

# Effects of nutrient loading and extreme rainfall events on coastal tallgrass prairies: invasion intensity, vegetation responses, and carbon and nitrogen distribution

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## Abstract

Soil fertility and precipitation are major factors regulating transitions from grasslands to forests. Biotic regulation may influence the effects of these abiotic drivers. In this study, we examined the effects of extreme rainfall events, anthropogenic nutrient loading and insect herbivory on the ability of Chinese tallow tree (*Sapium sebiferum*) to invade coastal prairie to determine how these factors may influence woody invasion of a grassland. We manipulated soil fertility (NPK addition) and simulated variation in frequency of extreme rainfall events in a three growing season, full factorial field experiment. Adding water to or pumping water out of plots simulated increased and decreased rainfall frequencies. We added *Sapium* seeds and seedlings to each plot and manipulated insect herbivory on transplanted *Sapium* seedlings with insecticide. We measured soil moisture, *Sapium* performance, vegetation mass, and carbon and nitrogen in vegetation and soils (0–10 cm deep, 10–20 cm deep). Fertilization increased *Sapium* invasion intensity by increasing seedling survival, height growth and biomass. Insect damage was low and insect suppression had little effect in all conditions. Recruitment of *Sapium* from seed was very low and independent of treatments. Vegetation mass was increased by fertilization in both rainfall treatments but not in the ambient moisture treatment. The amount of carbon and nitrogen in plants was increased by fertilization, especially in modified moisture plots. Soil carbon and nitrogen were independent of all treatments. These results suggest that coastal tallgrass prairies are more likely to be impacted by nutrient loading, in terms of invasion severity and nutrient cycling, than by changes in the frequency of extreme rainfall events.

*Keywords:* biological invasions, carbon, Chinese tallow tree, climate change, disturbance, nitrogen, rainfall, *Sapium sebiferum*

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## Introduction

Invasions by exotic plants are a leading cause of species extinctions and represent a large cost to society (Mack *et al.*, 2000; Pimentel *et al.*, 2000). Understanding the factors that contribute to their success is critical. One factor that is thought to contribute to the success of invasive species is disturbance, often from human activities (Vitousek, 1994; Davis *et al.*, 2000). This includes local scale disturbances from changing land use, dis-

turbances at large spatial scales such as those from anthropogenic nutrient inputs via atmospheric deposition and disturbances at global scales such as those from global climate change (Mack *et al.*, 2000). Because disturbances that are large in terms of spatial and temporal scale are especially difficult to manage in short time scales and cannot be effectively addressed by local land managers, it is especially important to understand and be able to predict the effects of such large-scale disturbances on invasions and plant community dynamics.

Predictions for future climate vary in degree of future warming due to differences in trace gas emission scenarios and differences in models that link climate

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changes to emissions (IPCC, 2001). This includes both temperature and precipitation. However, for most regions of the world, variations in model predictions among all scenarios are only differences in magnitude (extent of warming, perhaps only in winter or summer) but are not differences in direction of change. In every region of the world, all models and all scenarios predict warming if any predict warming.

Precipitation predictions are much more varied than those for temperatures (IPCC, 2001). Indeed, precipitation predictions vary both in direction, as well as magnitude for some parts of the world. In other words, depending on the choice of climate models and emission scenarios, climate may become wetter or drier in a region. However, only two regions of the world, Central North America (CNA) and Southern South America (SSA) have an inconsistent sign for both winter and summer precipitation (IPCC, 2001). Because ecosystems in the Gulf Coast of the United States are critically dependent on the availability of fresh water (Twilley *et al.*, 2001), this uncertainty in terms of whether precipitation is likely to increase or decrease makes it very difficult to predict the effects of climate change on ecosystems in this region.

