

Allelopathic effects of fruits of the Brazilian pepper *Schinus terebinthifolius* on growth, leaf production and biomass of seedlings of the red mangrove *Rhizophora mangle* and the black mangrove *Avicennia germinans*

Melinda J. Donnelly*, Danielle M. Green, Linda J. Walters

Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Orlando, FL 32816, USA

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Abstract

Exotic plant species can negatively affect native flora and fauna by changing the diversity and productivity of the system and altering successional processes. The novel weapons hypothesis has been suggested as one mechanism for invasion and spread of exotic plant species. It states that exotic species with “new weapons”, such as allelopathic chemicals, may have greater impacts on species in the invaded range without co-evolved defense strategies against the exotic chemicals. In Florida, one successful exotic species, *Schinus terebinthifolius* (Brazilian pepper), has invaded nearly every habitat throughout the state. Past studies have documented allelopathic properties of *S. terebinthifolius* negatively impacting the growth of native terrestrial flora. Here we document the effect of *S. terebinthifolius* for the first time on mangrove systems. We examined growth and survival of *Rhizophora mangle* (red mangrove) and *Avicennia germinans* (black mangrove) seedlings when exposed to a range of densities of intact and crushed *S. terebinthifolius* fruits (0, 25, 50) at two different salinities (15, 30 ppt). We also documented the natural density of *S. terebinthifolius* fruits beneath the tree canopy after fruit production in mangrove habitat. Growth and biomass were significantly reduced in *A. germinans* when exposed to the highest density of intact *S. terebinthifolius* fruits growing in 30 ppt saltwater. Trials with intact fruits had no significant effects on *R. mangle*; however, crushed fruits significantly decreased growth, and leaf production. The ecological importance of the different effects of crushed and intact fruits is supported by field observations which found equal or greater numbers of crushed fruits compared to intact fruits beneath the tree canopy of female *S. terebinthifolius*. In addition, abiotic factors, such as salinity, may interact with allelopathic chemicals in natural systems and needs to be addressed when planning future allelopathic studies.

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1. Introduction

Biological range expansions have occurred throughout evolutionary time, however, the increased transport of species by humans in recent times has significantly affected natural systems worldwide (Sharma et al., 2005). The total number of exotic species in the United States has increased for all taxa since the end of the eighteenth century and the threats posed by exotic species are expected to increase in future years (Wilcove et al., 1998). Not all exotics become invasive and colonize in local natural areas; exotic species are classified as invasive if

they negatively affect native biota by changing the diversity, structure and productivity of the system (Orr et al., 2005).

Multiple mechanisms have been suggested to explain why certain introduced species become invasive within the non-native range based on either resource or non-resource interactions between exotic and native species (Sharma et al., 2005). Resource interactions focus on the ability of exotics to compete with native species for limited resources (Sharma et al., 2005). Exotic plant species may out-compete native species because they possess certain characteristics, such as high growth rate, prolific seed production and tolerances to a variety of abiotic conditions, which facilitates the success of the exotic in the new environment (Sharma et al., 2005). Exotics may also have more success in their non-native range because of release from environmental controls limiting the species in its native range (Hiero and Callaway,

* Corresponding author. Tel.: +1 321 403 0278; fax: +1 407 823 5769.

E-mail address: mwtd@bellsouth.net (M.J. Donnelly).

2003; Carpenter and Cappuccino, 2005; Sharma et al., 2005). Carpenter and Cappuccino (2005) found that exotic plants had less herbivory than natives and low leaf herbivory was correlated with invasive potential. Reduced herbivory may also lead to enhanced competitive ability because the plant can spend less energy on defensive mechanisms and more energy on traits with competitive advantages (Sharma et al., 2005).

An alternate hypothesis to resource-based mechanisms for invasion is the novel weapons hypothesis (Callaway and Aschehoug, 2000; Orr et al., 2005; Sharma et al., 2005). Exotic species with “new weapons”, such as allelopathic chemicals or facilitators of microbial processes within the soil, may impact species in the invaded range more because the species in the invaded range have not been previously exposed and currently have no defense strategies (Callaway and Aschehoug, 2000; Orr et al., 2005; Sharma et al., 2005). These new weapons may increase the invasive potential of an exotic and allow it to out-compete native species (Herranz et al., 2006). Co-evolved species have adapted to each other, decreasing their susceptibility to each other’s allelopathic chemicals (Hiero and Callaway, 2003; Morgan and Overholt, 2005). When a species invades a new area, plants present in the new habitat may not be adapted to the exotics’ chemicals and may be very susceptible to the inhibitory effects (Hiero and Callaway, 2003; Morgan and Overholt, 2005). The production of allelopathic chemicals gives the exotic a competitive advantage over native flora and may rapidly lead to increases in the abundance of the exotic in the invaded habitat (Van Andel, 2005). The effect of allelopathic chemicals tends to be highly species-specific and this may increase the difficulty in identifying effects of allelopathy on native flora and fauna (Callaway and Aschehoug, 2000; Orr et al., 2005).

Although the production of allelopathic chemicals may increase the success of an exotic species, resource-based interactions may also be occurring, making it difficult to differentiate between chemical and competitive effects in the field (Herranz et al., 2006). The concentration of secondary chemicals within the plant is also related to resource availability, with plants growing in stressful environments having increased concentrations of secondary metabolites (Hiero and Callaway, 2003; Herranz et al., 2006). In addition, lower herbivory rates on exotic plants suggest that these species have strong chemical defenses, which may also have allelopathic properties, further confounding effects of allelopathy and other ecological factors (Carpenter and Cappuccino, 2005). The use of multiple mechanisms by an exotic during an invasion can make it more likely to successfully invade new habitats (Sharma et al., 2005). The successful invasion of *Tribulus terrestris* (puncture vine) (Hiero and Callaway, 2003) and *Lantana camara* (shrub verbena) (Sharma et al., 2005) into new habitats in the United States has been attributed to the use of both resource competition and allelopathic chemicals.

