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# Potential Allelopathic Interference by the Exotic Chinese Tallow Tree (Sapium sebiferum) (Abstract)

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# Potential Allelopathic Interference by the Exotic Chinese Tallow Tree (*Sapium sebiferum*)

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ABSTRACT.—The Chinese tallow tree (*Sapium sebiferum*) was introduced into the southeastern United States in late 1800s and has rapidly naturalized throughout the region's coastal ecosystems. Because tallow forms monotypic woodlands, we hypothesized that allelopathic interference is a mechanism by which tallow maintains and expands its presence. Laboratory experiments were performed using black willow (*Salix nigra*), baldcypress (*Taxodium distichum*) and tallow, as test species, to examine the hypothesis that aqueous tallow extracts inhibit seed germination and seedling root growth, shoot growth and mass. Extracts were prepared from tallow litter, woodland soil from under tallow trees and fresh tallow leaves. Samples were collected during October, January, April and July to determine any seasonal differences in allelopathic potential. Germination, root and shoot lengths and seedling mass differed ($P < 0.05$) among treatments for willow, baldcypress and tallow. Black willow germination did not vary ($P > 0.05$) among control and April litter or April soil treatments; the treatments designed to mimic conditions when black willow naturally germinates. Although germination was lower ($P < 0.05$) in April fresh leaf and July litter, soil and leaf treatments than control treatments, black willow does not germinate during July nor do black willow seeds contact fresh tallow leaves during April. Germination rates for baldcypress and tallow during April and July litter and soil treatments were higher ($P < 0.05$) than control treatments. Similarly, baldcypress seedling root length, shoot length and mass were the same or higher than control treatments ($P < 0.05$). Tallow seedling root length, shoot length and mass were lower ($P < 0.05$) in controls versus April and July litter and soil treatments. Our experiment questions the validity of allelopathic interference as a mechanism enhancing tallow invasion or maintaining woodlands once established. Because of its enhanced germination and seedling growth when exposed to its own experimental treatments, tallow may in fact be perpetuating its own woodland(s) by self facilitation, rather than inhibiting other plant survival by allelopathic interference.

## INTRODUCTION

Exploitative resource competition may be viewed as a primary mechanism by which native plant communities coexist, structure themselves and concomitantly resist invasion (Taylor and Aarssen, 1990; D'Antonio, 1993). Whereas resource competition can structure native communities, the same type of exploitation by exotic plants likely enhances their successful naturalization (Berkowitz *et al.*, 1995; Woods, 1997). However, even under strictly natural conditions, inter-and intraspecific interactions by resource competition do not occur in isolation from other potentially important ecological mechanisms such as facilitation, interference and allelopathy (Thijs *et al.*, 1994; Callaway and Walker, 1997; Inderjit and del Moral, 1997). Multiple mechanisms, such as resource competition, facilitation, site or resource pre-emption, direct physical factors and chemical interference by allelopathy, may drive ecosystem structure and function (D'Antonio, 1993; Rice, 1995; Callaway and Walker,

1997; Inderjit and del Moral, 1997). The overall impact of one species on others may be viewed as cumulative or synergistic.

Allelopathy is defined as the process by which plants release phytochemicals directly into their surrounding environment, inhibiting seed germination and seedling growth of neighboring species (Rice, 1995). Such impacts would provide producers competitive advantages (Gopal and Goel, 1993). However, it is difficult to isolate allelopathic interference from other community structuring mechanisms (Harper, 1977; Stowe, 1979; Thijs *et al.*, 1994), particularly when deciphering mechanisms of invasion by exotic species.

Tallow (*Sapium sebiferum* L. Roxb.) is an exotic deciduous tree that was introduced into the United States in the late 1800s (Bruce *et al.*, 1997), primarily since 1970 (NRCS, 1993) in the southeastern and south-central U.S. Tallow invasion in wetland and upland habitats has been favored by its rapid growth rates, large annual seed loads and modification of natural disturbance regimes (Scheld and Cowles, 1981; Scheld *et al.*, 1984; Cameron and Spencer, 1989; Harcombe *et al.*, 1993; Bruce *et al.*, 1997). Once naturalized, tallow forms monotypic woodlands with little or no woody understory (Bruce *et al.*, 1997). Reduction or absence of understory vegetation in a multilayered plant community is characteristic of allelopathic interference and tallow has been suspected of such on loblolly pine (*Pinus taeda*) regeneration (Gresham, 1986). Past studies have detected tannins and other potential allelochemicals in tallow leaves and bark (Cameron and LaPoint, 1978; Yang and Kinghorn, 1985) and its leaves are toxic to domesticated herbivores (Russell *et al.*, 1969). Tallow also drives some ecosystem-level processes by denitrifying soil and accelerating litter decomposition (Cameron and LaPoint, 1978; Cameron and Spencer, 1989).

Based upon these reports of its general biology and understory patterning indicative of potential allelopathy, we tested the hypothesis that tallow exerts allelopathic interference by inhibiting seed germination and seedling development in other species by allelochemical release from its leaves, litter and woodland soil. Native black willow (*Salix nigra*) and baldcypress (*Taxodium distichum*) and exotic tallow were used as target species.