Deposition of nutrients (Harpole, 2006), especially nitrogen (Vitousek, 1994; Bertness *et al.*, 2002; Minchinton & Bertness, 2003; Stevens *et al.*, 2004, 2006; Suding *et al.*, 2005; Power *et al.*, 2006), has the potential to change the diversity, species composition, and functional composition of ecosystems and to change the rates of biogeochemical processes. Currently, terrestrial ecosystems receive high levels of nutrients from aerial deposition, with nitrogen being an especially common pollutant (Galloway *et al.*, 1995). Changes in rates of supply of limiting nutrients can have important effects on the outcome of plant competition, especially when plants are from different functional groups with widely different root:shoot ratios (Wilson, 1998; Siemann & Rogers, 2003a).

Among the most aggressive invaders of terrestrial ecosystems in the Gulf Coast, and the most aggressive in many ecosystems throughout east Texas, is Chinese tallow tree [*Sapium sebiferum* (L.) Roxb., Euphorbiaceae, 'Sapium' hereafter, synonyms include *Stillingia sebifera* Willd. (Roxb. 1832) and *Triadica sebifera* (L.), nomenclature follows Hatch *et al.* (2001) throughout]. Because it grows rapidly and has seeds rich in oils, abundant flowers and colorful fall foliage, it has been widely planted as a biomass crop, oil crop, nectar crop and ornamental (Bruce *et al.*, 1997). *Sapium* has become naturalized from the Gulf Coast of Texas to the Atlantic Coast of North Carolina. It aggressively displaces native plants and forms monospecific stands. In the Gulf Coast, coastal tallgrass prairies have largely been con-

verted to *Sapium* woodland thickets and *Sapium* is aggressively invading wetlands and bottomland forests (Bruce *et al.*, 1997; Harcombe *et al.*, 1999). Previous work has shown that competitive superiority of *Sapium* is due to a combination of factors including low herbivore loads that contribute to high phenotypic and genetic increases in growth and reproduction (Siemann & Rogers, 2003b,c) such that it has faster growth than any native tree in a broad range of light conditions (Lin *et al.*, 2004), prolific seed production (Renne *et al.*, 2000), and tolerance of a wide range of abiotic conditions (Jones & McCleod, 1989; Butterfield *et al.*, 2004). It has been shown that nitrogen addition accelerates *Sapium* invasion into coastal tallgrass prairies under ambient hydrological conditions (Siemann & Rogers, 2003a). However, we do not know the relative importance of nutrient deposition vs. changes in hydrology for the intensity of *Sapium* invasions. We also do not know whether the effects of fertilization depend on hydrological conditions.

In order to predict the effects of climate change and nutrient deposition on woody invasions of grasslands, we performed an experiment in which we created appropriate environmental conditions. We simulated varying frequencies of extreme rainfall events together with fertilization treatments to examine: (1) effects on severity of *Sapium* invasion in coastal tallgrass prairies and (2) the ramifications for carbon and nitrogen distribution in the vegetation and soil.

## Methods

### Study site

The University of Houston Coastal Center is a 374 ha research area located ~50 km southeast of Houston, TX, USA (see Siemann & Rogers, 2003b for site description). Historically, this site was mostly tallgrass prairie. *Sapium* has invaded some areas while others have been protected from invasion by annual mowing. Mowed areas are dominated by graminoids (~75% of cover at the start of this experiment in this field), with *Schizachyrium scoparium* (Michx.) Nash, *Spartina patens* (Ait.) Muhl. and *Andropogon glomeratus* (Walt.) B.S.P., as the main species in the field in which this experiment took place (unpublished data). Forbs [~10% of cover, main species in this field: *Helianthus angustifolius* L. and *Hyptis alata* (Raf.) Shinnery] and woody plants (~5% of cover, main species in this field: *Rubus riograndis* Bailey, *Baccharis halimifolia* L., and *Myrica cerifera* L.) were also present. Mowing was stopped in experimental plots for the duration of these studies. Average annual rainfall is 1070 mm distributed fairly evenly throughout the year. Average temperature is 20.9°C. Soils are expansive Lake Charles Clay Vertisols (fine,

montmorillonitic, thermic Typic Pelludert) with a 40–60% clay content.