In Florida, the highly successful exotic species, *Schinus terebinthifolius* (Raddi) (Brazilian pepper), has invaded nearly every habitat throughout the state. It is native to South America and was introduced for use as an ornamental in two separate locations on the east and west coast of Florida in the mid-1800s (Williams et al., 2005). Although present in Florida for over one hundred years, *S. terebinthifolius* was not identified as a threat

until the 1950s when vegetation surveys conducted in Everglades National Park found it to be increasing in abundance (Ferriter, 1997). Surveys completed by the South Florida Water Management District in 1997 estimated that *S. terebinthifolius* occupied an estimated 700,000 ac throughout Florida (Ferriter, 1997).

S. terebinthifolius possesses multiple characteristics common to successful invaders, including high growth rates, high seed production, rapid recovery after damage, tolerance of a range of environmental conditions, pollination by insects, and animal-dispersed seeds (e.g. Rejmanek and Richardson, 1996; Jones and Doren, 1997; Mielke et al., 2005; Morgan and Overholt, 2005). This opportunistic exotic has been found in both disturbed and undisturbed areas of tropical hardwood forests, pine rocklands, sawgrass marshes, and mangrove swamps in Florida (Jones and Doren, 1997). *S. terebinthifolius* is classified as a Category 1 invasive plant species by the Florida Exotic Plant Pest Council because of its ability to alter the structure of natural habitats and negatively impact biodiversity of native ecosystems (Ferriter, 1997). *S. terebinthifolius* often forms monotypic stands in invaded areas of Florida, however, this is not observed in its native South American range where it is usually found as scattered individuals, co-existing with other flora (Ferriter, 1997).

S. terebinthifolius produces noxious secondary compounds (Inderjit and Callaway, 2003; Morgan and Overholt, 2005). One study from the 1970s tested the allelopathic properties of *S. terebinthifolius* on germination of native plants from the U.S. and found that the extract from the fruits had the greatest negative effect on germination (Morgan and Overholt, 2005). Laboratory trials found a decrease in germination of lettuce and *S. terebinthifolius* when exposed to extracts from exocarps of *S. terebinthifolius* seeds, suggesting that the exocarps of *S. terebinthifolius* seeds may contain inhibitory chemicals (Nilsen and Muller, 1980). In a later study by Morgan and Overholt (2005), aqueous extracts from *S. terebinthifolius* leaves decreased germination of seeds and biomass of seedlings in two native terrestrial plant species, *Bidens alba* (common beggar tick) and *Rivina humilis* (rougeplant). Although multiple publications have documented the allelopathic properties of *S. terebinthifolius* under laboratory conditions (e.g. Jones and Doren, 1997; Gordon, 1998; Ferriter, 1997), the effect on plants in the natural environment is still relatively unknown (Morgan and Overholt, 2005).

The focus of this study is on the allelopathic effects of *S. terebinthifolius* fruits on native Florida mangroves. The environmental conditions of mangrove habitat, such as high salinity levels, tidal fluctuations, anaerobic substrates and the accumulation of sulfides and heavy metals, inhibit the growth and survival of non-halophytic and terrestrial flora because they have not evolved the specialized adaptations needed to survive in the marine environment (Snedaker and Lahmann, 1988; Lugo, 1998). These conditions prevent invasions by both native and exotic species into mangrove habitat (Snedaker and Lahmann, 1988), unless the environmental conditions are changed due to natural or anthropogenic disturbances (Mytinger and Williamson, 1987; Lugo, 1998). Recent disturbances, such as hurricanes, habitat destruction and impoundment for mosquito control, have changed

the natural conditions in many of the mangrove ecosystems in Florida (Odum and McIvor, 1990; Lugo, 1998). These alterations potentially leave mangrove systems vulnerable to invasion by exotic plants, including *S. terebinthifolius*. This was demonstrated in a study in Indian River Lagoon, FL, where an increase in *S. terebinthifolius* seedlings was observed after pruning of the mangrove canopy (Parkinson et al., 1999). The productivity of the red mangroves decreased after pruning due to the loss of leaves, propagules and apical buds, giving *S. terebinthifolius* a competitive edge over the damaged mangroves (Parkinson et al., 1999).

Mytinger and Williamson (1987) found that germination of *S. terebinthifolius* seeds decreased with increased soil salinities. Survival of transplanted seedlings occurred only in the ecotone portion of the mangrove area, due to the lower soil saturation and salinity (Mytinger and Williamson, 1987). Ewe and da Silveira Lobo Sternberg (2005) evaluated growth and gas exchange of *S. terebinthifolius* at different salinities and compared the response of *S. terebinthifolius* to the responses found in four native species, including *Rhizophora mangle* (red mangrove) and *Laguncularia racemosa* (white mangrove). In response to salinity, *S. terebinthifolius* increased shoot biomass, resulting in taller plants and giving *S. terebinthifolius* a competitive edge over the native plants when competing for light (Ewe and da Silveira Lobo Sternberg, 2005). Ewe and da Silveira Lobo Sternberg (2005) concluded that morphological and physiological changes in *S. terebinthifolius* in response to salinity indicated salt tolerance at low to intermediate levels (<20 ppt).

These studies document the invasion of *S. terebinthifolius* into mangrove ecosystems of Florida. These invasions may have been facilitated by the production of allelopathic chemicals, increasing the potential for survival and spread of *S. terebinthifolius* in mangrove systems. We tested this hypothesis by determining the effects of *S. terebinthifolius* fruits on *R. mangle* (L. 1753) (red mangrove) and *A. germinans* (L. Stearn 1958) (black mangrove) seedlings. Additionally, we quantified the natural density of *S. terebinthifolius* fruits beneath the tree canopy after fruit production on the east coast of central Florida.

