Is The Exotic Brazilian Pepper, Schinus Terebinthifolius, A Threat To Mangrove Ecosystems In Florida?

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IS THE EXOTIC BRAZILIAN PEPPER, \textit{Schinus terebinthifolius}, A THREAT TO MANGROVE ECOSYSTEMS IN FLORIDA?

by

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B.S. University of Central Florida, 2002

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ABSTRACT

Mangrove ecosystems are critical to Florida, providing economic resources to humans, and untold ecological resources to estuarine organisms. In Florida’s estuaries, mangrove ecosystems have suffered significant losses due to natural and human disturbances; these disturbances potentially leave mangrove communities vulnerable to invasion by the opportunistic exotic, *Schinus terebinthifolius* (Brazilian pepper). Prior experiments have suggested that *Schinus terebinthifolius* is unable to survive under marine conditions and poses no long term threat to mangrove systems. However, this contradicts field observations where *Schinus terebinthifolius* was found growing in the intertidal zone of Mosquito Lagoon alongside three native species of mangroves, *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*. The purpose of my study was to evaluate competition between the invasive *S. terebinthifolius* and these three native species of mangroves in the coastal estuarine system along the east coast of Central Florida in Canaveral National Seashore. The effects of competition were evaluated by testing the ability of *S. terebinthifolius* to: 1) chemically inhibit growth of mangrove propagules, 2) invade new coastal habitats by dispersing seeds in the water, 3) alter species richness and abundance of the flora when present in a mangrove system, and 4) recruit and survive in mangrove habitat. By better understanding the invasibility and impact of *Schinus terebinthifolius* on mangroves, coastal resource managers will be able to develop the most effective management strategies to prevent this exotic from altering the structure and productivity of the mangrove ecosystem.
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CHAPTER 1: BACKGROUND

Mangrove ecosystems are one of the most productive ecosystems in the world (e.g. Odum and McIvor 1990, Lugo 1998, Imbert et al. 2000). Although floral biodiversity is typically less than other highly productive tropical systems (Lugo 1998), mangrove ecosystems provide numerous contributions to humans and support a large number of fauna from terrestrial, estuarine and marine environments (e.g. Odum and McIvor 1990, Lugo 1998, Imbert et al. 2000). Mangroves provide shoreline protection and stabilization (Imbert et al. 2000) and intercept nutrient-rich run-off from terrestrial sources (Odum and McIvor 1990). Mangrove ecosystems shelter and serve as a breeding and nursery grounds for numerous fauna, including many endangered or threatened species and economically important marine fishes and invertebrates (Odum and McIvor 1990).

Mangroves establish themselves in an ecological niche unavailable to many other species due to the high salinity levels, tidal fluctuations, anaerobic substrates and the accumulation of toxins, such as sulfides (e.g. Snedaker and Lahmann 1988, Lugo 1998). Mangroves survive this stressful environment with specialized adaptations, including aerial roots for support, gas exchange, and mechanisms for salt exclusion and excretion (Odum and McIvor 1990). The environmental conditions of mangrove habitat inhibit the growth and survival of non-halophytic and terrestrial flora, which have not evolved the specialized adaptations found in the mangroves (Snedaker and Lahmann 1988, Lugo 1998). The abiotic conditions of mangrove ecosystems prevent invasions by most native and exotic species (Snedaker and Lahmann 1988), unless the environmental conditions
are changed due to natural or human-mediated impacts (Mytinger and Williamson 1987, Lugo 1998).

Natural disturbances, such as hurricanes and freezing temperatures, and anthropogenic influences, such as development, impoundment, and pollution have damaged or changed the natural conditions in the mangrove ecosystems in Florida (Odum and McIvor 1990, Lugo 1998). These alterations potentially leave mangrove systems vulnerable to invasion by exotic plants, such as *Schinus terebinthifolius*, commonly known as Brazilian pepper (Figure 1). The purpose of this study is to evaluate competitive interactions between *Schinus terebinthifolius* and three native species of mangroves, *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*, in a coastal estuarine system in Canaveral National Seashore along the east coast of Central Florida. Despite the limiting abiotic conditions of mangrove habitat, mangroves and *Schinus terebinthifolius* grow side by side (Figures 2, 3). My research will focus on testing the ability of *Schinus terebinthifolius* to: 1) inhibit mangrove growth and survival, 2) invade coastal habitats through water dispersal, and 3) affect the biodiversity of invaded areas.

