

Restoring an Invaded Prairie by Mulching Live *Sapium* *sebiferum* (Chinese Tallow Trees): Effects of Mulch on *Sapium* Seed Germination

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Natural Areas Journal 26:244-253

ABSTRACT: The introduced *Sapium sebiferum* (Chinese tallow tree) has spread across the southeastern United States 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 two-year field experiment to evaluate the effectiveness of using large shredding mowers to mulch live *Sapium* trees and restore *Sapium*-invaded prairies. We predicted that *Sapium* mulch would damp diurnal soil temperature fluctuations and suppress *Sapium* seed germination because *Sapium* seed germination is highly dependent upon those fluctuations. We manipulated mulch depths and types (0, 10, and 15 cm deep *Sapium* mulch and hardwood and straw mulch) in the field and measured soil temperatures beneath them. Diurnal soil temperature fluctuations were damped at depths as little as 5 cm, and *Sapium* mulch significantly reduced *Sapium* seedling emergence. Deep layers of *Sapium* mulch (15 cm) reduced seedling survival and native vegetation cover as well. Comparisons among *Sapium* mulch and alternative mulch materials revealed no 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 first growing season. With no trees or stumps remaining on the site, a mowing regime can be implemented immediately regardless of the pre-mulching density of the trees. A heavy closed-canopy *Sapium* forest might result in mulch depths that slow the return of native vegetation and delay accumulation of adequate fuel loads to support prescribed burning.

Index terms: Chinese tallow, invasive species, prairie restoration, *Sapium sebiferum*

INTRODUCTION

The coastal prairie region is located along the northwestern coast of the Gulf of Mexico, extending from southwestern Louisiana to southern Texas. The range of ecological conditions in the region can support great native biodiversity. More than 70 species of vascular plants may be found in a hectare of prairie, and 350 to 400 species of migratory birds utilize coastal prairie (Smeins et al. 1992). Although it once covered 38,000 km², current estimates indicate that less than 1% now remains (Grace et al. 2001). Currently, monospecific *Sapium sebiferum* forests are rapidly replacing this diverse prairie.

The introduced *Sapium sebiferum* (L.) Roxb. (synonyms include *Triadica sebifera*, "*Sapium*" hereafter; nomenclature follows Hatch et al. 1990) (Chinese tallow tree) naturalized across the southeastern United States after its introduction on the East Coast in 1772 (Bruce et al. 1997). *Sapium* has rapid growth (Bruce et al. 1997), is tolerant of both flooding and drought (Conner 1994, Butterfield et al. 2004), and outperforms native species in both full sun and shade (Jones and McLeod 1989, Rogers and Siemann 2002, Siemann and Rogers 2003). These characteristics have contributed to *Sapium*'s displacement of native species throughout the coastal prairie, converting open grasslands to closed canopy forests in as little as 20

years (Bruce et al. 1995).

Once *Sapium* becomes established, it is very difficult to eradicate. Mature trees can produce 100,000 seeds annually (Lin et al. 1958) that persist in a seed bank (Renne et al. 2001). In addition, *Sapium* readily resprouts vegetatively; and, if stumps are not treated chemically, can grow two meters in height in one season. Consequently, effective restoration techniques have been elusive.

Land managers employ a variety of tools against *Sapium*. Herbicides are applied to individual trees or sprayed by airplane over extensive infestations, but the remaining trees (even if dead) hinder mowing, and rapid regeneration occurs from seeds. Individual trees can be removed manually, but large-scale invasions are often removed with heavy equipment that disturbs the soil and damages the root structures of perennial vegetation. Fire is an effective tool for preventing woody invasion but cannot be used to restore heavily invaded areas (Grace 1998). In this study, we examine a new management technique for eliminating *Sapium* trees and rapidly returning invaded grasslands to a condition in which native vegetation can be restored and effectively maintained.

Armand Bayou Nature Center ("ABNC" hereafter) is a non-profit nature center located 40 km southeast of Houston, Texas.

In August 1997 and August 1998, ABNC applied herbicide aerially to 45 ha of closed canopy *Sapium* forest to begin to restore it to tallgrass prairie. The chemically treated *Sapium* trees were left standing in 5 ha, but the standing trees in 40 ha were mulched with a large shredding mower in the summer of 2000. This mulch was left on the ground and was up to 15 cm deep in some places (pers. observation). 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 sparse, and herbaceous biomass was adequate to fuel a successful prairie burn the following winter. Understanding the mechanisms responsible for this successful restoration 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.