### Experimental design

In January 2002, we laid out twenty-four 3.6 m × 3.6 m plots. Plots were in three rows of eight plots with 2 m alleys between plots and around the outside of the experiment. The entire experiment was surrounded by a barbed wire fence to prevent incursion by feral hogs (*Sus scrofa*). Alleys were kept free of trees and shrubs above the level of the herbaceous vegetation by hand clipping but were otherwise unmanaged. Each plot was assigned two treatments in a randomized factorial design with four replicates. One treatment examined variation in water supply (three treatments: ambient, dry, wet). The other examined variation in fertility (two treatments: fertilized, unfertilized).

Two additional subexperiments were nested into each plot in a split-plot design. One examined recruitment of *Sapium* from seed (two treatments: seeds added vs. controls in which no seeds were added). The other examined performance of *Sapium* seedlings (two treatments: insect suppression vs. controls that were sprayed with water). For each nested subexperiment, there were two replicates in each plot that were averaged to increase precision.

### Water treatments

Recently, ecologists have been using rainout shelters to reduce soil moisture and mimic the effects of reduced rainfall on ecological communities (Fay *et al.*, 2000; Yahdjian & Sala, 2002; Chimner & Welker, 2005; English *et al.*, 2005; Harper *et al.*, 2005; Le Roux *et al.*, 2005). However, in coastal tall grass prairies, the water table is above the soil surface following periods of heavy rainfall (Smeins *et al.*, 1992) making a rainout shelter an ineffective way to change soil moisture in this ecosystem. So, in order to mimic reduced rainfall, we pumped water from plots following large rain events. Because soils are very dense, it is unlikely that subsurface water would enter the near-surface levels of plots.

Each reduced rainfall plot ('dry plot' hereafter) had a frame made of treated '2 by 12' lumber (3.8 cm × 29.2 cm, oriented so that boards were 29.2 cm high) that was trenched ~8 cm into the soil. Soil was packed back against boards after they were placed in the ground. The corner of each frame was a 60 cm long treated '4 by 4' post (8.9 cm × 8.9 cm) sunk 40 cm into the ground in order to prevent any movement of the frame boards that were screwed to it. All joints were sealed with commercial window sealing spray foam to make them watertight. The outside of the frame had sandbags filled with

commercial masonry sand placed along the entire perimeter to prevent water entering plots from aboveground flow. The center of each plot had a 10 cm diameter perforated plastic drain pipe sunk to a depth of 30 cm with 10 cm sticking above the ground. Each drainpipe had a 19 L min<sup>-1</sup> automatic switch marine bilge pump (Rule model 25S, ITT Industries, Gloucester, MA, USA) inserted down to the bottom. A piece of 1.3 cm inner diameter PVC pipe ran to the level of the soil surface where it was connected to a 1.6 cm inner diameter rubber garden hose that ran at least 5 m outside the experiment. The remote location made it impossible to plug pumps into a constant power supply. Rather, pumps were powered by a pair of deep-cycle marine batteries that were replaced with a freshly charged pair daily when conditions were wet enough to cause pumps to run.

When it rained a small amount, moisture would be absorbed by the soil and relatively little would be removed by pumps. Because soils are dense clay, their permeability is low and little water would move laterally to the pump casing. On the other hand, when there was a large rain event such that there would be water above the soil surface, pumps would remove it. Pumps were active from March through November, which corresponds with the major growing season.

Wet plots had frames installed that were identical to those in the dry plots. Three times during each growing season, at a time when there was not already water at or above the soil surface, each plot received an amount equivalent to approximately 10 cm of water across the plot. The source of the water was a nearby well that draws from the Chicot aquifer. Previous water tests indicated no detectable levels of toxins, nitrate concentrations of 0.2 mg L<sup>-1</sup>, and phosphate concentrations of 0.3 mg L<sup>-1</sup> (R. Capuano, unpublished results). Watering would have added 0.37 g of phosphorus (29 mg m<sup>-2</sup>) and 0.24 g of nitrogen (10 mg m<sup>-2</sup>) annually to each plot.