**Mangrove Biology**

The term mangrove refers to plants with specialized adaptations to the marine environment; these have evolved multiple times through evolutionary history from numerous terrestrial ancestors (Duke et al. 1998). The geographic range of mangroves extends from the sub-tropical and tropical regions of the eastern Atlantic and Pacific coasts and the Indo-West Pacific region (Duke et al. 1998). The eastern group consists of forty mangrove species, which are found in Australia, east Africa, southeast Asia, India
and western Pacific islands (Tomlinson 1994). The western group consists of eight species which are found in Florida, the Caribbean Islands, Central America, the subtropical and tropical coast of the Pacific Ocean of North America, both coasts of South America and west Africa (Tomlinson 1994).

**Mangroves in Florida**

In Florida, three species of true mangroves and one plant classified as a mangrove associate are found inhabiting the coastal regions (Odum and McIvor 1990, Tomlinson 1994). The three true mangrove species are: *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove) and *Laguncularia racemosa* (white mangrove) (Tomlinson 1994). The mangrove associate *Conocarpus erecta*, commonly called buttonwood mangrove, lacks the modified root systems to inhabit saturated soils with high salinity and the viviparous propagules found in the true mangrove species (Odum and McIvor 1990). *Conocarpus erecta* can tolerate the high saline soil, but does not survive prolonged flooding (Lugo 1998). It inhabits the drier, landward region of the mangrove ecosystems of Florida (Odum and McIvor 1990).

Temperature limits the northward distribution of mangroves on the east and west coasts of Florida (Odum and McIvor 1990). Fluctuations in temperature of more than 10°C and below freezing for greater than a few hours can be detrimental to mangroves (Tomlinson 1994), and mangroves rarely inhabit areas with a monthly mean air temperature below 20°C (Odum and McIvor 1990). *Avicennia germinans* is the most cold tolerant and its range in Florida extends north of St. Augustine on the east coast (Figure 4) and into the panhandle on the west coast (Odum and McIvor 1990, S. Leitholf, pers. comm.). After freeze damage, this species has the ability to regenerate from the
roots (Odum and McIvor 1990). *Rhizophora mangle* and *Laguncularia racemosa* are more susceptible to cold temperatures and the northern range for these two species is Ponce de Leon Inlet on the east coast and Cedar Key on the west coast (Odum and McIvor 1990) (Figure 4).

*Rhizophora mangle* (Rhizophoraceae) is characterized by prop roots which originate from the trunk or branches and penetrate the soil beneath the tree (Figure 5a). The prop roots stabilize the tree and contain specialized structures called lenticels (Odum and McIvor 1990). Lenticels are small, hydrophobic pores which allow oxygen to diffuse into the aerenchyma, an adaptation that allows them to survive in the anaerobic sediments (Odum and McIvor 1990). *Rhizophora mangle* can reach heights up to twenty-five meters and has deep green leaves which are paler green on their undersides (Tomlinson 1994). *Rhizophora mangle* flower year round (Fernandes 1999) and flowers are wind-pollinated and self-compatible (Figure 5b) (Tomlinson 1994). After flowering and pollination occur, long, buoyant propagules grow up to thirty centimeters long before dropping from the parent tree (Figure 5c) (Odum and McIvor 1990). These buoyant propagules disperse by water and are viviparous, with the growth of the embryo continuing throughout the dispersal stage (Rabinowitz 1978).