Temperature hypothesis

A mulch layer on the ground might suppress the germination of *Sapium* seeds by damping diurnal soil temperature fluctuations ("temperature hypothesis"). Pioneer species commonly germinate in response to diurnally fluctuating temperatures that often characterize vegetation gaps (Thompson and Grime 1983, Fenner 1985, Baskin and Baskin 1989, Ghera et al. 1992). In laboratory studies, *Sapium* has been shown to germinate in fluctuating temperatures but not in either constant warm or cool temperatures (Nijjer et al. 2002, Donahue et al. 2004). 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 to test the following predictions of the temperature hypothesis: (1) Plots with mulch will have fewer emerging *Sapium* seedlings than plots with the mulch removed, (2) thicker *Sapium* mulch layers will progressively suppress germination and emergence, and (3) subsequent seedling performance will be comparable across mulch treatments.

Mortality hypothesis

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). This may be because of insufficient food reserves in the seed to support growth until the soil surface is reached (Westoby et al. 1996, Dzwonko and Gawronski 2002) or because of fungal disease attack during germination or just before emergence (Fisher 1941, Boyce 1961, Agrios 1997). We planted *Sapium* seedlings into plots with different mulch depths to test the following predictions of the mortality hypothesis: (1) *Sapium* germination and emergence will not be affected by mulch treatments, and (2) subsequent survival and performance of seedlings will diminish with increasing mulch depth.

Allelopathy hypothesis

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 allelopathy compounds affect 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* L. germination and seedling growth. However, other studies found that water extracts of *Sapium* litter improved the performance of the native grass *Schizachyrium scoparium* (Michx.) Nash (Keay et al. 2000) and that of *Sapium* and *Taxodium distichum* (L.) L. Rich. (Conway et al. 2002), but had no effect on *Salix nigra* Marsh. (Conway et al. 2002). We replaced *Sapium* mulch with hardwood mulch or wheat straw in the

prairie restoration site to test the following predictions of the allelopathy hypothesis: (1) *Sapium*-mulched plots will have fewer emerging *Sapium* seedlings than plots with hardwood or wheat straw mulch, and (2) seedlings in *Sapium* mulch plots will have lower survivorship and reduced performance compared to those 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 (Wheeler 1976).

Historically, the area was tallgrass prairie, but it has become heavily invaded by *Sapium*. Within the experimental area, average *Sapium* density before stand removal ranged from 0.2 trees/m² in the east to 2.2 trees/m² in the west. However, dbh of individual trees decreased from east to west, from an average of 24.7 cm in the eastern-most block to 4.5 cm in the western-most block. Blocks with larger trees may have had more *Sapium* seeds in the soil at the start of the experiment. The percentage of the canopy that was open averaged 18.8% (range 14.2%-31.2%). Under the *Sapium* canopy, wetland species such as *Rynchospora* spp. dominated the herbaceous vegetation. Low densities of *Dicanthelium oligosanthos* Shult., *Muhlenbergia capillaris* (Lam.) Trin., *Axonopus affinis* Chase, *Croton capitatus* Michx., *Rubus* spp., and *Myrica cerifera* L. were also present, as well as climax prairie grass species such as *Schizachyrium scoparium*, *Paspalum plicatum* Michx., and *Panicum virgatum* L.

During the last week of September 2002, a machine, which is commonly called a "seppi," mulched 1 ha of *Sapium* forest. 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. Large stumps were individually treated with herbicide (Garlon 4 from Dow Chemical mixed with a JBL oil) to reduce resprouting.

Experimental design

Because of differences in pre-mulching *Sapium* density across the area, we used a randomized block design with three blocks. From east to west, the blocks slope down towards Taylor Bayou, and hereafter are called High, Medium, and Low, in reference to their elevation. 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 deep *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 using this management technique. The 10 and 15-cm *Sapium* mulch layers represented two additional depths that can reasonably be expected from mulching a denser 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 were 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.

The 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).

Six 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 in Galveston County. In 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. Conetainers were well watered. Seedlings were grown in the greenhouse until they had secondary leaves, and 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. We measured the height (mean 112 mm, range 83-161 mm) and number of leaves (mean 5.4, range 4-8) of each seedling at the time of planting. Since this was during a 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.

Data collection and analysis

Naturally germinating *Sapium* seedlings were first noted in the field on March 19, 2003. Approximately every two weeks during the 2003 growing season, through September 19, and on May 28, 2004, we counted all *Sapium* seedlings within a 0.25 m² area in the center of each plot. Once a month in 2003, and on May 28, 2004, we also measured the heights of the *Sapium* seedlings. On June 13, 2003, if more than ten seedlings were in a plot, ten were haphazardly selected and permanently marked with colored paper clips. Thereafter, a maximum of ten seedling heights was measured in each plot. In total, seedlings were counted 13 times and measured six times in 2003. Vegetation cover was estimated once a month as the percentage of the 0.25 m² area covered by vegetation other than *Sapium*. Survival of added seedlings planted in plots was evaluated 98 days after the initial planting.