## METHODS

In 1995 and 1996 tallow litter, soil and fresh leaf samples were collected from a monotypic tallow woodland in the Brazoria National Wildlife Refuge (BNWR) (29°10′N 95°8′W) in Brazoria County, Texas. The woodland was dominated by tallow trees (Conway *et al.*, 1999) with a mean canopy height of 9.75 m. Although the area was previously native riparian habitat, no native woody trees existed at the site.

Black willow and baldcypress were selected as test species because they are native and found in wetland habitats throughout the Texas coast (Smeins *et al.*, 1992) and formerly existed at the study site (J. F. Bergan, pers. comm.). Black willow trees do presently exist at BNWR although they did not occur in the woodland in which the study was conducted (pers. obs.). Baldcypress seeds were collected from native stands located near Houston, Texas. Baldcypress seeds were rinsed twice in alcohol to remove resins and scarify the seed coat (Bonner, 1974a) and then subjected to a continual cold water (22 C) rinse for 36 h and placed in a refrigerator (8 C) for 40 d. We randomly collected black willow seeds at The Nature Conservancy of Texas' Mad Island Marsh Preserve (MIMP) (28°10′N 95°8′W) in Matagorda County, Texas. No seed pretreatment is necessary for black willow seeds (Brinkman, 1974; Hupp, 1992), as mature seeds are viable for a short time (Brinkman, 1974). To prolong viability willow seeds were placed in plastic bags and stored in a freezer (<0 C) (Brinkman, 1974). We collected undamaged, ripe tallow seeds from randomly selected trees (n = 15) during September, October and November 1995 from the MIMP and BNWR (Conway *et al.*, 2000). Seeds were placed in paper bags and stored at 20 C (Bonner,

1974b). No seed pretreatment protocol has been developed for tallow (Bonner, 1974b; Conway *et al.*, 2000).

*Tallow extract preparation.*—We collected 30 g samples (300 g total) each of fresh tallow leaves, litter and soil from 10 randomly selected tallow trees at the BNWR during October, 1995, January, April and July 1996. These sampling periods correspond to leaf litter decay (January), the beginning of the growing season and native woody plant germination (April), the middle of the growing season (July) and during leaf fall, after the growing season (October). Only undamaged leaves were collected to prevent potential release of internal compounds (Richardson and Williamson, 1988). We did not collect fresh tallow leaves in January 1996 because leaves were not present (Conway *et al.*, 1999). Tallow litter (*i.e.*, leaves, twigs and seed hulls) samples were collected <1 m from the base of the selected tree directly from the woodland floor. We collected soil samples 180° from where litter samples were removed to a depth of 2.5 cm. The woodland floor was cleared of litter, after which soil samples were removed using a small hand shovel. Leaf, litter and soil samples were placed in separate paper bags and placed on dry ice to prevent enzymatic degradation (Wilson *et al.*, 1975).

When preparing aqueous tallow extracts we used composite samples to reduce potential variability among samples within each sampling date (Lodhi, 1975). We placed 200 g (*i.e.*, 20 g from each 30 g sample) of each material (*i.e.*, tallow leaves, litter or soil) in 2 L of distilled water to make a 1:10 mass to volume (m:v) aqueous extract. After samples were immersed into the distilled water, containers were sealed and refrigerated at (6–8 C) for 36 h under dark conditions. Each sample was filtered through Whatman No. 2 filter paper. Once filtered, filtrate was replaced into the extract container which was resealed and stored at <0 C, so as not to degrade potential allelochemicals (Waterman and Mole, 1994; Zhu and Mallik, 1994).

*Germination experiments.*—Germination experiments were performed in 10 cm sterilized petri dishes. Each dish was lined with a single sheet of Whatman No. 1 filter paper and irrigated with 5 ml of a particular experimental tallow aqueous extract, as prepared (*i.e.*, 1:10 m:v). We sowed each dish with 20 seeds of a test species (*i.e.*, black willow (BW), baldcypress (BC) or tallow (CT)). There were 40 dishes (*i.e.*, 10 BW, 10 BC and 20 CT) for each month (January, April, July, October) and type (*i.e.*, aqueous tallow leaf, litter or soil extract) treatment combination. Treatments in which tallow was the test species consisted of 20 dishes, due to the difficulty of germinating those seeds (Conway *et al.*, 2000). The control treatment consisted of 40 dishes (10 BW, 10 BC and 20 CT), each sown with 20 seeds and irrigated with 5 ml of distilled water (Zhu and Mallik, 1994).

After petri dishes were sown they were placed into a Stults Scientific 100% humidity germination chamber. Germination experiments were performed from June through mid-August 1996, maintaining a temperature/light regime of 20 C for 8 h dark and 30 C for 16 h light (Zhu and Mallik, 1994). Baldcypress dishes remained in the germination chamber for 28 d (Richardson and Williamson, 1988), black willow for 14 d because of their rapid germination, and tallow for 35 d, due to difficulty germinating these seeds (Conway *et al.*, 2000).