Ambient water plots did not have water removed or added. In lieu of a frame, they had four metal corner posts to delineate the plots.

### Fertilization

Plots assigned to the fertilizer treatment received 4 g m<sup>-2</sup> nitrogen, 1.3 g m<sup>-2</sup> phosphorus, and 2.6 g m<sup>-2</sup> potassium twice during each growing season (June and July) as a commercial fertilizer blend that also included micronutrients. Fertilizer was hand broadcast before forecast rain.

### Seed collection

In November 2001, we hand collected seeds from *Sapium* trees in Harris and Galveston Counties (TX).

Seeds were stored at room temperature in the dark after collecting until they were planted in the field (seed addition experiment) or in germination flats (seedling addition experiment).

#### *Seed additions*

In each plot, we installed four wire mesh cages (1 cm square mesh) that were 20 cm tall and 20 cm in diameter. Cages were 45 cm in from each corner of the plot. We randomly selected two cages in each plot to receive 50 *Sapium* seeds. Seeds were surface sown in April 2002. At that time there were no naturally occurring *Sapium* seedlings in any of the cages. We censused *Sapium* seedlings and all other woody seedlings in each cage three times during each of the following three growing seasons.

#### *Seedlings*

In February 2002, we planted *Sapium* seeds in germination trays filled with commercially available topsoil that were located in an unheated greenhouse in Houston, TX. Once a seed germinated, it was transferred to a 115 mL container (Stuewe & Sons, Corvallis, OR, USA) filled with field soil collected from the margin of the experiment. Once seedlings had primary leaves, they were transferred outside under a 50% shade cloth to harden off. Four seedlings were planted into each plot in April, 2002. Seedlings were located 1 m from the middle of each side of the plot.

Seedlings were randomly assigned to an insect herbivore treatment (two of each treatment in each plot). Insect suppression seedlings were sprayed approximately every two weeks throughout the growing season with Esfenvalerate (DuPont, Wilmington, DE, USA). We have used this insecticide in other experiments and have found no phytotoxic effects or fertilization effects and have found it to be effective at reducing insect damage (Siemann & Rogers, 2003b). Seedlings that were assigned to the control treatment were sprayed with water.

We checked seedling survival five times in the first growing season and three times in the second and third growing seasons. We measured seedling height, counted the number of leaves and visually estimated the average percent of leaves removed by chewing insect herbivores three times during each growing season. We calculated height growth rate as  $\ln[\text{end height}/\text{start height}]$ . In August 2004 (854 days after planting), seedlings were clipped at ground level, dried and weighed.

#### *Physical measurements*

Twice during each growing season, we measured gravimetric soil moisture in the top 1 cm of the soil using a

small diameter (3 mm) cork borer. These measurements occurred between adjacent watering events.

At the conclusion of the experiment, we clipped a 1 m × 1 m area of vegetation in each plot at ground level. Vegetation was dried and weighed. The sample was ground in a cyclone mill and 4 subsets of this ground sample were analyzed for percent carbon and percent nitrogen in an autoanalyzer (Model CE 440, LeeMann Labs Inc. Elemental Analyzer, Hudson, NH, USA).

At the conclusion of the experiment, we extracted four 2.2 cm diameter, 20 cm deep soil cores from each plot. Before pulling each core, we pushed aside surface litter. Cores were split into two samples representing top (0–10 cm deep) and bottom (10–20 cm deep) sections of the sample. These samples were dried, ground and analyzed for percent carbon and percent nitrogen in an autoanalyzer.

#### *Analyses*

We used split-plot ANOVAs to examine effects of experimental treatments on *Sapium* seedling survival time, average chewing insect damage to seedlings in the first growing season, height growth rates of seedlings, and their final aboveground mass. For each of these response variables we used the average of the two seedlings with the same insecticide treatment in the plot. Mass was log-transformed to meet the assumption of normality in ANOVA. Whole-plot factors were fertilization treatment, water treatment and their interaction. We used Fisher's least significant difference (LSD) *post hoc* tests to examine whether water treatments differed in cases where it was a significant predictor. Split-plot terms were insecticide treatment and its interaction with whole-plot factors.