Three factors were included in full-interaction ANOVA evaluations: mulch treatment, block, and seedling addition. The seedling addition factor included 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. All evaluations were full-interaction ANOVA's unless otherwise indicated.

We tested whether seedling emergence (cumulative emergent seedlings in plots) over the full term of the experiment differed among bare soil and the three different depths of *Sapium* mulch (0-cm mulch and 5, 10, and 15-cm *Sapium* mulch). A similar evaluation was made for the number of seedlings alive in May 2004 (final count). We separately tested whether seedling emergence or 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 back-transformed for graphical presentation. We used Fisher's PLSD to reveal significant differences among categories within individual factors.

The survival percentage of naturally occurring seedlings was calculated by dividing end-of-season count of seedlings in September 2003 by cumulative emergence over the first growing season. We analyzed 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. We separately tested whether survival varied among the

10-cm *Sapium* mulch layer and the alternative hardwood or straw mulch.

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 planted seedling survival (eliminating the 15-cm *Sapium* mulch depth).

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 in 2003. Heights were log-transformed to achieve normality. We also tested for possible variation in average seedling height among the 10-cm *Sapium* mulch depth and the two alternative mulch treatments.

Vegetation cover in 2003 and 2004 were square root transformed to achieve normality and evaluated for dependence on *Sapium* mulch treatment (0, 5, 10, and 15-cm *Sapium* mulch), block, and seedling addition with a repeated measures ANOVA. Separate correlation Z tests were used to determine if 2003 seedling counts or average heights were correlated with vegetation cover. Regression was then used to determine the relationship

between average seedling height and vegetation cover. Data from 2003 were used in these seedling tests to consistently include vegetation and seedlings from the same growing season.

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

RESULTS

Seedling emergence and final counts depended significantly on *Sapium* mulch treatment (0 cm > 5 cm > 10 cm ≥ 15 cm), block, seedling addition, and the interactions of all of these variables (Table 1, Table 2, Figure 1). The significant mulch × block interaction reflects a high number of seedlings in the 0-cm mulch in the High block. The mulch × seedling term results from the high seedling emergence in 0-cm mulch plots that received an added seedling. A large positive effect of seedling addition in plots in the drier High block, especially in the 0-cm mulch plots, likely contributed to the significance of the block × seedling as well as the third level interaction terms.

Excluding bare plots in the High block did not change the significance of any terms except seedling addition (P=0.10)

Table 1. Full factor analysis of variance table for effect of *Sapium* mulch treatment (0, 5, 10, 15 cm) on square root transformed seedling emergence (cumulative emergent seedlings in plots) and final count in 2004.

Factor	df	Cumulative Emergence			Final Count		
		SS	F	P ^a	SS	F	P ^a
Treatment	3	130.1	17.5	****	94.9	16.3	****
Block	2	41.3	8.3	***	42.6	11.0	****
Seedling	1	16.1	6.5	*	19.5	10.0	**
Treatment * Block	6	80.8	5.4	****	62.1	5.3	****
Treatment * Seedling	3	25.5	3.4	*	21.5	3.7	*
Block * Seedling	2	39.4	7.9	***	36.7	9.5	****
Treatment * Block * Seedling	6	88.2	5.9	****	70.6	6.1	****
Residual	144	357.0			279.4		
Overall Model	23	421.5	7.4	****	347.8	7.8	****

^a P-value: NS, not significant; * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001; **** ≤ 0.0001.

Table 2. Mean (+ 1 SE) number of seedlings per plot for all mulch treatments (0 cm - 15 cm = *Sapium*) by block (High = eastern block that is higher and drier, Medium = middle block that is intermediate in elevation and moisture, and Low = west block that is lowest and wettest) and whether or not an added seedling was planted in the plot. Data were square root transformed for analysis and back-transformed for presentation.

