Raddi, or Brazilian peppertree (Wheeler et al. 2001; Hight et al. 2003), and *Melaleuca quinquenervia* (Cav.) Blake, or punktree (Costello et al. 2003; Johnston et al. 2003). Mulching might be an effective control method for other invasive woody species as well.

Germination and emergence from under 10 cm of mulch was not significantly different from that from bare soil (P = 0.6575), and there was no consistent trend in germination rates as mulch depth increased. This supports a conclusion that the indirect effect of mulch on soil temperature oscillations is more important than mulch depth alone for *Sapium* seed germination. It is encouraging for the potential success of this restoration method that only 5 cm of mulch in the field was required to damp the soil temperature oscillations sufficiently (Fig. 3.1) to achieve the germination suppression evidenced by the low oscillation treatment in Figure 3.2.

The cotyledons of the seedlings in 10 cm of mulch were on long attenuated stems. The large *Sapium* seed (0.16 g/seed, Bonner 1989) apparently provides adequate resources for the seedling to emerge through deep mulch before reaching light where it can begin to photosynthesize. Several studies in different environments have shown a positive correlation between seed mass and ability for seedlings to become established

(Dzwonko & Gawronski 2002; Christie & Armesto 2003). When they modeled the emergence response of weed seeds to burial depth, Grundy et al. (2003) also found that some species had adequate reserves to emerge from a wider range of depths than might be expected in the field, as *Sapium* demonstrated in the present study. This may contribute to *Sapium*'s ability to invade and exploit many different environmental conditions.

To be useful, the mulching treatment should have minimal effects on native prairie species. Foster and Gross (1998) found that prairie forbs and the prairie grass, *Andropogon gerardi*, were able to establish a significant number of seedlings in intact plant litter, even though the densities in litter were significantly lower than where litter was removed. In multiple-site studies, Foster and Gross (1997) and Foster (1999) found that accumulated litter affected *Andropogon gerardi* seedling establishment in some sites but not in others. Also, when examining tallgrass prairie recolonization mechanisms after soil disturbance by pocket gophers, Rogers and Hartnett (2001) found that vegetative regrowth after burial under soil was the dominant recolonization mechanism. Therefore, possible mulch-induced seed germination suppression could be expected to have little impact on native vegetation. Finally, the high flotation rubber tires of the mulching equipment limit damage to the root structure of existing perennial vegetation.

Techniques for control of invasive vegetation include biological, herbicidal, mechanical, or some combination of these. While herbicide use appears to be necessary because of resprouting from stumps (Jubinsky & Anderson 1996), this study indicates that mulching live trees can be an effective initial mechanical treatment that reduces

subsequent seedling numbers, and thereby reduces the frequency and intensity of herbicide treatments.

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