*Avicennia germinans* (Avicenniaceae) is characterized by a shallow system of laterally extending roots emerging from the substrate, known as cable roots (Figure 6a) (Tomlinson 1994). The cable roots contain pneumatophores with lenticels on the exposed portion that can extend up to twenty centimeters above the substrate (Odum and McIvor 1990). *Avicennia germinans* reaches heights of twenty meters and has narrow, elliptical leaves which are deep green on the upper surface and white on the lower surface.
The leaves of *Avicennia germinans* are encrusted with secreted salt (Odum and McIvor 1990). White flowers form in the early summer months in Florida (Figure 6b) and are the largest in this genus at ten to thirteen millimeters (Tomlinson 1994). The flowers are pollinated by short-tongued insects, particularly honeybees (Tomlinson 1994). Its propagules are smaller than the red mangrove, measuring two to three centimeters in length (Figure 6c). These ovoid-shaped propagules are viviparous, with the embryo germinating immediately after release from the parent tree (Tomlinson 1994).

The third mangrove species found in Florida is the white mangrove, *Laguncularia racemosa* (Combretaceae) (Figure 7a). *Laguncularia racemosa* lacks prop or cable roots, but contains lenticels on the lower portion of the trunk (Odum and McIvor 1990). *Laguncularia racemosa* trees can reach a height of fifteen meters or more and have flat, oval shaped leaves that are up to seven centimeters long (Odum and McIvor 1990). This species is usually dioecious; however, there is some evidence of monoecious trees with self-fertilizing flowers (Tomlinson 1994). The flowers are four to five millimeters in diameter, have a greenish-yellow color (Figure 7b) and form in the summer months in Florida (Tomlinson 1994). Flowers are pollinated by insect vectors, mostly bees (Tomlinson 1994). The small, ovoid-shaped propagules measure approximately two centimeters and are viviparous (Figure 7c) (Odum and McIvor 1990, Tomlinson 1994).

**Propagule Characteristics and Dispersal**

*Rhizophora mangle, Avicennia germinans* and *Laguncularia racemosa* have developed effective reproductive strategies that allow them to widely disperse and
establish in new habitats. Vivipary, germination that occurs while attached to the tree, enables all three species to omit a resting stage prior to germination (Odum and McIvor 1990). After fertilization, the zygote develops continuously through the embryonic stage to seedling stage without a dormancy period (Rabinowitz 1978). This is especially noticeable in R. mangle, where the hypocotyl emerges from the embryo and can grow up to thirty centimeters while still attached to the tree (Tomlinson 1994). Rabinowitz (1978) determined that all mangrove propagules have an obligate floating period during dispersal to complete germination and prepare to initiate root growth. This obligate floating period is eight days for L. racemosa, fourteen days for A. germinans and forty days for R. mangle (Rabinowitz 1978).

Unique characteristics of propagules from the three native mangrove species affect their distribution in the intertidal region. The small propagules of A. germinans always float, so they require a stranding period on higher ground for establishment to occur (Rabinowitz 1978). The amount of time needed to root into new substrate is seven days (Rabinowitz 1978). They are unable to establish in the low intertidal region because the propagules will be washed away with the tide before forming roots (Rabinowitz 1978). Laguncularia racemosa propagules lose their buoyancy after a floating period of eight days (Rabinowitz 1978). Though some growth can occur while submerged, the propagules need five days above the waterline in order to establish roots (Rabinowitz 1978). The large propagules of R. mangle sink after a forty day obligate floating period (Tomlinson 1994). If in still water, the roots can establish while submerged (Tomlinson 1994). Rabinowitz (1978) showed propagules of R. mangle needed fifteen days in order
to establish roots. However, seeds can regain buoyancy if initial attempts to establish are unsuccessful, allowing for additional dispersal (Rabinowitz 1978).

**Salt Tolerance and Adaptations**

Mangrove species are facultative halophytes and do not require saltwater for growth (Odum and McIvor 1990). However, mangroves are rarely found in freshwater habitats due to competition with other freshwater vascular plants (Odum and McIvor 1990). Because of the specialized adaptations that allow them to survive in marine environments, mangroves flourish in habitats unavailable to most other species (Odum and McIvor 1990).

Soil salinity tolerance of *R. mangle* is between 60-65 ppt (Odum and McIvor 1990). *Laguncularia racemosa* and *A. germinans* both have soil salinity tolerances greater than *R. mangle*, at approximately 80-90 ppt (Odum and McIvor 1990).