Percent germination was calculated for each dish. Seeds were considered germinated if radicles emerged from the seed (Groves and Anderson, 1981). Root length (mm), shoot length (mm) and seedling mass (g) were measured for each seedling (Zhu and Mallik, 1994). Due to small seedling size, dry mass could not be accurately measured for black willow seedlings. Consequently, we measured fresh mass for all seedlings (Klein *et al.*, 1991), an appropriate measure for evaluating allelopathic potential (Inderjit, 1996). For black

willow seedlings, total seedling length was measured rather than separate root and shoot lengths, due to small seedling size.

*Chromatographic analysis.*—Tallow leaf, litter and soil aqueous extracts were subjected to chromatographic analysis to assess the presence of potential allelochemicals. We divided each composite tallow extract into three subsamples and subjected them to chromatographic analyses. Analyses were performed by the Veterinary, Anatomy and Public Health Department of Texas A&M University, College Station, Texas, U.S.A., during June–July 1997. All gas chromatography/mass spectrophotometry (GC/MS) analyses and methodology were conducted following standard protocol (Clement *et al.*, 1997). Analyses were performed using a Hewlett Packard Model 5970 C system equipped with a splitless heated injection port. Grade 0 helium was used as the carrier gas and the transfer line was maintained at 280 C. Initial sample preparation was performed using a methanol soxhlet boiling procedure which disintegrates plant cellular integrity, leaving extractable material. Chloroform was added to the sample, which was then evaporated to a dry state, leaving a chloroform extract. This extract was suspended in a water soluble solvent, washed with water, washed with 10% hydrochloric acid (HCl) and then washed with 10% sodium chloride (NaCl). The final solute was passed through an anion exchange column. The chromatographic column was a Hewlett Packard-Ultra 1 cross-linked methyl silicone. Mass spectral data were collected as the total ion chromatograms in the operating range of 35 to 800 amu. Preliminary compound identification was made by library comparison, but final identification was performed by direct spectral comparison using the sample compound and an authentic sample generated using the GC/MS system. Authentic samples were either purchased or prepared by standard chemical procedures.

*Data analysis.*—For each test species we used a 2-way factorial analysis of variance (ANOVA) to analyze differences in percent germination, root length, shoot length and seedling mass. Independent variables were tallow aqueous extract type (litter, soil and fresh leaf), month (January, April, July and October) and controls. Initial analyses were conducted among months and the controls, between soil and litter treatments only. Fresh leaf extract treatments were excluded from these initial analyses to compensate for an unbalanced design where there was no January leaf extract treatment. If interactions ($P < 0.05$) occurred during the 2-way ANOVA, analyses were performed within extract type (*i.e.*, within litter or soil extract type) among months and the controls. We compared the control against all month x extract type combinations. When testing for differences including leaf extract treatments, we first performed a 2-way ANOVA among litter, soil and leaf extract treatments among April, July and October only. If interactions ($P < 0.05$) occurred among types and months, subsequent analyses were conducted within leaf extract treatments among months and the control.

Analyses performed using percent germination data included all data points, whereas analyses conducted on seedling root length, seedling shoot length and seedling mass were conducted on nonzero data only. Black willow percent germination was not transformed (Shapiro-Wilks'; $W = 0.98$; $P = 0.799$), but black willow seedling mass data, all tallow data and baldcypress seedling mass data were rank transformed (Conover and Iman, 1981). We square root transformed baldcypress percent germination, seedling root and shoot length data and black willow seedling length data (Conover and Iman, 1981). If differences ($\alpha < 0.05$) occurred, we conducted least squares mean separation (Zar, 1996). We did not use Bonferroni confidence intervals during mean separation. Consequently, in instances where no differences were detected ($P > 0.05$), we attempted to avoid committing Type II errors by maintaining a higher alpha level, which is a more conservative approach (Zar, 1996). Analyses were conducted using SAS (1995). All reported means were back transformed.