2. Methods

2.1. Study species

S. terebinthifolius (Brazilian pepper) is in the family Anacardiaceae and is native to Brazil, Paraguay and Argentina (Jones and Doren, 1997). This evergreen, woody perennial can reach heights of 7 m and has a multiple-stemmed trunk (Jones and Doren, 1997). *S. terebinthifolius* is dioecious and produces small flowers on branched inflorescences in the fall, usually from August–October in Florida (Ferriter, 1997). Flowers are pollinated by multiple species of native insects, including wasps and flies (Ferriter, 1997). After flowering, female trees produce large quantities of small, fleshy, red berries containing individual seeds from November through February (Ferriter, 1997).

R. mangle (Rhizophoraceae), the red mangrove, is characterized by prop roots which originate from the trunk or branches and penetrate the soil beneath the tree. The prop roots

stabilize the tree and contain specialized structures called lenticels, which assist with gas exchange (Odum and McIvor, 1990). *R. mangle* can reach heights up to 25 m and has deep green leaves which are paler green on the undersides (Tomlinson, 1994). *R. mangle* flowers year-round throughout its range (Fernandes, 1999) and flowers are wind-pollinated and self-compatible (Tomlinson, 1994). Following pollination, viviparous propagules grow up to 30 cm before leaving the parent tree and dispersing by water (Odum and McIvor, 1990).

Avicennia germinans (Avicenniaceae), the black mangrove, is characterized by a shallow system of laterally extending roots emerging from the substrate (Tomlinson, 1994). *A. germinans* reaches heights of 20 m and has narrow, elliptical leaves, encrusted with secreted salt (Odum and McIvor, 1990). White flowers form in the early summer months in Florida that are ten to 13 mm in diameter (Tomlinson, 1994). Propagules are two to 3 cm, ovoid-shaped and viviparous (Tomlinson, 1994).

3. Experimental methods

3.1. Density of crushed and intact *S. terebinthifolius* fruits

The density of crushed and intact *S. terebinthifolius* fruits on substrate beneath the *S. terebinthifolius* canopy was estimated by counting the number of each type of fruit within four 0.16 m² quadrats beneath four reproductive male and six female *S. terebinthifolius* trees. Quadrats were haphazardly tossed to four locations beneath each tree canopy, all fruits were counted, and the condition of the fruit exocarps was evaluated. Those with damaged exocarps were recorded as crushed and those without damage were recorded as intact. Surveys were conducted in May 2006.

3.2. Impact of *S. terebinthifolius* fruits on mangrove survival and growth

Collection of mangrove propagules and *S. terebinthifolius* fruits occurred in Mosquito Lagoon in Canaveral National Seashore, located on the east coast of central Florida directly south of New Smyrna Beach (28° 56.0 N, 80°49.2 W). Mangrove propagules were planted in August 2004 (*R. mangle*) and October 2004 (*A. germinans*). Each propagule was individually planted in a 3.8 L plastic pot containing top soil (Southland Topsoil). Pots with propagules were kept in rectangular holding trays (24 m × 24 m) lined with 6 mm thick plastic sheets and filled with either 15 ppt or 30 ppt saltwater ($n=125$ for each species × salinity combination).

Water depth in holding trays was kept at 15 cm, which submerged the lower portion of the pot to ensure constant absorption of water by the soil through the four 1.75 cm holes in the bottom of each pot. Water depth and water salinity was monitored every two days. Salts (Instant Ocean Sea Salts) and freshwater were added as needed to maintain depth and salinity.

In August 2005, intact *S. terebinthifolius* fruits were added to pots containing *R. mangle* and *A. germinans* seedlings in one of three densities: 0, 25 or 50 fruits. For each mangrove species, there were six treatments ($n=20$): 3 fruit densities × 2 water salinities. Initial height (distance from surface of soil to apical

meristem) and number of leaves was recorded when *S. terebinthifolius* fruits were added. Sixteen weeks after fruits were added (December 2005), the final heights and number of leaves were recorded and all above ground biomass for each plant was removed, dried at 70°C for 24 h and weighed. In January 2006, the above methods were repeated with *R. mangle* seedlings using crushed *S. terebinthifolius* fruits ($n=16/\text{treatment}$). Fruits were crushed by hand in a plastic bag prior to adding fruits to the mangrove pots. We did not run crushed fruit trials with *A. germinans* seedlings as there were too few available for experimental manipulations.

Normality of data was determined by examining boxplots and homogeneity of variances was determined by using Levene's test for equality (SPSS, 13.0). Comparisons were made between treatments for *A. germinans* and *R. mangle* with two-way ANCOVAs (salinity \times fruit density) for change in height, change in number of leaves and biomass. The experiments with *R. mangle* were run during different seasons due to logistical constraints and all statistics were run on intact and crushed treatments separately to prevent confounding effects of season on growth (SPSS, 13.0). Significant main effects were further tested with a posteriori contrasts for significant differences between treatments (SPSS, 13.0).

4. Results

4.1. Density of crushed and intact *S. terebinthifolius* fruits

No fruits were found in any quadrats beneath male *S. terebinthifolius* trees. The overall mean number (\pm SE) of fruits per 0.16 m² quadrat beneath female *S. terebinthifolius* trees was 73.70 \pm 17.71 intact fruits and 155.30 \pm 54.90 crushed fruits (Table 1). The number of intact fruits per 0.16 m² quadrat beneath each female *S. terebinthifolius* trees ranged from 0 to 256 fruits. In comparison, the number of crushed fruits ranged from 0–1206 fruits for each female tree (Table 1).

