THE ROLE OF ALLELOPATHY IN THE INVASION OF THE CHINESE TALLOW TREE (*SAPIUM SEBIFERUM*)

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Abstract.—The rapid transition from grassland to Chinese tallow tree (*Sapium sebiferum*) woodland may be partly due to allelopathic effects on native plants. A bioassay was performed using aqueous extracts of *Sapium* or little bluestem (*Schizachyrium scoparium*) and *Schizachyrium* seeds. *Schizachyrium* germination rates and germination timing were unaffected by watering treatments. Growth of *Schizachyrium* seedlings was significantly facilitated by watering with *Sapium* extracts versus watering with water. These results suggest that allelopathic effects are not responsible for the competitive success of *Sapium* in coastal prairies.

The Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) (Euphorbiaceae) was originally introduced to Georgia in 1772 through seeds provided by Benjamin Franklin (Bell 1966; Bruce et al. 1997). 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 (Lieux 1975; Scheld et al. 1980; Scheld & Cowles 1981; Scheld et al. 1984; Rockwood et al. 1993; Bruce et al. 1997; Grace 1998). Unfortunately, *Sapium* may be the most serious threat to the biotic integrity of native coastal prairies and floodplain forests. The gravity of the *Sapium* invasion problem is underscored by the Nature Conservancy naming the Chinese tallow tree as one of the worst alien plant species in the U.S. (Flack & Furlow 1996).

Sapium has become naturalized throughout the southeastern United States from the Gulf Coast of Texas to the coast of North Carolina with range limits apparently determined largely by climate (Bruce et al. 1995; Jubinsky 1995; Bruce et al. 1997). It often aggressively displaces native plants and forms monospecific stands (Helm et al. 1991; Bruce et al. 1995; Burks 1996; Jubinsky & Anderson 1996; Bruce et al. 1997; Gordon 1998). A considerable amount of the remaining native coastal prairies of Texas, formerly dominated by little bluestem (*Schizachyrium scoparium*), have been converted to *Sapium* woodlands. *Sapium* has also become the most abundant sapling in floodplain forests of the Big Thicket National Preserve in eastern Texas (Harcombe et al. 1999).

The dynamics of *Sapium* invasion in coastal prairie are characterized by a slow 10 year increase in *Sapium* cover ("establishment") followed by a dramatic increase in *Sapium* over the next 10 years ("displacement"). Within 30 years of the appearance of the first *Sapium* seedling, a coastal prairie is converted into a biotically depauperate woodland that is highly dominated by *Sapium*. These woodlands appear to be self-replacing with *Sapium* also dominating recruitment into the canopy (Bruce et al. 1995).

It has been suggested that the rapid transition from coastal prairie to *Sapium* woodland and the extreme dominance of *Sapium* in these woodlands result from allelopathic effects of *Sapium* on other plant species (Flack & Furlow 1996; Conway 1997). Evidence in favor of this hypothesis includes a sparse, low diversity understory in *Sapium* woodlands. Allelopathy can impact germination (Halligan 1975; Wicklow 1977; Keeley et al 1985; Tanrisever et al 1988), growth (Petranka & McPherson 1979; Barnes & Putnam 1987; Callaway et al. 1991; Mahall & Callaway 1992), and/or survival rates of competitors (Muller 1953; Chapin et al 1994). Although bioassays have the limitation of low correlation between field distribution and bioassay results (Stowe 1979; Myster & Pickett 1992) they do have the advantage of providing a rapid, replicated and precisely controlled method of screening for allelopathic effects (del Moral & Cates 1971; Blum 1999; Inderjit & Dakshini 1999).

A greenhouse bioassay experiment was conducted to test for allelopathic effects of *Sapium* litter on *Schizachyrium* germination rates and growth. If allelopathy plays a role in the rapid invasion of *Sapium*, then it would be predicted that *Sapium* litter would reduce *Schizachyrium* germination and growth.

Materials and Methods

Extract solutions.—Two solutions of aqueous extract were prepared in order to test the hypothesis that *Sapium* has an allelopathic effect on *Schizachyrium*. Clipped tallow twigs and leaves and clipped native coastal prairie vegetation obtained at the University of Houston Coastal Center (primarily *Schizachyrium*; Harcombe et al. 1993) were weighed and then submerged in deionized water in five gallon plastic buckets. A small subsample of the clipped biomass of each type was oven dried to provide a dry weight estimate. Plant biomass was submerged and soaked for 23 days, 15 of which were in a cold room with an aeration tube bubbling in each bucket.