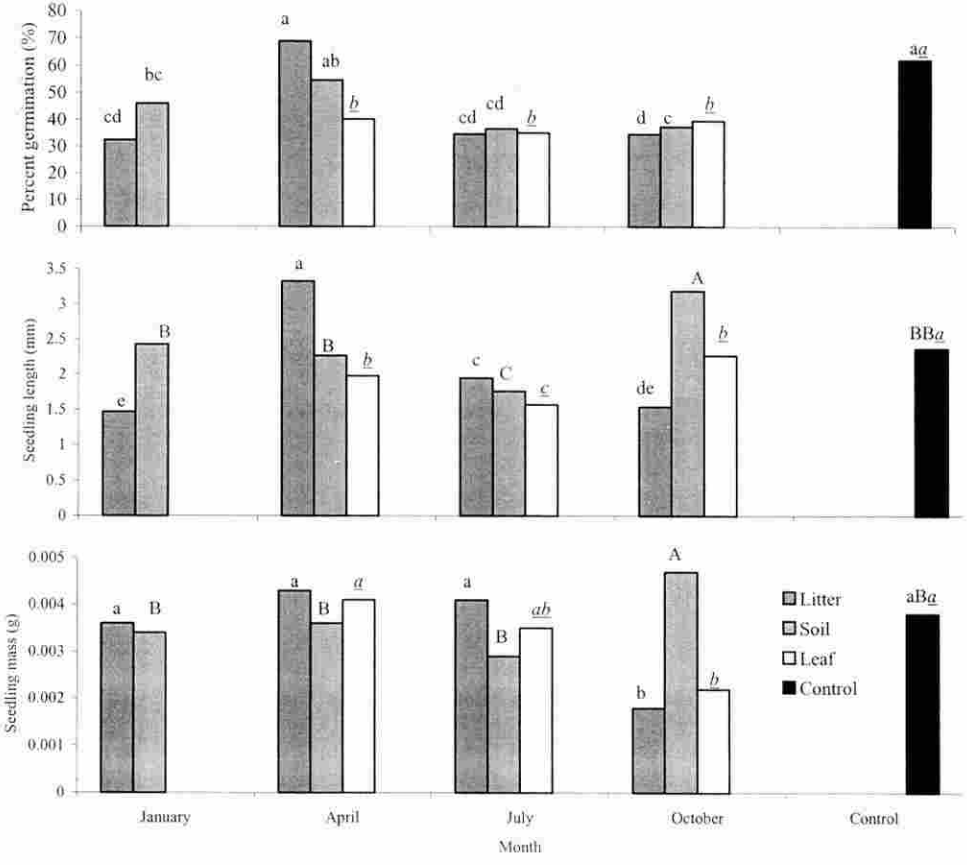


FIG. 1.—Means of percent germination, seedling length and mass for black willow seeds exposed to aqueous Chinese tallow extracts during seed germination experiments. Several interactions ($P < 0.05$) occurred during analyses, such that bars below the same letter and same letter type (*i.e.*, a, b, *a*, *b*, A, B, etc). are not different ($P > 0.05$)

## RESULTS

*Black willow.*—Percent germination varied among months ($F = 11.96_{3,81}$, $P < 0.001$) among litter and soil extract treatments and differed ($F = 4.06_{2,36}$, $P = 0.014$) for fresh leaf treatments (Fig. 1). Highest germination rates were observed for control and April litter treatments, but were reduced in July litter and soil treatments compared to the control ($F = 12.25_{1,81}$, $P < 0.001$). Seedling length was greatest ($F = 23.96_{3,44}$, $P < 0.001$) in April litter treatments and October soil treatments ($F = 10.79_{3,44}$, $P < 0.001$), but was reduced in October litter and July soil treatments. Seedling mass was greater ($F = 4.45_{1,44}$, $P = 0.041$) in October soil treatments than the control, but April and July litter treatments did not vary ($F = 3.09_{1,44}$, $P = 0.086$) from the control. Seedling mass varied among months ($F = 4.75_{3,35}$, $P = 0.007$) within fresh leaf extract treatments, but were not consistently less than the control ($F = 3.74_{1,35}$, $P = 0.061$) (Fig. 1).

*Baldcypress.*—Germination rates were higher ($F = 4.07_{1,81}$, $P = 0.047$) in all litter and soil treatments than in the control (Fig. 2). Percent germination was higher ($F = 6.22_{2,36}$,