4.2. Impact of *S. terebinthifolius* fruits on mangrove growth

4.2.1. *R. mangle*

The mean initial height of *R. mangle* seedlings for the intact fruit trials was 32.77 \pm 0.46 cm and 30.73 \pm 0.64 cm for seedlings

Table 1

The number of intact and crushed *S. terebinthifolius* fruits was counted in four quadrats (0.16 m²) under the canopy of each of six female *S. terebinthifolius* trees ($n=6$) in Canaveral National Seashore, FL in May 2006

Tree	Intact fruits		Crushed fruits	
	Mean (\pm SE) (# fruits quadrat ⁻¹)	Range	Mean (\pm SE) (# fruits quadrat ⁻¹)	Range
1	131.50 (\pm 44.10)	0–184	559.50 (\pm 251.10)	0–1206
2	15.25 (\pm 9.80)	0–43	54.50 (\pm 13.20)	25–88
3	0.25 (\pm 0.25)	0–1	4.25 (\pm 2.01)	0–9
4	0.00 (\pm 0.00)	0	1.75 (\pm 1.75)	0–7
5	165.25 (\pm 41.20)	56–256	175.75 (\pm 28.70)	91–217
6	129.75 (\pm 30.60)	64–210	135.00 (\pm 37.79)	92–242
Overall mean	73.70 (\pm 17.71)		155.30 (\pm 54.90)	

The mean (\pm SE) and range of intact and crushed fruits for each tree and the overall mean for all trees combined are presented.

Table 2

Results from two-way ANCOVAs comparing the effects of fruit density and salinity on change in height, change in number of leaves, and aboveground biomass of *R. mangle* grown with intact *S. terebinthifolius* fruits

Variable	Source	df	Mean square	F	p
Change in height	Salinity	1	0.24	0.05	0.832
	Fruit density	2	6.42	1.19	0.306
	Salinity * fruit density	2	0.06	0.01	0.989
	Error	113	5.36		
Change in # leaves	Salinity	1	54.04	1.18	0.279
	Fruit density	2	80.75	1.76	0.175
	Salinity * fruit density	2	83.93	1.83	0.164
	Error	113	45.66		
Biomass	Salinity	1	26.29	2.77	0.099
	Fruit density	2	22.24	2.34	0.101
	Salinity * fruit density	2	11.24	1.18	0.309
	Error	112	1.19		

grown in 15 and 30 ppt saltwater, respectively. The mean increase in height for *R. mangle* seedlings grown in 15 and 30 ppt saltwater with intact fruits was not significantly different among the three fruit densities (ANCOVA, $F=1.19$, $p=0.306$) or salinities (ANCOVA, $F=0.05$, $p=0.832$) (Table 2, Fig. 1a). At the start of the crushed fruit trials, the mean initial height of *R. mangle* seedlings was 32.05 \pm 0.73 cm grown in 15 ppt saltwater and 34.19 \pm 0.55 cm in the 30 ppt saltwater treatment. The change in height for treatments with crushed fruits did show significant main effects for both salinity (ANCOVA, $F=9.33$, $p=0.003$) and fruit density (ANCOVA, $F=8.15$, $F=0.001$) but not the interaction term (Table 3). Similar changes in height (\sim 0.80 cm) were observed in both fruit densities in 15 ppt saltwater, but were less than the control group (Fig. 1b). However, in the 30 ppt saltwater treatment, the mean change in height (cm \pm SE) for the plants grown with 50 crushed fruits was 0.26 \pm 0.05 cm compared to 0.46 \pm 0.58 cm for the lower fruit density (Fig. 1b). Comparisons with a posteriori contrasts found significant variation between the two salinities ($p=0.003$). Within the 15 ppt saltwater treatment, significant differences were found between the control group and 25 fruit density ($p=0.012$) and 50 fruit density ($p=0.012$) (Fig. 1b). In 30 ppt saltwater, significant differences were found between the control group and 50 fruit density treatment ($p=0.006$) (Fig. 1b).

The mean number of leaves of *R. mangle* at the start of the intact fruit trials was 11.32 \pm 0.26 leaves and 12.33 \pm 0.67 leaves for plants grown in 15 and 30 ppt saltwater, respectively. All intact fruit treatments showed a positive increase in number of leaves during the experiment period (Fig. 1c) and there was no significant difference in the change in number of leaves of *R. mangle* seedlings between fruit densities (ANCOVA, $F=1.77$, $p=0.175$) or salinities (ANCOVA, $F=1.18$, $p=0.279$) (Table 2). However, treatments with crushed fruits had a significant decrease in number of leaves in plants exposed to *S. terebinthifolius* fruits, compared to the control (Fig. 1d, Table 3). The initial mean number of leaves for the crushed fruit trials was \sim 18 leaves for seedlings grown in both 15 and 30 ppt saltwater. The mean change in number of leaves (\pm SE) of *R. mangle* seedlings grown in 15 ppt saltwater was positive for the control group (6.50 \pm 1.42 leaves), but was negative for both fruit density treatments (Fig. 1d). Two of the sixteen plants lost all leaves in the highest fruit density treatment in 15 ppt