Solutions were autoclaved for one hour at 110 degrees C in order to eliminate any bacterial or fungal agents that may influence seed germination and plant growth. Because the purpose of this study was to screen for allelopathic effects of *Sapium* litter on germination and growth of *Schizachyrium* the following spring, potential loss of volatile compounds is unlikely to be important. Autoclaved solutions were filtered to remove debris and sediment. The solutions were transferred to Nalgene carboys and diluted to a standard concentration of 1 g dry weight per 200 mL. All solutions were refrigerated during the experiment. The control solution was deionized water.

Seedlings.—For each of the three treatments, sixty 255 mL plastic cups were used. Cups without drain holes were filled with potting soil moistened with 50 mL of deionized water. A thin layer of horticultural charcoal was placed in the bottom of each cup to prevent root rot in the non-draining pots and to keep the soil mixture fresh. Ten seeds of field collected *Schizachyrium scoparium* were planted in each cup. An additional fifteen pots did not receive seeds in order to monitor the effects of solutions and sterility of the soil mixture (i.e., seeds, fungus).

Seeds were planted into cups on 15 January 1999 to a depth of ≈ 0.5 cm. All pots received 50 mL of the appropriate treatment solutions on the following day. Pots were watered with 50 mL of the appropriate treatment solution semi-weekly. All pots were randomly located on a laboratory table beneath incandescent and fluorescent gro-lights on a 14 hour light/10 hour dark cycle and rotated frequently.

Pots were checked for germinating plants daily. Each plant was harvested eight weeks after its germination date. Roots were carefully washed from the soil. They were dried to constant mass and the root and shoot dry mass were weighed separately.

Analyses.—*ANOVA* was used to test whether *Schizachyrium* germination rate, time of germination (days after planting), shoot mass at eight weeks, root mass at eight weeks and total mass at eight weeks depended on watering treatment (three level categorical variable). Fisher's Least Significant Difference Test was used to test whether treatment means differed.

Table 1. The dependence of *Schizachyrium* root mass, shoot mass and total mass at 8 weeks post-germination on watering with distilled water (Control), *Schizachyrium* extracts (Schiz) or *Sapium* extracts (Tallow). Overall model results are from *ANOVA* and means contrasts are Fisher's Least Significant Difference tests.

	Overall Model		Means Contrasts		
Variable	$F_{2,41}$	*P*-value	C, S	C, T	S, T
Germination rate	0.6	0.55	0.56	0.28	0.59
Germination timing	0.5	0.62	0.33	0.46	0.85
Root mass	3.3	<0.05	0.09	<0.05	0.37
Shoot mass	3.1	0.06	0.11	<0.05	0.34
Total mass	3.6	<0.05	0.08	<0.05	0.32

RESULTS

Schizachyrium germination rate and timing were independent of watering treatment (Table 1). Overall germination percentage was 3%. Final shoot mass did not depend significantly on watering treatment but seedlings watered with *Sapium* extracts were significantly larger than controls in means contrasts (Figure 1, Table 1). Final root mass and final total mass both depended significantly on watering treatments in an *ANOVA* and seedlings watered with *Sapium* extracts were significantly larger than controls in means contrasts (Figure 1, Table 1).

DISCUSSION

Sapium extracts did not reduce or slow germination of *Schizachyrium* seeds compared to *Schizachyrium* extracts or controls (Table 1). Growth of *Schizachyrium* was significantly increased by watering with *Sapium* extracts versus watering with controls. This facilitation is possibly due to nutrients in the extract since growth of *Sapium* watered and *Schizachyrium* watered seedlings were not significantly different from each other. This suggests that allelopathy does not play an important role in the displacement of coastal prairie vegetation by Chinese Tallow Tree. However, there are a number of ways to test for allelopathy (Rice 1984); this study is not definitive but rather represents a single piece of negative evidence.