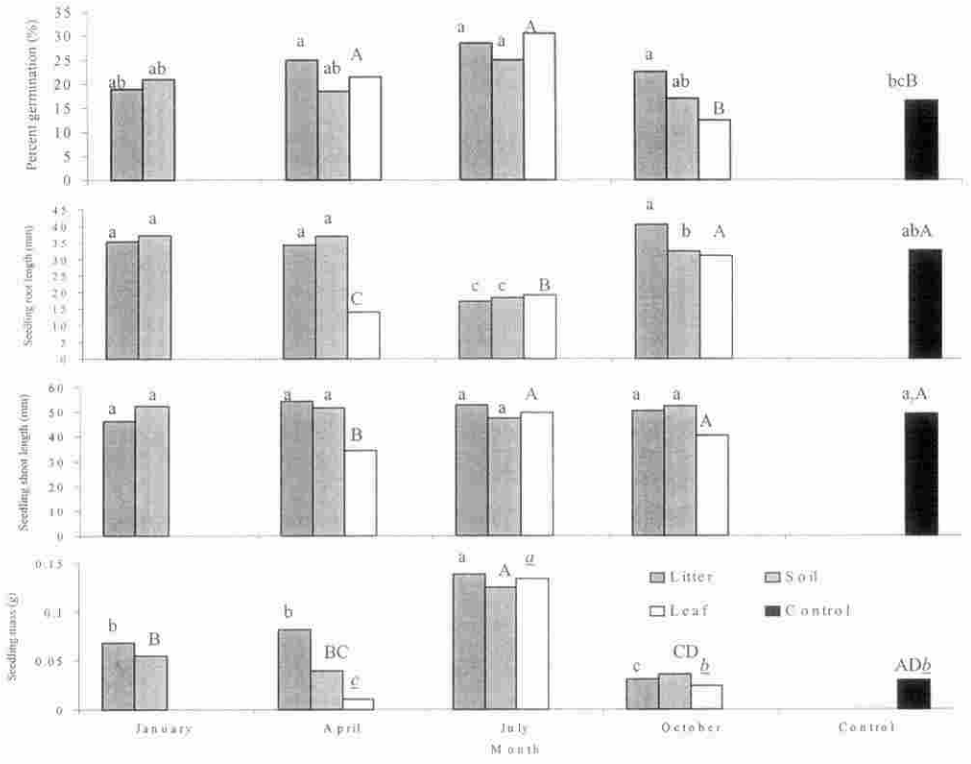


FIG. 2.—Means of percent germination, root length, shoot length, and seedling mass for baldcypress seeds exposed to Chinese tallow extracts during seed germination experiments. Several interactions ($P < 0.05$) occurred during analyses, such that bars below the same letter and same letter type (*i.e.*, a, b, *a*, *b*, A, B, etc), are not different ($P > 0.05$).

$P = 0.016$) in April and July fresh leaf extract treatments than October treatments. Root length was reduced in July soil and litter treatments ($F = 4.13_{1,79}$, $P = 0.046$) and April and July fresh leaf treatments as ($F = 22.78_{1,33}$, $P < 0.001$) as compared to the control. Seedling shoot length varied ($F = 5.68_{3,79}$, $P < 0.001$) among months, but litter and soil treatments were generally similar to the control ($F = 1.39_{1,79}$, $P = 0.242$). Shoot length was less ($F = 4.19_{3,34}$, $P = 0.012$) in April fresh leaf treatments as compared to July and October fresh leaf treatments. Seedling mass was greater in April and July litter ($F = 22.49_{3,43}$, $P < 0.001$) and soil ($F = 9.98_{3,44}$, $P < 0.001$) treatments than the control ($F = 22.85_{1,43}$, $P < 0.001$), ($F = 14.61_{1,44}$, $P < 0.001$), respectively (Fig. 2).

*Tallow.*—Percent germination varied among months ($F = 17.84_{3,95}$, $P < 0.001$) ($F = 5.41_{3,95}$, $P = 0.002$) and germination was higher than the control ($F = 18.70_{1,95}$, $P < 0.001$) ($F = 20.77_{1,95}$, $P < 0.001$) for litter and soil treatments, respectively (Fig. 3). Root length varied among months ($F = 15.10_{3,103}$, $P < 0.001$) for litter and soil treatments, where root lengths were greatest in January and October soil treatments. Shoot length varied by month ($F = 5.87_{3,27}$, $P = 0.003$), where shoot lengths were greatest in January, April and October soil treatments. Seedling mass varied by month ($F = 8.80_{3,48}$, $P < 0.001$) ($F = 5.69_{3,56}$, $P = 0.002$) and differed from the distilled water control ($F = 4.83_{1,48}$, $P = 0.033$) ($F = 8.80_{1,56}$, $P = 0.004$) for litter and soil treatments, respectively (Fig. 3).

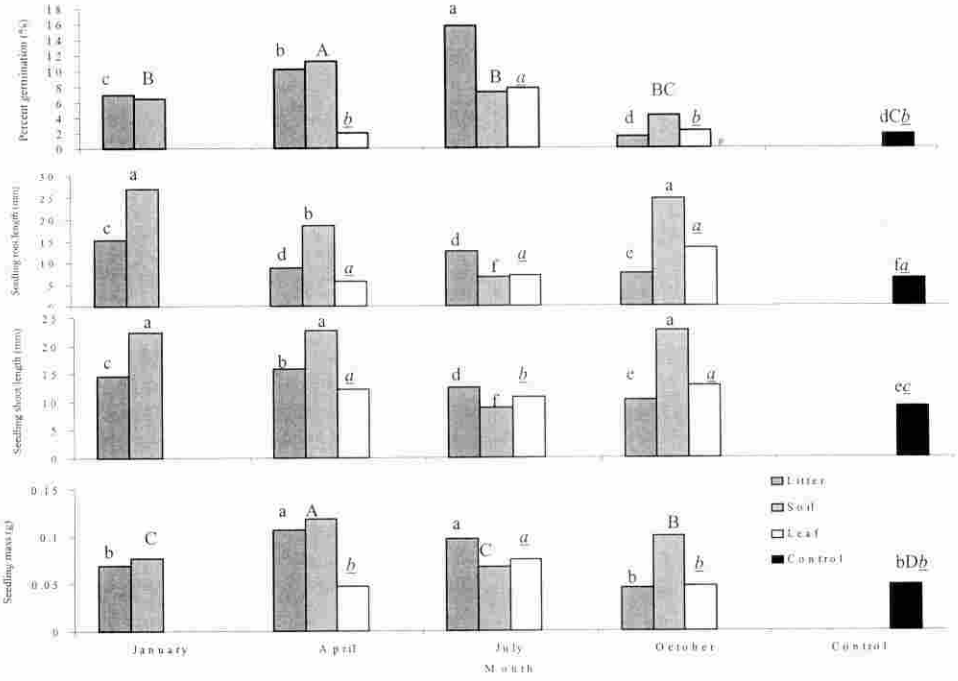


FIG. 3.—Means of percent germination, root length, shoot length and seedling mass for Chinese tallow seeds exposed to Chinese tallow extracts during seed germination experiments. Several interactions ($P < 0.05$) occurred during analyses, such that bars below the same letter and same letter type (*i.e.*, a, b, *a*, *b*, A, B, etc). are not different ($P > 0.05$)