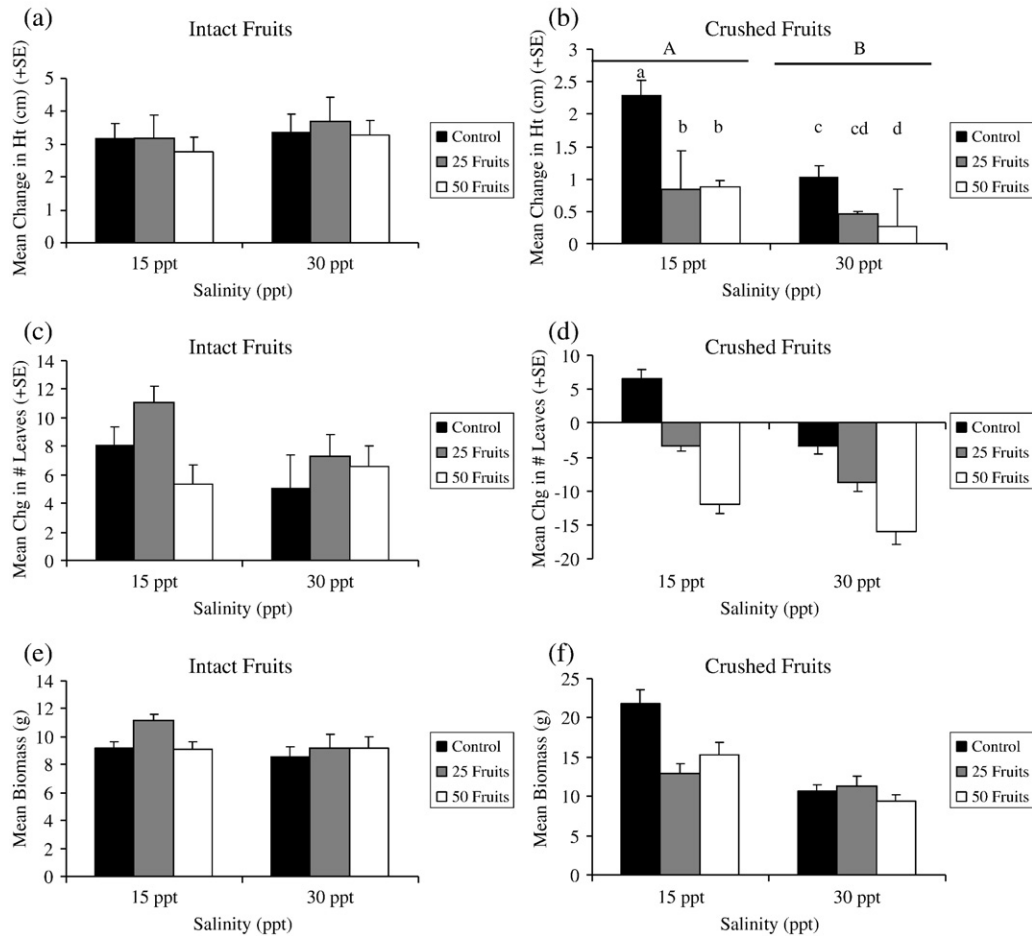


Fig. 1. (a, b) Mean change in height (cm +SE), (c, d) mean change in number of leaves (+SE), and (e, f) mean aboveground biomass (g +SE) of the red mangrove *R. mangle* grown in 15 and 30 ppt saltwater with one of three densities (0, 25, 50) of either intact or crushed *S. terebinthifolius* fruits. Letters on the change in height of crushed fruits graph (b) represent significant differences between the two salinities (capital letters) and fruit densities (lower case letters) when compared with a posteriori contrasts.

saltwater. The mean change in number of leaves for *R. mangle* seedlings grown in 30 ppt saltwater with crushed fruits was negative for all treatments, with the greatest loss observed in the highest fruit density treatment (-16.06 ± 1.81 leaves) (Fig. 1d). In 30 ppt saltwater, 37.5% (6/16) and 25.0% (4/16) of plants in the 50 fruits and 25 fruits treatments, respectively, lost all leaves after the

addition of *S. terebinthifolius* fruits. A significant interaction between salinity and fruit density (ANCOVA, $F=4.05, p=0.021$) was found for the change in number of leaves in the mangrove seedlings grown with crushed fruits (Table 3).

There was not a significant difference in the biomass of *R. mangle* in the two salinities (ANCOVA, $F=2.72, p=0.099$) or

Table 3
Results from two-way ANCOVAs comparing the effect of fruit density and salinity on change in height, change in number of leaves, and above ground biomass of *R. mangle* grown with crushed *S. terebinthifolius* fruits

Variable	Source	df	Mean square	F	p
Change in height	Salinity	1	19.63	9.33	0.003
	Fruit density	2	17.16	8.15	0.001
	Salinity * fruit density	2	2.62	1.25	0.293
	Error	89	2.10		
Change in # leaves	Salinity	1	979.96	43.63	<0.001
	Fruit density	2	1617.42	72.02	<0.001
	Salinity * fruit density	2	90.98	4.05	0.021
	Error	89	22.45		
Biomass	Salinity	1	892.03	30.07	<0.001
	Fruit density	2	179.44	6.05	0.003
	Salinity * fruit density	2	160.92	5.42	0.006
	Error	88	29.66		

Table 4
Results from two-way ANCOVAs (salinity × fruit density) comparing the effects of fruit density and salinity on change in height and number of leaves, and above ground biomass of *A. germinans* grown with intact *S. terebinthifolius* fruits

Variable	Source	df	Mean square	F	p
Change in height	Salinity	1	55.82	3.58	0.061
	Fruit density	2	19.05	1.22	0.298
	Salinity * fruit density	2	81.83	5.25	0.007
	Error	113	15.57		
Change in # leaves	Salinity	1	235.73	2.50	0.117
	Fruit density	2	272.75	2.89	0.060
	Salinity * fruit density	2	275.78	2.92	0.058
	Error	113	94.30		
Biomass	Salinity	1	12.70	9.27	0.003
	Fruit density	2	5.13	3.74	0.027
	Salinity * fruit density	2	7.53	5.49	0.005
	Error	112	1.37		

three fruit densities (ANCOVA, $F=2.34$, $p=0.101$) for intact fruits (Table 2, Fig. 1e). The highest mean biomass for seedlings in the crushed fruit treatments was in control group grown in the 15 ppt saltwater (21.75 ± 1.87 g) (Fig. 1f). There was a significant interaction between salinity and fruit density (ANCOVA, $F=5.42$, $p=0.006$) for the plants grown with crushed fruits (Table 3).