Block	Cumulative Emergence - by mulch treatment					Final Count - by mulch treatment						
	0 cm	5 cm	10 cm	15 cm	Hardwood	Straw	0 cm	5 cm	10 cm	15 cm	Hardwood	Straw
No seedling-												
High	9.1 + 2.0	9.1 + 2.8	2.6 + 1.3	1.6 + 0.7	2.3 + 1.2	1.8 + 2.4	5.4 + 1.1	6.7 + 2.0	1.9 + 0.9	0.5 + 0.3	1.8 + 0.8	1.6 + 2.1
Medium	4.7 + 3.5	10.4 + 3.7	6.4 + 1.8	3.1 + 2.7	5.6 + 3.4	6.8 + 3.9	2.7 + 2.4	6.5 + 2.5	4.2 + 1.2	1.8 + 1.2	3.9 + 2.6	3.9 + 2.2
Low	14.4 + 9.0	6.2 + 1.5	0.2 + 0.3	1.9 + 1.1	4.8 + 2.4	0.8 + 0.6	8.0 + 5.4	3.8 + 0.9	0.1 + 0.2	1.0 + 0.7	3.6 + 2.0	0.5 + 0.4
With seedling-												
Medium	6.8 + 7.4	8.2 + 3.7	3.9 + 1.8	2.6 + 1.1	7.9 + 4.1	2.4 + 2.2	5.2 + 5.9	6.2 + 2.9	3.4 + 1.8	1.1 + 1.2	7.0 + 3.5	2.0 + 1.8
Low	5.7 + 1.8	4.8 + 1.8	7.8 + 5.0	0.8 + 0.8	5.5 + 2.2	2.8 + 1.7	2.4 + 0.7	3.2 + 1.3	5.4 + 4.8	0.3 + 0.5	3.9 + 1.9	1.6 + 0.9

and treatment by seedling addition ($P=0.32$).

The pattern of highest seedling emergence in 0 cm to lowest in 10 and 15-cm *Sapium* mulch (Figure 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 (Figure 2).

There was no difference in seedling emergence or final counts among 10-cm *Sapium* mulch and alternative mulch treatments (Table 3).

Sapium mulch treatment had a significant effect on the survival of naturally occurring seedlings in 2003 ($F_{3,118} = 9.9, P < 0.0001$). Survival was significantly higher in 5 cm of mulch than in 0 cm ($P < 0.05$), but then tended to be lower in the 10-cm mulch so that it did not differ from that in either 5 cm ($P = 0.40$) or 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 between 10-cm *Sapium* and alternative mulches ($F_{2,68} = 0.5, P = 0.60$).

The probability of an added seedling's survival in 2003 was not dependent on its initial height when planted ($\chi^2 = 0.5, 1 \text{ d.f.}, P = 0.47$), but survival was affected by *Sapium* mulch depth. The odds of survival were lower at greater mulch depths ($\chi^2 = 9.5, 3 \text{ d.f.}, P < 0.05$); however, this effect was eliminated when the

15-cm *Sapium* mulch depth was excluded ($\chi^2 = 0.4, 2 \text{ d.f.}, P = 0.83$). Survival of added seedlings did not vary among 10-cm *Sapium* mulch and the alternative mulch treatments ($\chi^2 = 0.5, 2 \text{ d.f.}, P = 0.77$).

Final seedling heights did not vary among *Sapium* mulch depths (0, 5, 10, and 15 cm, $F_{3,107} = 1.0, P = 0.41$) nor among alternative mulch treatments (10-cm *Sapium*, hardwood, and straw, $F_{2,63} = 2.1, P = 0.13$) in 2003. Seedlings in the Low block were shorter than in the other blocks among the *Sapium* mulch depths, resulting in an overall block effect ($F_{2,107} = 5.2, P < 0.01$).

Sapium mulch depth significantly reduced vegetation cover in both years (Figure 3, $F_{3,144} = 55.8, P < 0.0001$) with vegetation cover in 0 cm > 5 cm > 10 cm \geq 15 cm. Vegetation cover was lower in seedling addition plots ($F_{1,144} = 10.0, P < 0.01$). There was no correlation between vegetation cover and final seedling count in the *Sapium* mulch plots in 2003 ($P = 0.11$). *Sapium* seedling height was positively correlated with vegetation cover in the *Sapium* mulch plots in 2003 ($R^2 = 0.03, P < 0.05$).

DISCUSSION

Mulch effects

Only a shallow layer of *Sapium* mulch was required to suppress *Sapium* seedling emergence (Figure 1). Mulch also reduced native vegetation cover in early spring 2003, limiting its possible interference with subsequent *Sapium* seedling success. Heavier layers of mulch further suppressed seedling emergence, but also greatly reduced native vegetation cover into the second year (Figure 3). As a result, a mowing regime could be implemented soon after restoration regardless of the density of the *Sapium* coverage, but the mulch from a closed canopy forest might delay prescribed burning for a few years until a sufficient herbaceous fuel load accumulates.