*Chromatographic analysis.*—The only chemical detected in any of the aqueous tallow extracts was inositol. There was not sufficient sample to identify the exact inositol isomers detected, but they were probably myo-inositol or epi-inositol (B. Clement, pers. comm., Texas A&M Univ. College Station, TX). Inositols were detected in every aqueous tallow extract. The January soil extract sample showed the highest peak, but in each instance, inositol appeared after 73–74 min in the chromatographic column.

## DISCUSSION

*Lack of allelopathic interference.*—Our experiments showed varied responses by black willow, baldcypress and tallow seeds and seedlings exposed to tallow extract treatments, but no inhibition. Although our statistical approach was conservative, if allelopathic interference were important, inhibition of seed germination and reductions in seedling size and mass would have been particularly observed during the April and July germination and growing season treatments. Our results corroborate another study of allelopathic interference by Chinese tallow upon little bluestem (*Schizachyrium scoparium*), where inhibition did not occur, but germination and growth rates of bluestem were actually facilitated by tallow extracts (Keay *et al.*, 2000).

Seed germination of black willow naturally occurs during April (Hupp, 1992; Walters and Reich, 1996), but in the April litter and soil treatments, germination did not vary from the control. Germination in the April fresh-leaf treatments was lower than the control, but fresh

leaves are not present on woodland floors during this time of year (Cameron and Spencer, 1989). July treatments reduced willow germination, but analogous with the April leaf treatments, willow seeds are not normally viable in July (Brinkman, 1974) under natural conditions. Similarly, seedling length and mass were either greater or the same in the April litter and soil treatments compared to the control. If allelopathic interference by tallow were an important mechanism for preventing black willow germination and growth, it would have been observed during the April treatments.

Germination and establishment of baldcypress generally occurs later in the growing season than black willow, closer to July than April. However, no reduction in germination was observed for either the July or April treatments for baldcypress; in fact, germination rates were higher in the July and April treatments than the control. If baldcypress successfully germinated, without any reduction in germination rates resulting during April, then seedling establishment and growth would occur during July. In the July litter and soil treatments seedling mass was either greater or the same as the control for these treatments. Although the July baldcypress results for root and shoot lengths were variable, seedling mass for all the July treatments were at least three times greater than controls.

Results of the germination experiments are supported by the GC/MS analysis. Although GC/MS analysis does not purify or isolate compounds, this analysis is the most sensitive technique available for identifying unknown compounds (Waterman and Mole, 1994). Inositol was the only phytochemical identified from GC/MS analyses. Inositols are typically crystalline, water soluble, high melting point compounds commonly found as latex derivatives (Pigman and Goepp, 1948) with little or no allelopathic potential (Rice, 1995).

No common water soluble (*i.e.*, tannins, phenols, alkaloids, etc.) (Muller, 1969; Rice, 1995) allelochemicals were detected in any of the aqueous tallow extracts, because such compounds would not be detectable based upon the procedures used here to prepare extracts. Our GC/MS results differ from previous research, which reported tannins in fresh and fallen tallow leaves (Cameron and LaPoint, 1978; Cameron and Spencer, 1989), roots and bark (Yang and Kinghorn, 1985) and in ephemeral tallow woodland ponds after leaf fall (Cameron and LaPoint, 1978). However, in those studies actual plant material was analysed using an acidified vanillin test (Cameron and LaPoint, 1978; Cameron and Spencer, 1989) which uses methanol to destroy cell walls, releasing cell contents to extract tannins (Waterman and Mole, 1994). Comparing results from methanol-extracted material versus aqueous extracts is incompatible in terms of relating to allelopathic interference (Stowe, 1979; Heisey and Delwiche, 1985). The extraction procedures used in our study were designed to: (1) simulate rainfall or flooding events and (2) eliminate confounding factors (*i.e.*, chemical, physical or biological interactions) found under natural conditions. Consequently, when exposing test species to experimental treatments, such interactions were removed to focus upon the impacts of prepared aqueous extracts on test species.

*Tallow: potential self facilitation.*—Tallow seeds exposed to control treatments had poor (1.75%) germination rates, but germination has proven difficult under laboratory conditions (Conway *et al.*, 2000). Enhancement of response variables (*i.e.*, germination and seedling size and mass) in experimental treatments as compared to controls was observed in all month/treatment type combinations when tallow was the test species. Although tallow germination rates were generally low among treatments, no germination inhibition nor seedling growth reduction was observed when exposed to treatments. Allelopathic treatments consistently enhanced tallow germination and growth. Such results have potentially important implications in terms of future tallow expansion and woodland maintenance and control (Conway *et al.*, 1999).