Biochemical mechanisms assisting in salt regulation vary among mangrove species and include changes in the stomata, an increase in leaf thickness as the tree ages to develop succulent leaves for water storage, and changes in enzyme activation and protein synthesis (e.g. Odum and McIvor 1990, Tomlinson 1994).

*Avicennia germinans* and *L. racemosa* are salt-excreting species (Tomlinson 1994). These trees contain salt glands that actively transport salts out of the plant (Odum and McIvor 1990). *Avicennia germinans* contains abundant salt glands contained in shallow pits on the upper and lower surface of the leaves (Tomlinson 1994). *Laguncularia racemosa* has shallow pits on leaf surface that excrete salt and epidermal sites resembling salt glands that also assist in salt excretion (Tomlinson 1994). The salt concentration of the sap is up to ten times higher in the excreting species compared to the
salt excluding species (Odum and McIvor 1990). Salt excretion requires more energy than salt exclusion (Odum and McIvor 1990).

*Rhizophora mangle* is a salt excluding species that prevents the salt from entering the cells of the root surface by reverse osmosis (Tomlinson 1994). This is accomplished by keeping a high negative pressure in the xylem (Odum and McIvor 1990). Sulfide is also excluded and can cause sulfides to build up in areas not regularly flushed by tides (Odum and McIvor 1990). Even though the mangroves live in an area inundated regularly with saltwater, they exhibit characteristics found in plants living in xeric habitats, including succulent leaves, thick cuticles and sunken stomata on the leaf surface to aid in conservation of water (Odum and McIvor 1990). These adaptations serve to prevent water loss and lower the metabolic cost of osmoregulation in the marine environment (Odum and McIvor 1990).

Another characteristic of mangrove species that enables them to grow in the marine environment is that they are evergreen (Snedaker and Lahmann 1988). Snedaker and Lahmann (1988) hypothesized this characteristic decreases the metabolic expenditure of the plants. Annual shedding of the leaves would result in the mangroves living a portion of the year without photosynthetic productivity and needing reserves in order to reproduce the leaves at a later time, resulting in a higher metabolic cost to the mangroves (Snedaker and Lahmann 1988). By being evergreen, mangroves have photosynthetic production year-round; this may compensate for the increased metabolic requirements of living in the stressful intertidal habitat (Snedaker and Lahmann 1988). This hypothesis is supported by the fact that almost all species of true mangroves are evergreen with the exceptions being members of the genera *Xylocarpus, Lumnitzera*, and *Exocarpia*.
(Snedaker and Lahmann 1988). These deciduous plants typically live in habitats frequently inundated with freshwater, where the metabolic cost is believed to be less than those species living in a marine environment and the annual shedding and production of leaves is not as metabolically taxing to the plant (Snedaker and Lahmann 1988).

Mangrove canopies are highly effective at absorbing light to maximize photosynthetic activity (Snedaker and Lahmann 1988). The upper four meters of the canopy contains ninety percent of aboveground biomass of mangroves and intercepts almost ninety-five percent of incoming light, creating highly shaded conditions in the understory (Odum and McIvor 1990). Mangroves and other intertidal halophytes are shade intolerant and this tends to prevent the establishment of propagules and seedlings within the mangrove canopy (Snedaker and Lahmann 1988). Snedaker and Lahmann (1988) hypothesized the high metabolic cost of living in the marine environment prevents the establishment of understory species in the highly shaded area of the mangrove canopy. To survive under these stressful conditions, plants must maximize photosynthetic capabilities to offset the metabolic costs of living in the marine habitat (Snedaker and Lahmann 1988). This explains why the understory is typically absent, except in areas with high rainfall, low soil salinity or near the higher, landward region where metabolic costs are decreased (Snedaker and Lahmann 1988).