Mulch likely suppressed *Sapium* seedling emergence by reducing the diurnal soil

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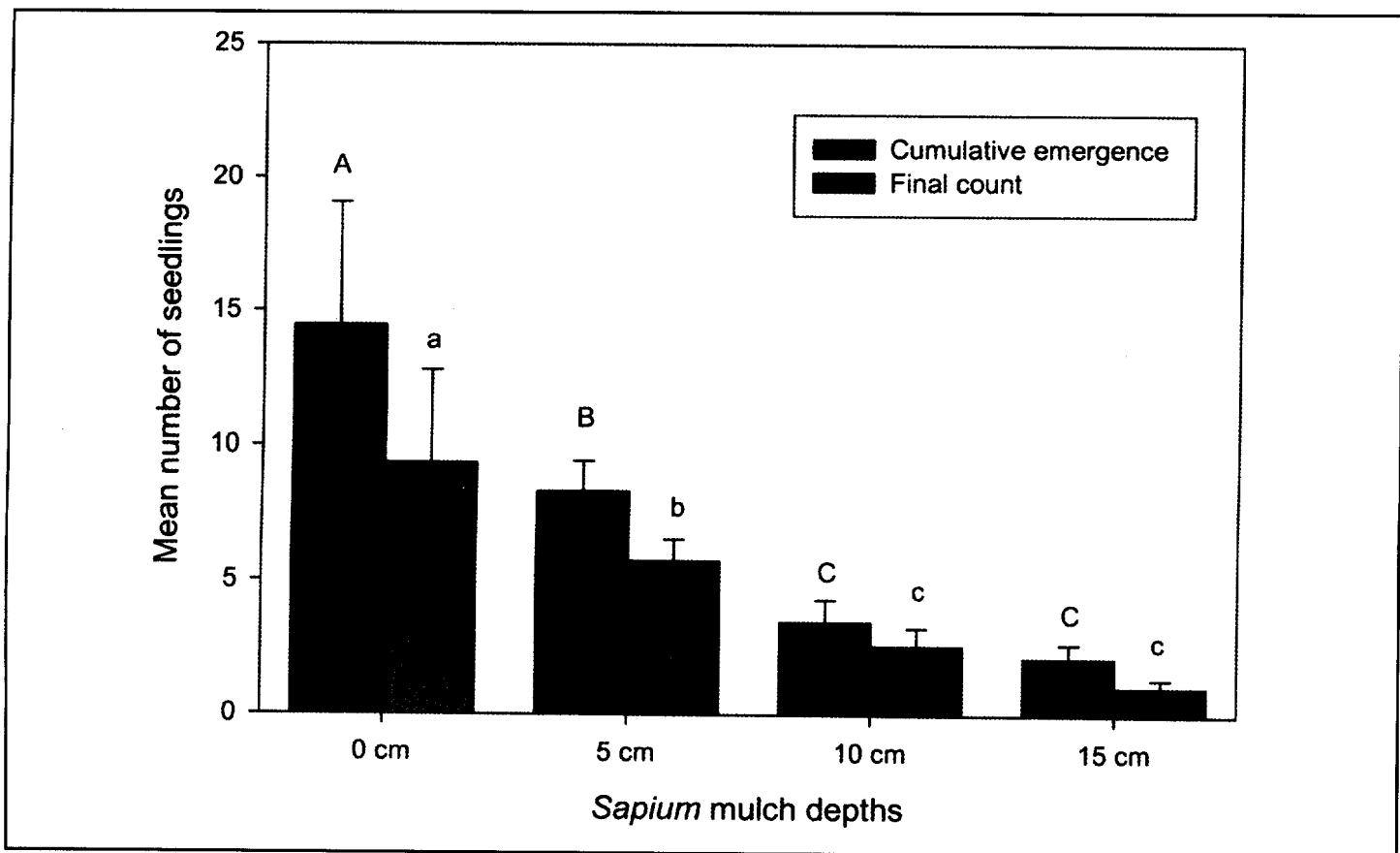


Figure 1. The effect of *Sapium* mulch depth on the cumulative count of new seedlings in a plot over the entire term of the experiment (cumulative emergence) and the number of seedlings alive in May of the second growing season (final count). Seedling counts were square root transformed for analysis and back-transformed for presentation. Error bars indicate + 1 SE. Different letters indicate means that were significantly different in Fisher's PLSD means contrasts for cumulative emergence (capital letters) or final count (lower case letters).

temperature fluctuations that *Sapium* seeds use as germination cues (Nijjer et al. 2002, Donahue et al. 2004). Mulch depths of 5 and 10 cm progressively damped soil surface temperature fluctuations from those evident at 0-cm mulch (Figure 2), and the same pattern was seen in seedling emergence (Figure 1). Neither soil temperature fluctuations nor seedling emergence differed between 10 and 15-cm of mulch (Figures 1, 2). These results support the temperature hypothesis: mulch layers reduced diurnal fluctuations in soil temperature, and seedling emergence was lower as mulch depth increased. At mulch depths where daily soil temperature fluctuations ceased to diminish, seedling emergence also leveled off.