Tallow drives the soil-nutrient distribution in its woodlands by large annual autumn leaf

loads and rapid leaf decomposition (Cameron and Spencer, 1989; Harcombe *et al.*, 1993). These leaf decomposition/nutrient release cycles likely enhance tallow establishment (Cameron and Spencer, 1989; Harcombe *et al.*, 1993) rather than inhibit germination and growth of other species (sensu Ramakrishnan and Vitousek, 1989; Vitousek and Walker, 1989; Vitousek, 1990). These patterns observed from prior field studies (Cameron and Spencer, 1989; Harcombe *et al.*, 1993), combined with results from the present study, suggest that tallow promotes its own growth and survival rather than inhibits establishment of other species. Rather than specifically inhibiting establishment of other species, tallow engages in a successful self-perpetuating establishment/naturalization cycle, heightened by its own rapid growth, ability to vigorously resprout, large seed loads (4500 kg seeds $ha^{-1}$ $yr^{-1}$) and rapid leaf decomposition cycles (Scheld and Cowles, 1981; Scheld *et al.*, 1984). Consequently, future control and management efforts as well as basic ecological/coexistence studies need to focus upon this self-perpetuating/self-facilitation aspect of tallow ecology.

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## LITERATURE CITED

BERKOWITZ, A. R., C. D. CANHAM AND V. R. KELLY. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. *Ecology*, **76**:1156–1168.

BONNER, F. T. 1974a. *Taxodium distichum* (L.) Rich. Baldcypress, p. 796–798. *In:* C. S. Schopmeyer (ed.). Seeds of woody plants in the United States. United States Department of Agriculture, Forest Service Agricultural Handbook No. 450. Washington, D.C.

———. 1974b. *Sapium sebiferum* (L.) Roxb. Tallowtree, p. 760. *In:* C. S. Schopmeyer (ed.). Seeds of woody plants in the United States. United States Department of Agriculture, Forest Service Agricultural Handbook No. 450. Washington, D.C.

BRINKMAN, K. A. 1974. *Salix* L.Willow, p. 746–750. *In:* C. S. Schopmeyer (ed.). Seeds of woody plants in the United States. United States Department of Agriculture, Forest Service Agricultural Handbook No. 450. Washington, D.C.

BRUCE, K. A., G. N. CAMERON, P. A. HARCOMBE AND G. JUBINSKY. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb). *Nat. Areas J.*, **17**:255–260.

CALLAWAY, R. M. AND L. R. WALKER. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**:1958–1965.

CAMERON, G. N. AND T. W. LAPOINT. 1978. Effects of tannins on the decomposition of Chinese tallow leaves by terrestrial and aquatic invertebrates. *Oecologia*, **32**:349–366.

——— AND S. R. SPENCER. 1989. Rapid leaf decay and nutrient release in a Chinese tallow forest. *Oecologia*, **80**:222–228.

CLEMENT, B. A., C. M. GOFF AND T. D. A. FORBES. 1997. Toxic amines and alkaloids from *Acacia berlandieri*. *Phytochemistry*, **46**:249–254.

CONOVER, W. J. AND R. L. IMAN. 1981. Rank transformations as a bridge between parametric and nonparametric tests. *Am. Stat.*, **35**:124–129.

CONWAY, W. C., L. M. SMITH, R. E. SOSEBEE AND J. F. BERGAN. 1999. Total nonstructural carbohydrate trends in Chinese tallow. *J. Range Manage.*, **52**:539–542.

———, ——— AND J. F. BERGAN. 2000. Evaluating germination protocols for Chinese tallow (*Sapium sebiferum*) seeds. *Tex. J. Sci.*, **52**:267–270.

D'ANTONIO, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology*, **74**:83–95.

GOPAL, B. AND U. GOEL. 1993. Competition and allelopathy in aquatic plant communities. *Bot. Rev.*, **59**:155–210.

GRESHAM, C. A. 1986. Potential allelopathic interactions of *Sapium sebiferum* on loblolly pine germination and seedling growth. Proceedings of the Fourth Biennial Southern Silvicultural Research Conference United States Forest Service General Technical Report SE-42.

GROVES, C. R. AND J. E. ANDERSON. 1981. Allelopathic effects of *Artemesia tridentata* leaves on germination and growth of two grass species. *Am. Midl. Nat.*, **106**:73–79.

HARCOMBE, P. A., G. N. CAMERON AND E. G. GLUMAC. 1993. Above-ground net primary productivity in adjacent grassland and woodland on the coastal prairie of Texas, U.S.A. *J. Veg. Sci.*, **4**:521–530.

HARPER, J. L. 1977. Population biology of plants. Academic Press, Inc., New York, N.Y. 892 p.

HEISEY, R. M. AND C. C. DELWICHE. 1985. Allelopathic effects of *Trichostema lanceolatum* (Labiatae) in the California annual grassland. *J. Ecology*, **73**:729–742.

HUPP, C. R. 1992. Riparian vegetation recovery patterns following stream channelization: a geomorphic perspective. *Ecology*, **73**:1209–1226.

INDERJIT. 1996. Plant phenolics in allelopathy. *Bot. Rev.*, **62**:186–202.