4.2.2. *A. germinans*

There was a significant interaction between salinity and fruit density on the change in height with *A. germinans* seedlings (ANCOVA, $F=5.25$, $p=0.007$) (Table 4). Mean initial heights of seedlings were 20.11 ± 0.74 cm and 21.07 ± 0.80 cm, grown in 15 and 30 ppt saltwater, respectively. The mean change in height (cm \pm SE) for seedlings grown in 30 ppt saltwater was lowest at the 50 fruits density, while the control treatment had the least growth in 15 ppt saltwater (Fig. 2a).

The mean number of leaves at the start of trials was 10.93 ± 0.99 leaves for seedlings in 15 ppt saltwater and 16.17 ± 1.21 leaves for seedlings grown in 30 ppt saltwater. All treatments had a positive increase in the number of leaves (Fig. 2b). No significant effect was found for salinity (ANCOVA, $F=2.50$, $p=0.117$) or fruit density (ANCOVA, $F=2.89$, $p=0.060$) on the change in number of leaves for the three treatment groups (Table 4).

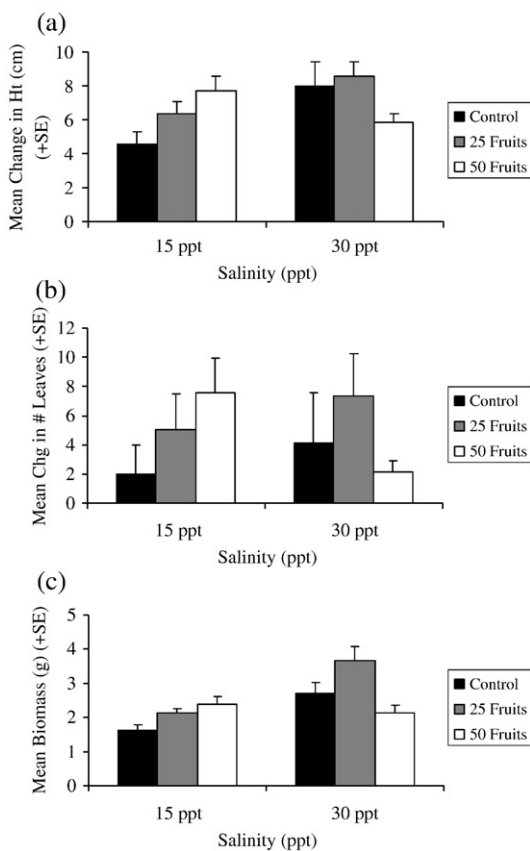


Fig. 2. (a) Mean change in height (cm \pm SE), (b) mean change in number of leaves (+SE), and (c) mean total biomass (g \pm SE) of the black mangrove *A. germinans* grown in 15 and 30 ppt saltwater with one of three densities (0, 25, 50) of intact *S. terebinthifolius* fruits.

The mean biomass of *A. germinans* seedlings grown in 15 ppt saltwater was similar among the control and treatment groups and ranged between 1.5 g and 2.5 g for the three treatments (Fig. 2c). In 30 ppt salinity, the lowest mean aboveground biomass was in the treatment with the 50 fruits treatment (Fig. 2c). There was a significant interaction (ANCOVA, $F=5.49$, $p=0.005$) between salinity and fruit density for the biomass of *A. germinans* (Table 4).

5. Discussion

S. terebinthifolius has invaded many habitats in central and south Florida and has changed natural community structure and functioning of the invaded systems (Williams et al., 2005). *S. terebinthifolius* is a successful colonizer in both disturbed and undisturbed habitats and a competent resource competitor with native flora. Past studies have documented allelopathic properties of *S. terebinthifolius* negatively impacting the growth of native flora (Nilsen and Muller, 1980; Morgan and Overholt, 2005). This study documents the negative effects of *S. terebinthifolius* fruits on two native Florida mangroves. The black mangrove, *A. germinans*, had a reduction in growth and biomass when exposed to the highest density of *S. terebinthifolius* fruits when growing in 30 ppt saltwater. The red mangrove, *R. mangle*, also showed significant effects of both salinity and fruit density on growth rate and leaf production when grown with crushed *S. terebinthifolius* fruits. In the trials with crushed fruits at 30 ppt, 6 mangrove seedlings in the 50 fruit density treatment and 4 mangrove seedlings in the 25 fruit density treatment lost all leaves after exposure to the fruits. Loss of leaves equals loss of photosynthetic capabilities, decreasing the growth capabilities of the mangrove seedlings when exposed to *S. terebinthifolius* fruits. In natural habitats, the mangrove seedlings may recover from the initial leaf loss, but *S. terebinthifolius* seedlings germinating in the same location would have a competitive advantage over the recovering mangrove seedlings in the short term.