Mulch depth alone is known to reduce seedling emergence (Fenner 1985). 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 (Donahue et al. 2004). We found seedling emergence was significantly higher with high diurnal temperature fluctuations compared to 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 that temperature fluctuation and not mulch depth *per se* is the factor responsible for lower seedling emergence.

The gradient in pre-mulching tree density likely influenced the effects of the mulch treatments. Larger, more mature trees in

the High block graded to smaller trees in the Low block before treatment. This might have resulted in a larger seed bank in the High block, which would result in more germinating seedlings, especially in the bare soil plots where no suppression occurred. Suppression effects of mulch were most pronounced in the High block.

Deeper mulch did not progressively reduce seedling performance. The effects of mulch on seedling survival varied between naturally occurring seedlings and planted seedlings, but deep mulch decreased seedling survival in both groups. Some mulch (5 cm) increased seedling survival among naturally occurring seedlings, possibly because it reduced the effects of summer drought in 2003. This pattern was not seen among planted seedlings probably because they were watered. Mulch treatment did not affect average seedling height. Because mulch depth had mixed effects on seedling

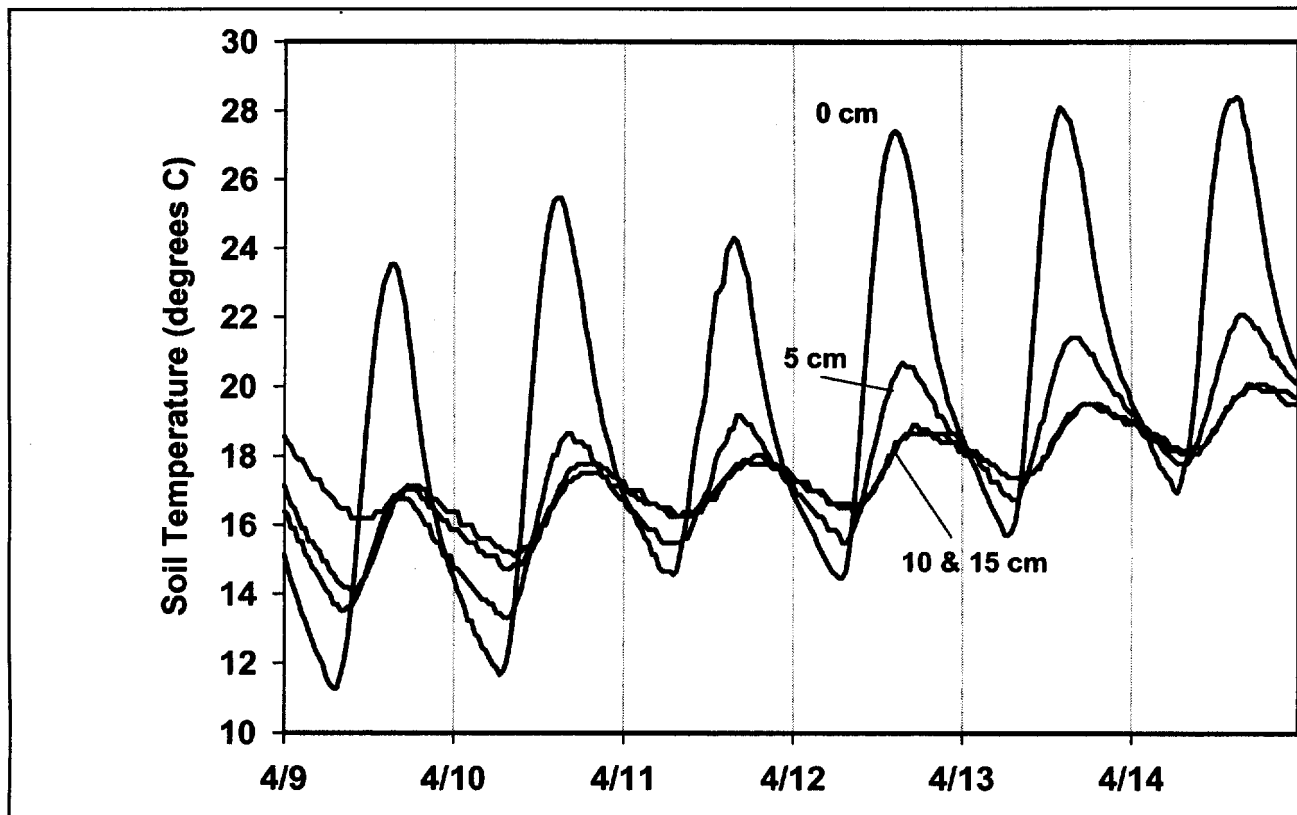


Figure 2. Diurnal soil temperature fluctuations in the field for different depths of *Sapium* mulch for six days in April 2003. *Sapium* mulch depths are indicated on the graphs.

survival and no effect on height, the mortality hypothesis was not supported.

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 westernmost Low block through March 2003 may have contributed to later germination of seedlings in that block and the resultant

shorter height of the naturally occurring seedlings.

The poor survival of planted seedlings in the 15-cm *Sapium* mulch was likely

Table 3. Full factor analysis of variance table for effects of 10 cm *Sapium* mulch, hardwood mulch, and straw mulch treatments on square root transformed seedling emergence (cumulative emergent seedlings in plots) and final count in 2004.

Factor	df	Cumulative Emergence			Final Count		
		SS	F	P ^a	SS	F	P ^a
Treatment	2	6.6	2.0	NS	7.9	2.8	NS
Block	2	7.4	2.2	NS	6.6	2.3	NS
Seedling	1	4.2	2.5	NS	4.5	3.2	NS
Treatment * Block	4	1.8	0.3	NS	1.7	0.3	NS
Treatment * Seedling	2	2.6	0.8	NS	3.1	1.1	NS
Block * Seedling	2	9.5	2.8	NS	3.6	1.3	NS
Treatment * Block * Seedling	4	8.3	1.2	NS	5.8	1.0	NS
Residual	90	151.2			126.7		
Overall Model	17	40.4	1.4	NS	33.2	1.40	NS

^a P-value: NS, not significant; * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001; **** ≤ 0.0001.