We used ANOVA to examine effects of experimental treatments on plot level variables: vegetation mass (log transformed), amount of carbon and nitrogen in vegetation, percent carbon and nitrogen in vegetation, and percent carbon and nitrogen at the two soil depths. For gravimetric soil moisture, we used a repeated measures ANOVA with annual means. We used Fisher's LSD *post hoc* tests to examine whether water treatments differed in cases where it was a significant predictor.

## **Results**

#### *Seed additions*

In total, five *Sapium* seedlings were observed in seed cages during the experiment: four in seed addition cages (plots: fertilized, ambient water; unfertilized, dry; fertilized, wet; unfertilized, ambient water) and one in a no seed addition cage (fertilized, dry plot). Only the seedling in the unfertilized, ambient water

plot was alive at the end of the experiment. On average, the germination rate was 0.17% (4 in addition cages – 1 in no addition cages)/(2400 seeds added to addition cages). Germination in a single season in a greenhouse for this same batch of seeds was 30.3% (unpublished results). One *Ulmus* seedling germinated in a unfertilized, ambient water, no seed addition cage. No other tree seedling recruitment occurred during the three growing seasons.

### Seedlings

*Sapium* seedling survival times were longer on average in fertilized plots than in unfertilized plots (Tables 1 and 2). Their survival times depended on water treatment on average but the water treatment means did not differ from each other in means contrast tests (Tables 1 and 2). The interaction of fertilization and water treatment significantly affected survival time with fertilization increasing survival time in dry conditions and ambient water conditions but not in wet conditions. Insect suppression only affected seedling survival in interaction with water treatment but not as a main effect or in interaction with other terms (Table 2). Survival times were lower with insecticide applications in dry (704 vs. 670 days) and wet plots (794 vs. 722 days) but higher in ambient water conditions with insecticide applications (708 vs. 826 days). However, insect damage was low (on average 0.67% of leaf area removed) and independent of all factors (Table 2). Seedling height growth rates and final mass (Fig. 1) were higher in fertilized plots than in unfertilized plots but independent of all other factors. (Tables 1 and 2).

### Physical measurements

Gravimetric soil moisture depended on water treatment ( $F_{2,18} = 15.8, P < 0.0001$ ) and time ( $F_{5,90} = 11.7, P < 0.0001$ ) but not on any other factors ( $P$  values : fert = 0.98, fert  $\times$  water = 0.28, time  $\times$  fert = 0.99, time  $\times$  water = 0.65, time  $\times$  fert  $\times$  water = 0.14). All three water treatments differed in mean gravimetric soil moisture (dry = 0.43, ambient = 0.51, wet = 0.62).

Vegetation mass was higher in fertilized plots and it depended on water treatment (Table 2, Fig. 1). Vegetation mass was lower in ambient plots than dry plots. The amount of carbon contained in vegetation showed the same pattern in terms of significance of factors and contrasts among water treatments (Tables 1 and 3). The amount of nitrogen contained in vegetation was higher in fertilized plots than in unfertilized plots (Table 1). Over the course of the experiment, 24 g m<sup>-2</sup> of nitrogen had been applied. The percent carbon in vegetation was higher in fertilized plots than in unfertilized plots but it was independent of other factors (Tables 1 and 3). The model for percent nitrogen in vegetation was not significant (Tables 1 and 3). Soil percent carbon and percent nitrogen in both horizons were independent of all factors (Table 2). The dry mass of soil averaged 110 kg m<sup>-2</sup> for each of the horizons. There was approximately 6.0 kg carbon m<sup>-2</sup> and 470 g nitrogen m<sup>-2</sup> in the top 20 cm of soil.