Exposure to high salinity soils and saltwater is physiologically stressful to mangroves (Ewe and da Silveira Lobo Sternberg, 2005) and may make the plants more susceptible to inhibitory compounds in high concentrations. The native mangroves, *R. mangle* and *A. germinans* have numerous adaptations for survival in the marine environment (Odum and McIvor, 1990; Tomlinson, 1994), however, these mechanisms can be physiologically costly to the plant, potentially leaving it more susceptible to allelopathic compounds. In our study, there was a significant interaction between salinity and fruit density on both mangrove species, suggesting that the higher salinity may make the plants more susceptible to inhibitory chemicals. The impact of allelopathic chemicals on native flora can interact with environmental factors and competition for resources (Herranz et al., 2006) and this may be important when determining the effects of these compounds on plants within estuarine environments. Resource availability and environmental stressors in limiting environments can also increase the production of secondary chemicals in exotic plants (Hiero and Callaway, 2003; Herranz et al., 2006). The increase in production of chemical compounds can reduce other competitive interactions and increase the success of the plant in the invaded area (Hiero and Callaway, 2003; Herranz et al., 2006). To

evaluate the potential of exotic species using allelopathic chemicals in native habitats, further studies are needed to better understand the role of resource competition and environmental factors in the production of secondary compounds in the exotic species and its effect on native flora.

R. mangle did not show a depression in growth or biomass when exposed to intact *S. terebinthifolius* fruits. The intact fruits used in this trial may not release a high enough concentration of chemicals to cause a depression in growth of *R. mangle*. In comparison, significant effects on growth and leaf production were observed when *R. mangle* seedlings were grown with crushed *S. terebinthifolius* fruits. The crushed fruits may release higher concentrations of chemicals into the soil, causing a greater negative impact on neighboring plants. Crushed fruits also caused greater mortality of brine shrimp in comparison to intact fruits during laboratory bioassay trials (M. Alphonse and L. Walters, unpublished data).

Counts of fruits dropped from female *S. terebinthifolius* trees in Canaveral National Seashore showed a range in density of fruits beneath any given *S. terebinthifolius* tree (Table 1). For the trees with a high number of fruits, the number of crushed was equal or greater to the number of intact fruits (Table 1). The fruits are popular forage for frugivorous birds and small mammals and attract a large number of animals to the trees when fruits are produced (Ferriter, 1997). This may lead to high numbers of fruits being crushed in the tree canopy and on the ground. The surface area of pots used in this study was ~ 0.30 m² and, compared to the fruit densities measured in the field, the densities used in these trials are less than what plants would be exposed to in the field and are conservative estimates of effects.

Growth of *A. germinans* was depressed by *S. terebinthifolius* fruits (Fig. 2). This is ecologically significant because both *A. germinans* and *S. terebinthifolius* are usually found in the landward portion of mangrove habitat adjacent to Florida estuaries because the soil is not inundated as often as in the intertidal region (Mytinger and Williamson, 1987; Odum and McIvor, 1990). There is a high probability that the two species would come into contact under normal growing conditions in Florida and *A. germinans* may be excluded due to the chemical compounds produced by *S. terebinthifolius*. *R. mangle* tends to grow in the saturated soil of the intertidal region (Odum and McIvor, 1990), where it might be expected to have less contact with *S. terebinthifolius*, as the latter does tolerate some periods of soil inundation, but not frequent saturation of the soil (Mytinger and Williamson, 1987). Mielke et al. (2005) found a decrease in both stomatal conductance and whole plant biomass in *S. terebinthifolius* when exposed to saturated soil conditions. However, human disturbances to the mangrove environment can alter the elevation of the substrate, which restricts mangroves to a narrow fringe in the intertidal region and allows *S. terebinthifolius* to grow immediately behind it (Donnelly, 2006). Additionally, Spector and Putz (2006) found that *S. terebinthifolius* exhibits extensive plasticity in growth forms, including the production of a large crown, which can extend into adjacent areas where it is unable to root. Fruits from the overhanging *S. terebinthifolius* are dropped into the intertidal region, even though this exotic cannot directly grow there (M. Donnelly, pers. obs.). Within the intertidal region, regular tidal flushing may

prevent the build-up of toxic concentrations of allelopathic chemicals produced by *S. terebinthifolius*, decreasing the effect of the inhibitory chemicals. However, areas with less frequent inundation or altered hydrological regimes because of anthropogenic factors may experience high concentrations of chemicals.

The concentration of chemicals may also increase during decomposition of the fallen fruit in the anaerobic soils of mangrove habitat. During the decomposition of a variety of different plant species' fruits and tree litter, the chemical concentration of phytotoxins was highest during the onset of decomposition and decreased over time (Bonanomi et al., 2006). However, decomposition in anaerobic soil can lead to increased concentrations and prolonged persistence in the soil (Bonanomi et al., 2006). The persistence of allelopathic chemicals within the soil negatively impacted plant nutrient absorption and decreased competitive abilities in native flora (Bonanomi et al., 2006).

In many areas, the primary method for control and eradication of *S. terebinthifolius* is herbicide application (Ferriter, 1997) and the plant material is left to decompose after death. Recruitment and recovery of native flora may be negatively impacted by the accumulation of these chemicals within the mangrove habitat, slowing restoration efforts. The removal of the dead trees would be both time-consuming and costly, but other methods may reduce the amount of chemicals left behind. This study and numerous other studies have shown a significant effect of chemicals from the fruits being highly allelopathic (Nilsen and Muller, 1980; Morgan and Overholt, 2005); therefore, treating mature female *S. terebinthifolius* trees prior to fruit production may reduce the amount of decomposing material and eliminate the fruit as a source of allelopathic chemicals.

Allelopathic chemicals may be an additional mechanism for the successful invasion of *S. terebinthifolius* into central and southern Florida habitats. Exotic species with multiple mechanisms for out-competing native flora have greater potential of invasion success (Sharma et al., 2005). *S. terebinthifolius* is an effective resource competitor under a range of environmental conditions (Jones and Doren, 1997). This study supports the results of past research showing that this exotic produces allelopathic chemicals which can negatively impact a variety of native flora (Nilsen and Muller, 1980; Morgan and Overholt, 2005). To effectively manage this exotic plant species, understanding both the allelopathic capabilities of *S. terebinthifolius* under a range of environmental factors in the field and how resource competition can influence these effects is needed. *S. terebinthifolius* causes wide-spread changes after invading natural systems and the more we know about the mechanisms it uses to invade, the better we can control, predict and prevent the spread of this exotic in the future.