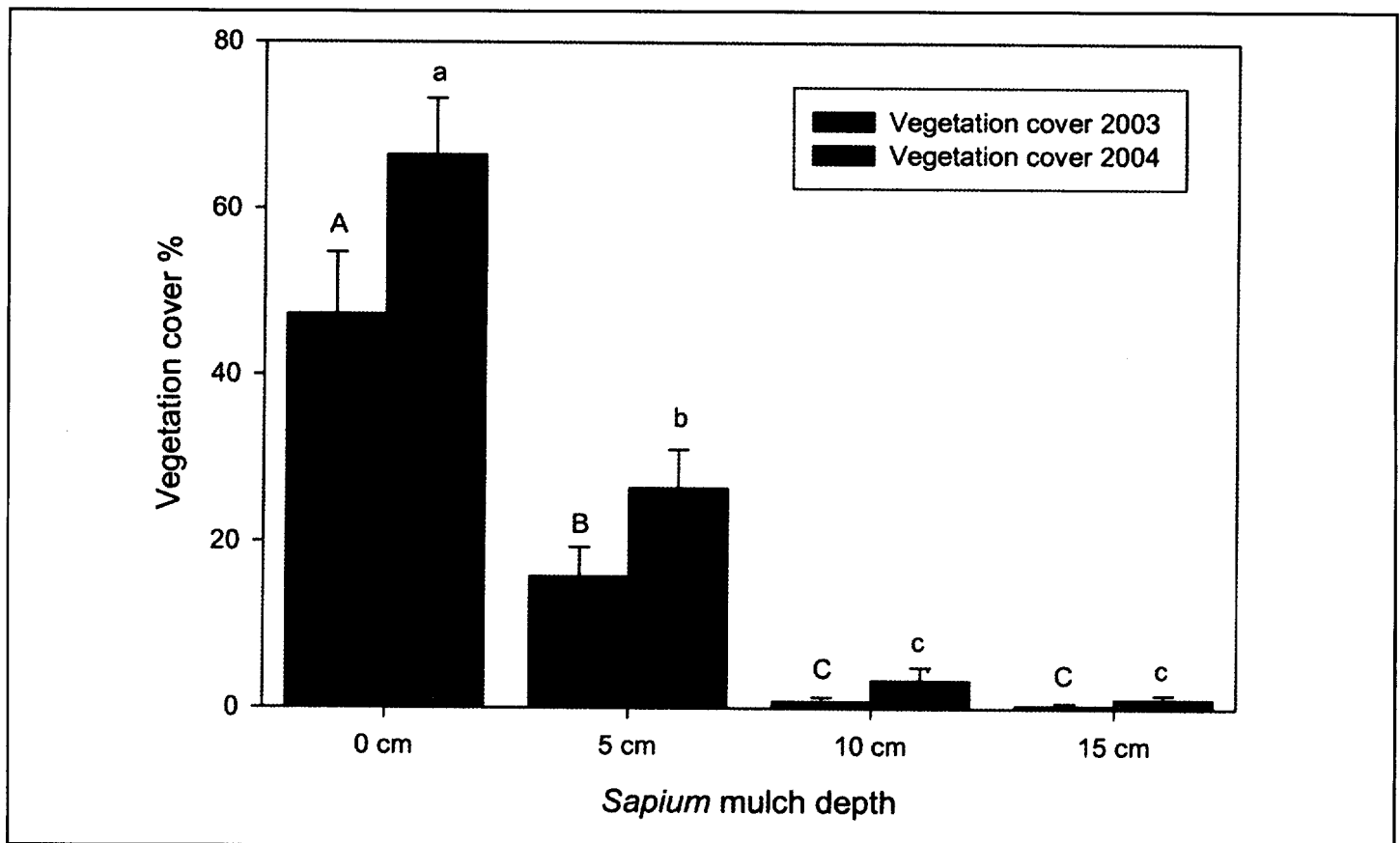


Figure 3. Average vegetation cover per plot at the end of the growing season in 2003 and in May 2004 for each depth of *Sapium* mulch. Vegetation cover was estimated as the percentage of the area covered by non-*Sapium* vegetation (remaining percentage would be *Sapium*, mulch, or bare soil). Vegetation cover was square root transformed for analysis and back-transformed for presentation. Error bars indicate + 1 SE. Different letters indicate means that were significantly different in Fisher's PLSD means contrasts for 2003 (capital letters) or 2004 (lower case letters).

because many seedlings were completely covered in this treatment (average seedling height at planting was 112 mm) after they had invested significant seed resource reserves in production of true leaves. *Sapium* has a relatively large seed (Bonner 1989c), especially compared to native pioneer tree species (Bonner 1989a,b), and larger seeds have been shown to increase seedling establishment in many environments (Silvertown 1989, Burke and Grime 1996, Gray and Spies 1997, Jakobsson and Eriksson 2000, Thompson et al. 2001, Grundy et al. 2003). *Sapium*'s large seed size may have contributed to the lack of a negative correlation between vegetation cover and final seedling count in the experimental plots. In addition, in our lab experiment (Donahue et al. 2004), *Sapium* seedlings emerged through 10 cm of mulch. However, these seedlings planted into the field had invested seed energy reserves in true leaves before burial in the mulch. Therefore, mortality

in the 15-cm mulch depth likely resulted from insufficient energy reserves rather than direct mulch effects.