### Discussion

Fertilization had strong effects on *Sapium* invasion independent of hydrological conditions (Tables 1 and 2, Fig. 1). A separate factorial nutrient addition experiment showed that nitrogen addition, but not the addi-

**Table 1** Dependence of response variables on the combination of fertilizer and water treatment (mean  $\pm$  SE)

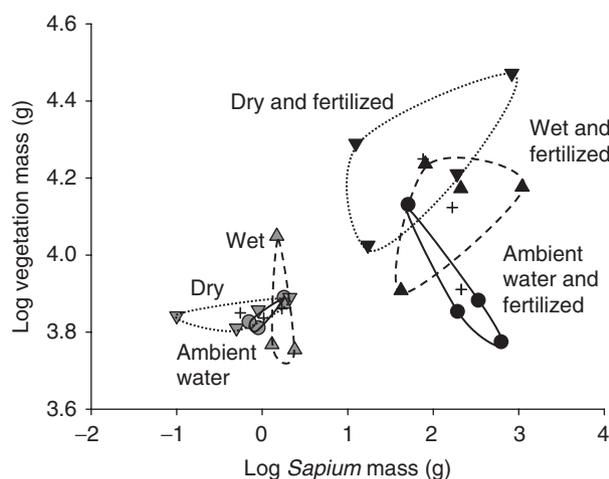
Variable	Unfertilized			Fertilized		
	Ambient	Dry	Wet	Ambient	Dry	Wet
<i>Sapium seedlings</i>						
Survival time (days)	774 $\pm$ 42	633 $\pm$ 50	707 $\pm$ 40	827 $\pm$ 26	741 $\pm$ 49	742 $\pm$ 46
Height growth rate (mm m day <sup>-1</sup> )	1.04 $\pm$ 0.32	1.18 $\pm$ 0.36	1.02 $\pm$ 0.15	2.76 $\pm$ 0.15	2.70 $\pm$ 0.20	2.99 $\pm$ 0.14
<i>Vegetation</i>						
Carbon (g m <sup>-2</sup> )	226 $\pm$ 8	232 $\pm$ 9	250 $\pm$ 44	284 $\pm$ 60	670 $\pm$ 149	491 $\pm$ 76
Nitrogen (g m <sup>-2</sup> )	3.34 $\pm$ 0.26	3.74 $\pm$ 0.23	4.59 $\pm$ 1.17	5.33 $\pm$ 0.61	10.11 $\pm$ 2.29	8.78 $\pm$ 1.78
Carbon (% dry mass)	42.4 $\pm$ 0.4	42.2 $\pm$ 0.2	42.6 $\pm$ 0.7	42.4 $\pm$ 0.6	45.2 $\pm$ 1.2	45.6 $\pm$ 0.8
Nitrogen (% dry mass)	0.62 $\pm$ 0.03	0.68 $\pm$ 0.03	0.75 $\pm$ 0.07	0.84 $\pm$ 0.06	0.68 $\pm$ 0.01	0.81 $\pm$ 0.08
<i>Soil</i>						
Top C (% dry mass)	3.14 $\pm$ 0.12	3.23 $\pm$ 0.22	3.21 $\pm$ 0.13	3.34 $\pm$ 0.07	3.51 $\pm$ 0.15	3.37 $\pm$ 0.17
Top N (% dry mass)	0.25 $\pm$ 0.01	0.26 $\pm$ 0.02	0.25 $\pm$ 0.01	0.25 $\pm$ 0.01	0.27 $\pm$ 0.01	0.27 $\pm$ 0.01
Bottom C (% dry mass)	2.08 $\pm$ 0.07	2.15 $\pm$ 0.08	2.14 $\pm$ 0.09	2.05 $\pm$ 0.13	2.19 $\pm$ 0.08	2.29 $\pm$ 0.09
Bottom N (% dry mass)	0.16 $\pm$ 0.01	0.17 $\pm$ 0.01	0.17 $\pm$ 0.01	0.16 $\pm$ 0.01	0.17 $\pm$ 0.01	0.19 $\pm$ 0.01

Top = 0–10 cm deep; bottom = 10–20 cm deep. *Sapium* and vegetation mass are shown in Fig. 1.