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References

- Bonanomi, G., Sicurezza, M.G., Caporaso, S., Esposito, A., Mazzoleni, S., 2006. Phytotoxicity dynamics of decaying plant materials. *New Phytol.* 169, 571–578.
- Callaway, R.M., Aschehoug, E.T., 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290, 521–523.
- Carpenter, D., Cappuccino, N., 2005. Herbivory, time since introduction and the invasiveness of exotic plants. *J. Ecol.* 93, 315–321.
- Donnelly, M., 2006. Is the exotic *Schinus terebinthifolius* a threat to mangrove ecosystems in Florida? Masters Thesis, University of Central Florida.
- Ewe, S.M., da Silveira Lobo Sternberg, L., 2005. Growth and gas exchange responses of Brazilian pepper (*Schinus terebinthifolius*) and native South Florida to salinity. *Trees* 19, 119–128.
- Fernandes, M.E.B., 1999. Phenological patterns of *Rhizophora* L., *Avicennia* L. and *Laguncularia* Gaertn. F. in Amazonian mangrove swamps. *Hydrobiologia* 413, 53–62.
- Ferriter, A. (Ed.), 1997. Brazilian pepper management plan for Florida: a report from The Florida Exotic Pest Plant Council's Brazilian pepper task force. 26 pg. Retrieved December 23, 2005 www.fleppc.org/Manage_Plans/schinus.pdf.
- Gordon, D.R., 1998. Effect of non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecol. Appl.* 8, 975–989.
- Herranz, J.M., Ferrandis, P., Copete, M.A., Duro, E.M., Zalacain, A., 2006. Effect of allelopathic compounds produced by *Cistus ladanifer* on germination of 20 Mediterranean taxa. *Plant Ecol.* 184, 259–272.
- Hierro, J.L., Callaway, R.M., 2003. Allelopathy and exotic plant invasion. *Plant Soil* 256, 29–39.
- Inderjit, Callaway, R.M., 2003. Experimental designs for the study of allelopathy. *Plant Soil* 256, 1–11.
- Jones, D.T., Doren, R.F., 1997. The distribution, biology and control of *Schinus terebinthifolius* in Southern Florida, with special reference to Everglades National Park. In: Brock, J.H., Wade, M., Pysek, P., Green, D. (Eds.), *Plant Invasions: Studies from North America and Europe*. Backhuys Publishers, Leiden, pp. 81–93.
- Lugo, A.E., 1998. Mangrove forests: a tough system to invade but an easy one to rehabilitate. *Mar. Pollut. Bull.* 37, 8–12.
- Mielke, M.S., Furtado de Almeida, A.A., Gomes, F.P., Mangabeira, P.A.O., Da Costa Silva, D., 2005. Effects of soil flooding on leaf gas exchange and growth of two neotropical pioneer tree species. *New For.* 29, 161–168.
- Morgan, E.C., Overholt, W.A., 2005. Potential allelopathic effects of Brazilian pepper (*Schinus terebinthifolius* Raddi, Anacardiaceae) aqueous extract on germination and growth of selected Florida native plants. *J. Torrey Bot. Soc.* 132 (1), 11–15.
- Mytinger, L., Williamson, G.B., 1987. The invasion of *Schinus* into saline communities of Everglades National Park. *Fla. Sci.* 50, 9–11.
- Nilsen, E.T., Muller, W.H., 1980. A comparison of the relative naturalization ability of two *Schinus* species in southern California. I. Seed germination. *J. Torrey Bot. Club.* 107, 51–56.
- Odum, W.E., McIvor, C.C., 1990. Mangroves. In: Myers, R.L., Ewel, J.J. (Eds.), *Ecosystems of Florida*. University of Central Florida Press, Orlando, pp. 517–548.
- Orr, S.P., Rudgers, J.A., Clay, K., 2005. Invasive plants can inhibit native tree seedlings: testing potential allelopathic mechanisms. *Plant Ecol.* 181, 153–165.
- Parkinson, R.W., Perez-Bedmar, M., Santangelo, J.A., 1999. Red mangrove (*Rhizophora mangle*) litter fall response to selective pruning (Indian River Lagoon, FL, USA). *Hydrobiologia* 413, 63–76.
- Rejmanek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? *Ecology* 77, 1655–1661.
- Sharma, G.P., Raghubanshi, A.S., Singh, J.S., 2005. *Lantana* invasion: an overview. *Weed Biol. Manag.* 5, 157–165.
- Snedaker, S.C., Lahmann, E.J., 1988. Mangrove understorey absence: a consequence of evolution? *J. Trop. Ecol.* 4, 311–314.
- SPSS for Windows Student Version, Rel. 13.0.2004. Chicago: SPSS, Inc.
- Spector, T., Putz, F.E., 2006. Biomechanical plasticity facilitates invasion of maritime forests in the southern USA by Brazilian pepper (*Schinus terebinthifolius*). *Biol. Invasions* 8, 255–260.
- Tomlinson, P.B., 1994. *The Botany of Mangroves*. University of Cambridge Press, Cambridge.
- Van Andel, J., 2005. Species interactions structuring plant communities. In: van der Maarel, E. (Ed.), *Vegetation Ecology*. Blackwell Publishing, Oxford, pp. 238–264.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48, 607–615.
- Williams, D.A., Overholt, W.A., Cuda, J.P., Hughes, C.R., 2005. Chloroplast and microsatellite DNA diversities reveal the introduction history of Brazilian pepper (*Schinus terebinthifolius*) in Florida. *Mol. Ecol.* 14, 3643–3656.