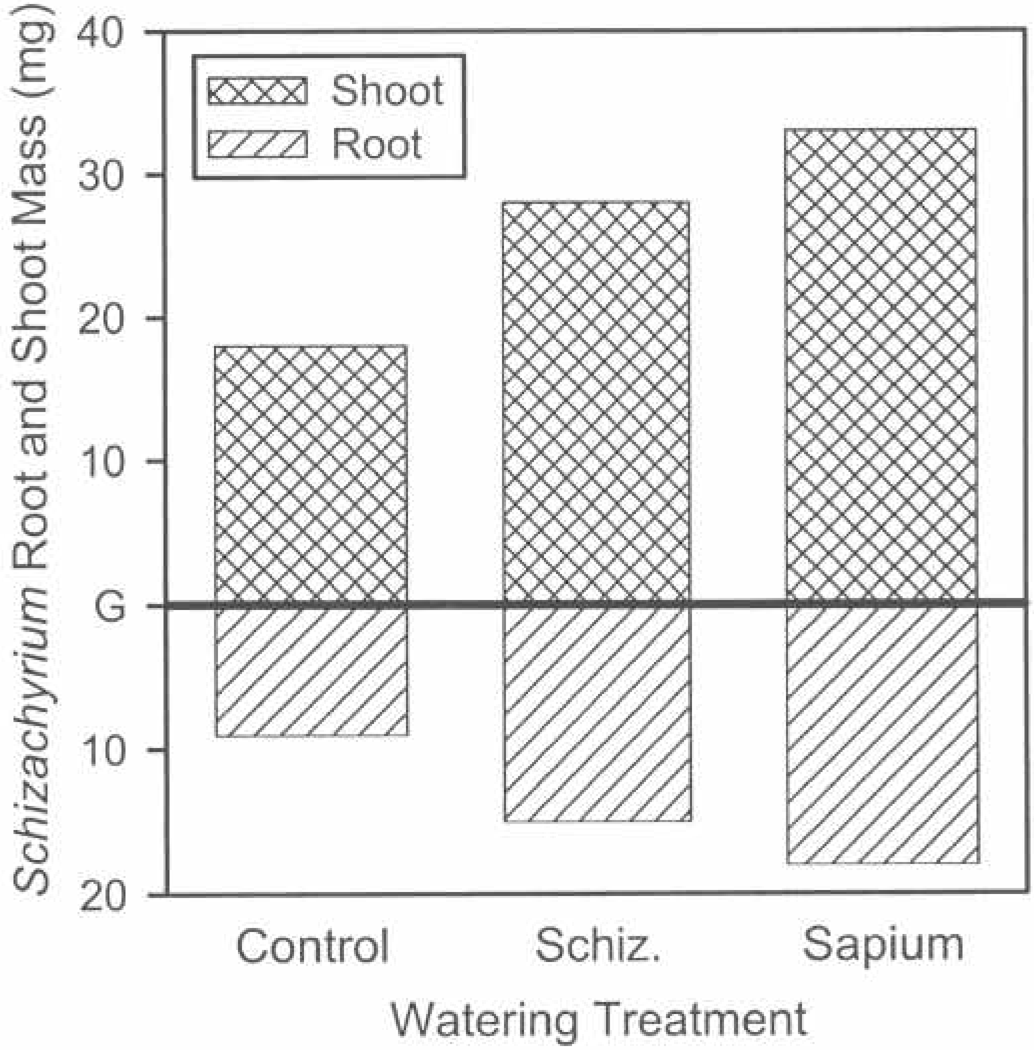

Figure 1. Dependence of *Schizachyrium* root and shoot mass at 8 week harvest on watering with water (Control), *Schizachyrium* extracts (Schiz.) and *Sapium* extracts (Sapium). G=ground.

Conway (1997) performed a bioassay to determine whether aqueous *Sapium* extracts or *Sapium* litter impacted the germination or growth of black willow (*Salix nigra*), baldcypress (*Taxodium distichum*), *Sapium* or lettuce from seeds. He found that *Sapium* extract sometimes enhanced germination or growth but never significantly reduced germination or growth of these species. He was not able to isolate any known allelochemicals in his aqueous extracts. His results, together with those presented here, suggest that allelopathy does not likely play a role in the invasion of *Sapium* into any Gulf Coast habitats.

Other factors that cause a rapid transition from coastal prairie to *Sapium* woodland include: high local seed supply or facilitation of *Sapium* establishment by changes in resources under *Sapium* trees. In fact, the density of *Sapium* seeds under a *Sapium* tree in a prairie observed during this study was two orders of magnitude higher than in a coastal prairie in the early stages of invasion without seed producing trees. The success of seedlings may also be higher under a *Sapium* tree in coastal prairie. In a greenhouse experiment, increasing soil fertility or lowering light availability to levels found under a mature Tallow tree promoted *Sapium* invasion into mature prairie sod. These results together with those of this allelopathy bioassay suggest that allelopathic effects are not responsible for rapid transition of coastal prairie to *Sapium* woodland.

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