**Table 2** The dependence of *Sapium* seedling survival time (days since planting), average chewing insect damage in the first growing season, height growth rate [ $\ln(\text{end height}/\text{start height})$ ], and aboveground mass (log transformed) on fertilization (fert), water treatment (water), insect suppression treatment (Insect) and their interaction in split-plot ANOVAs

Factor	Survival time			Insect damage			Height growth rate			Aboveground mass		
	df	F	P	df	F	P	df	F	P	df	F	P
Fert	1	<b>6.7</b>	<b>&lt;0.05</b>	1	0.8	0.37	1	<b>74.5</b>	<b>&lt;0.0001</b>	1	<b>63.8</b>	<b>&lt;0.0001</b>
Water	2	<b>4.1</b>	<b>&lt;0.05</b>	2	0.7	0.52	2	0.4	0.66	2	0.2	0.8
Fert × water	2	<b>3.8</b>	<b>&lt;0.05</b>	2	0.7	0.5	2	0.3	0.76	2	<0.1	0.96
WP error	18			18			17			17		
Insect	1	<0.1	0.89	1	0.8	0.39	1	1.6	0.15	1	1.2	0.29
Insect × fert	1	0.2	0.69	1	0.1	0.74	1	<0.1	0.96	1	0.1	0.75
Insect × water	2	<b>3.6</b>	<b>&lt;0.05</b>	2	0.3	0.71	2	0.8	0.47	2	0.3	0.76
Insect × fert × water	2	2.5	0.11	2	1.5	0.26	2	1.8	0.2	2	0.6	0.56
SP error	18			23			13			13		

WP, error is the whole-plot error term; SP, error is the split plot error term. Significant results are shown in bold.



**Fig. 1** The vegetation mass and *Sapium* mass in plots that differ in treatments. Each point represents the value for a single plot. The outline is a visual guide to show the range of variation within a treatment combination. The average value for a treatment combination is indicated by a cross.

tion of either phosphorus or potassium alone, has a comparable effect on *Sapium* growth in these prairies (Siemann & Rogers, 2007). Therefore, nitrogen appears to have been the element responsible for the *Sapium* responses observed here with the addition of nitrogen, phosphorus and potassium. Indeed, the same study with factorial nutrient additions showed that both nitrogen and phosphorus had to be added to see any detectable response in terms of prairie vegetation biomass. Nevertheless, because the response of *Sapium* was so strong when nitrogen was added compared with the response of prairie vegetation, additional input of soil nutrients has the potential to cause large increases in the intensity of *Sapium* invasion. This agrees well with other studies on fertilization and invasion that have found

acceleration of invasions by nutrient addition including *Phragmites* invasions into coastal wetlands (Bertness *et al.*, 2002; Minchinton & Bertness, 2003) and woody plant invasions into grasslands (Daehler, 2003; Stevens *et al.*, 2004).

*Sapium* invasion from seed was extremely low and independent of all treatments. *Sapium* has been shown to have very specific germination requirements such that it rarely germinates in the absence of disturbance (Nijjer *et al.*, 2002). In particular, it requires oscillating temperatures, typically from heating of exposed soil during the day, to break seed dormancy (Nijjer *et al.*, 2002; Donahue *et al.*, 2004, 2006). If changes in fertility or rainfall frequency are uncorrelated with disturbance, our seedling results should predict *Sapium* invasion success from seed as well.

During our experiment, soil nutrient concentrations did not respond to changes in water regimes or to fertilization (Tables 1 and 3). Similarly, concentrations of nutrients in vegetation had little dependence on our treatments such that the amount of carbon and nitrogen in vegetation mirrored the amounts of biomass in plots that had different treatments. However, by facilitating conversion from grassland to *Sapium* monoculture forests, fertilization may cause large changes in soil nutrient content as soils under such forests have much higher concentrations of nitrogen than those in the grasslands they replace (Cameron & Spencer, 1989). The effect of such conversions on soil carbon pools is unknown but work on other woody invasions into grasslands has shown that soil carbon can sometimes be sensitive to woody plant abundance (Gill & Burke, 1999; McCulley *et al.*, 2004) but that site characteristics such as soil type can have a role in determining carbon and nitrogen pools (Hibbard *et al.*, 2003; Hughes *et al.*, 2006).