———, AND R. DEL MORAL. 1997. Is separating resource competition from allelopathy realistic? *Bot. Rev.*, **63**:221–230.

KEAY, J., W. E. ROGERS, R. LANKAU AND E. SIEMANN. 2000. The role of allelopathy in the invasion of the Chinese tallow tree (*Sapium sebiferum*). *Texas J. Sci.*, **52**:57–64.

KLEIN, R. M., T. D. PERKINS, J. TRICOU, A. OATES AND K. CUTLER. 1991. Factors affecting red spruce regeneration in declining areas of Camels Hump Mountain, Vermont. *Am. J. Bot.*, **78**:1191–1198.

LODHI, M. A. K. 1975. Allelopathic effects of hackberry in a bottomland hardwood forest. *J. Chem. Ecol.*, **1**:171–182.

MULLER, C. H. 1969. Allelopathy as a factor in ecological processes. *Vegetatio*, **18**:348–357.

NATURAL RESOURCE CONSERVATION SERVICE. 1993. Special practice-exotic species: Chinese tallow tree control justification. U.S. Department of Agriculture. Agricultural Stabilization and Conservation Service, Angleton, TX. 4 p.

PIGMAN, W. W. AND R. M. GOEPP, JR. 1948. Chemistry of the carbohydrates. Academic Press, Inc., New York, NY.

RAMAKRISHNAN, P. S. AND P. M. VITOUSEK. 1989. Ecosystem-level processes and the consequences of biological invasions, p. 281–300. *In:* J. A. Drake, H. A. Mooney, F. diCastri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson (eds.). Biological invasions: a global perspective. John Wiley and Sons, Inc., Chichester, U.K.

RICE, E. L. 1995. Biological control of weeds and plant diseases: advances in applied allelopathy. University of Oklahoma Press, Norman, OK. U.S.A. 439 p.

RICHARDSON, D. R. AND G. B. WILLIAMSON. 1988. Allelopathic effects of shrubs of the sand pine scrub on pines and grasses of the sandhills. *For. Sci.*, **34**:592–605.

RUSSELL, L. H., W. L. SCHWARTZ AND J. W. DOLLAHITE. 1969. Toxicity of Chinese tallow tree (*Sapium sebiferum*). *Am. J. Vet. Res.*, **30**:1233–1238.

SAS. 1995. SAS 6.12. SAS Institute, Cary, NC.

SCHELD, H. W. AND J. R. COWLES. 1981. Woody biomass potential of the Chinese tallow tree. *Econ. Bot.*, **35**:391–397.

———, ———, C. R. ENGLER, R. KLEIMAN AND E. B. SCHULTZ, JR. 1984. Seeds of the Chinese tallow tree as a source of chemicals and fuels, p. 81–101. *In:* E. B. Schultz, Jr. and R. P. Morgan (eds.). Fuels and chemicals from oilseeds: technology and policy options. Westview Press, American Association for Advancement of Science, Boulder, CO.

SMEINS, F. E., D. D. DIAMOND AND C. W. HANSELKA. 1992. Coastal prairie, p. 269–290. *In:* R. T. Coupland (ed.). Ecosystems of the world: natural grasslands in the western hemisphere. Elsevier Science Publ. Co., Inc., New York, N.Y.

STOWE, L. G. 1979. Allelopathy and its influence on the distribution of plants in an Illinois old field. *J. Ecol.*, **67**:1065–1085.

TAYLOR, D. R. AND L. W. AARSSEN. 1990. Complex competitive relationships among genotypes of three perennial grasses: implications for species coexistence. *Am. Nat.*, **136**:305–327.

THIJS, H., J. R. SHANN AND J. D. WEIDENHAMER. 1994. The effect of phytotoxins on competitive outcome in a model system. *Ecology*, **75**:1959–1964.

VITOUSEK, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos*, **57**:7–13.

———, AND L. R. WALKER. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecol. Monogr.*, **59**:247–265.

WALTERS, M. B. AND P. B. REICH. 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology*, **77**:841–853.

WATERMAN, P. G. AND S. MOLE. 1994. Analysis of phenolic plant metabolites. Blackwell Scientific Publications, Oxford, U.K. 238 p.

WILSON, R. T., B. E. DAHL AND D. R. KRIEG. 1975. Carbohydrate concentrations in honey mesquite roots in relation to phenological development and reproductive condition. *J. Range Manage.*, **28**:286–289.

WOODS, K. D. 1997. Community response to plant invasion, p. 56–68. *In:* J. O. Luken and J. W. Thieret (eds.). Assessment and management of plant invasions. Springer-Verlag, Inc. New York, N.Y.

YANG, P. AND D. KINGHORN. 1985. Coumarin constituents of the Chinese tallow tree (*Sapium sebiferum*). *J. Natur. Prod.*, **48**:486–488.

ZAR, J. H. 1996. Biostatistical analysis. Prentice-Hall, Inc., Upper Saddle River, N.J. 918 p.

ZHU, H. AND A. U. MALLIK. 1994. Interactions between *Kalmia* and black spruce: isolation and identification of allelopathic compounds. *J. Chem. Ecol.*, **20**:407–421.

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