We found no evidence of allelopathic effects of *Sapium* mulch on *Sapium* seeds or seedlings. There was no difference in seedling emergence (Table 3) or seedling survival between *Sapium* and alternative mulch plots, and seedling height was unaffected by *Sapium* versus alternative mulches. One study has shown negative effects of *Sapium* on a native tree species (Gresham and Edwards 1995). Some studies have found positive effects of *Sapium* litter extracts on growth of some 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 in the laboratory.

Conclusions and implications

This experiment demonstrated that using shredding mowers to mulch live *Sapium* trees in an invaded prairie could be a rapid restoration technique. Modern native prairie management involves mimicking the historic forces of grazing and fire that shaped prairies over time (Axelrod 1985, Smeins et al. 1992). Grazing is often replaced by mowing, and this technique aids mowing by removing all of the *Sapium* to ground level. Therefore, although heavier mulch layers reduced *Sapium* seedling emergence and may help future management, mulching trees and removing mulch also appears to be a viable restoration technique. 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). Therefore, mulching eliminated the trees, reduced subsequent *Sapium* seedling emergence, and facilitated future native prairie management.

ACKNOWLEDGMENTS

The authors would like to thank Armand Bayou Nature Center for access and assistance, Saara DeWalt for comments on the manuscript, Philemon Chow, Maria Hartley, Zach McLemore, Summer Nijjer, Megan Rua, Rachel Tardif, Liz Urban, and Terris White for field assistance, and Wray-Todd Fellowship, US EPA (R82-8903), and US NSF (DEB-9981654) for financial support.

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