**Table 3** The effects of fertilization (fert), water treatment (water), and their interaction on aboveground vegetation mass (log transformed), mass of C and N in vegetation, and percent C and N in vegetation and soil in ANOVAS

Factor	df	Vegetation Mass		C in Vegetation		N in Vegetation	
Fert	1	<b>21.6</b>	<b>&lt;0.001</b>	<b>23.1</b>	<b>&lt;0.0001</b>	<b>15.3</b>	<b>&lt;0.001</b>
Water	2	<b>3.9</b>	<b>&lt;0.05</b>	<b>4.1</b>	<b>&lt;0.05</b>	2.4	0.12
Fert × water	2	3.2	0.06	3.5	0.05	1.4	0.27
Error	18	<b>35.2</b>	<b>&lt;0.0001</b>	<b>7.8</b>	<b>&lt;0.001</b>	<b>4.6</b>	<b>&lt;0.01</b>

		Vegetation %C		Vegetation %N		Soil %C top	
Fert	1	<b>12.2</b>	<b>&lt;0.01</b>	4.7	<0.05	3	0.1
Water	2	3	0.07	2	0.16	0.4	0.68
Fert × water	2	3	0.08	2.2	0.14	0.9	0.92
Error	18	<b>4.8</b>	<b>&lt;0.01</b>	2.5	0.07	0.8	0.57

		Soil %C bottom		Soil %N top		Soil %N bottom	
Fert	1	0.5	0.5	2.2	0.16	1	0.34
Water	2	1.3	0.3	0.7	0.52	1.5	0.24
Fert × water	2	0.5	0.64	0.1	0.95	0.6	0.55
Error	18	0.8	0.56	0.9	0.49	1.3	0.32

Top = 0–10 cm deep; bottom = 10–20 cm deep. The pair of numbers for each variable are the *F*-value and *P*-value, respectively. The model *F*-value and *P*-value are in the row for the model error term. Significant results are shown in bold.

The responses of *Sapium* to changing water availability were surprising (Tables 1 and 2, Fig. 1) because it has been predicted that disturbance in general should facilitate invasions (Davis *et al.*, 2000; Mack *et al.*, 2000) and studies have shown increases in invasion with changes in abiotic conditions (e.g. Burke & Grime, 1996). Our results indicate that the current hydrological conditions are such that either drier or wetter conditions would lead to lower relative *Sapium* success in these coastal tallgrass prairies (i.e. *Sapium* vs. prairie vegetation, Fig. 1, Tables 1–3). However, the difference in *Sapium* success in different water treatments was minor without fertilization compared with the differences with fertilization (Tables 1–3, Fig. 1). This suggests that anthropogenic nutrient addition makes the hydrological variation more important than it is in low fertility conditions. It is not what we had predicted nor do we know any hypothesis that predicts such a result. Nonetheless, it does suggest that there are at least two constraints on *Sapium* growth and survival that each becomes more severe at more extreme hydrological conditions.

Together the strong increase in *Sapium* success with fertilization and the peak in *Sapium* success with the current frequency of extreme rainfall events suggest that anthropogenic nutrient loading poses a far greater risk to coastal tallgrass prairies than does changing precipitation patterns. However, it is possible that our experiments that mimicked changing frequencies

of extreme rainfall events are not a reliable predictor of the effects of changing precipitation in general. Furthermore, changing patterns of rainfall are expected to alter the balance between grasslands and forests partly through changes in the frequency and intensity of fires that favor the maintenance of grasslands (Twilley *et al.*, 2001). This would strengthen our conclusion that reduced frequencies of extreme rainfall events will hinder *Sapium* success but would weaken the result for increased frequencies of such rainfall events. Because exotic plant invasions are often so intense and pose such a great risk to natural ecosystems (Mack *et al.*, 2000), understanding how changing climate and other human caused disturbances impact the intensity of biological invasions is critically important.

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