**Mangrove Distribution Factors**

The distribution of mangroves depends on numerous factors, including climate, wave action, substrate, environmental disturbances, tidal fluctuations, and seed predation (Odum and McIvor 1990). An early hypothesis proposed by J. H. Davis, Jr. in the 1940s compared mangrove zonation to stages of succession, with *R. mangle* being the pioneer
plant, *A. germinans* and *L. racemosa* representing the older, more mature vegetation and the upland hammock being the climax community (Odum and McIvor 1990). It was believed that *R. mangle* built up the soil and expanded the land area (Odum and McIvor 1990). However, recent research has shown that mangroves stabilize existing soil more than building up the substrate and the current hypothesis is that mangrove zonation is influenced by multiple factors (Odum and McIvor 1990).

The location of *R. mangle* is typically in the lowest portion of the intertidal region with its prop roots submerged in saltwater due to its buoyant propagules and lower tolerance to soil salinity (Odum and McIvor 1990). The primary productivity of this species is negatively correlated with an increase in soil salinity, restricting it to areas where evaporation rates are lower (Imbert et al. 2000). *Rhizophora mangle* does not oxidize anaerobic soils as efficiently as *A. germinans*, making them less able to compete with *A. germinans* in reducing substrates higher in the intertidal zone (Odum and McIvor 1990). Duke et al. (1998) found the presence of burrowing crustaceans may increase soil aeration and increase growth in established trees, reducing the competitive edge of *A. germinans* in reducing substrates in the drier, landward portion of mangrove habitat.

*Avicennia germinans* commonly occurs higher in the intertidal zone, where soils may have elevated salinity content due to less tidal flushing and water levels do not submerge the cable roots (Imbert et al. 2000). *Laguncularia racemosa* tends to dominate landward areas in brackish, saturated soils (Imbert et al. 2000). Studies have shown *L. racemosa* grows well in all areas of the intertidal region; however, it dominates on the higher ground with greater soil salinity, where it has the competitive advantage over *R. mangle* (Odum and McIvor 1990). *Laguncularia racemosa* usually colonizes areas
created by disturbances, such as lightning strikes, hurricanes or human influences, often being the first mangrove species able to exploit newly available resources (Odum and McIvor 1990).

Seed predation may be influential in the distribution of mangroves (Odum and McIvor 1990). Heavy predation by crabs and mollusks accounts for the majority of damage to propagules and seedlings around the world (Snedaker and Lahmann 1988), particularly those of the genus *Rhizophora* and *Avicennia* (Smith et al. 1989, Duke et al. 1998). Grapsid crabs, living in high intertidal areas, damage more red mangrove propagules than other mangrove species and may prevent red mangroves from dominating higher in the intertidal region (Duke et al. 1998). A dominance-predation model has been suggested to explain the relationship between seed predation and distribution of mangroves (McGuiness 1997). The model proposes an inverse relationship between the dominant mangrove species in the canopy and the rate of seed predation (McGuiness 1997). However, support for this model has been mixed (e.g. Smith et al. 1989, McKee 1995; McGuiness 1997; Clarke and Kerrigan 2002), indicating that predation may only influence distribution in some regions. For example, studies have shown that the seed predation is an important factor in the distribution of mangroves in Australia (Snedaker and Lahmann 1988), but was less important than other factors in Florida (Smith et al. 1989).

**Environmental Contributions of the Mangrove Ecosystem**

Primary productivity of the mangrove ecosystem ranks as one of the highest in the world (Imbert et al. 2000). The mangrove ecosystem provides numerous ecological services to the surrounding environment and any alteration to the system could bring
about major changes in neighboring systems as well (Imbert et al. 2000). Litter fall from mangroves trees is considered one of the greatest inputs of organic carbon for consumption by the inhabitants of the ecosystem (Odum and McIvor 1990). Net primary production is estimated at 1-12 grams of carbon m$^{-2}$ day$^{-1}$ (Odum and McIvor 1990). This rate often depends on the amount of nutrients entering the system from terrestrial sources (Odum and McIvor 1990). Areas with the greatest tidal activity, and thus greater influx of nutrients, are more productive than areas where the water is more stagnant (Odum and McIvor 1990). When comparing the three native species in Florida, *Rhizophora mangle* has the highest rates of primary productivity, *Avicennia germinans* is the intermediate, and *Laguncularia racemosa* has the lowest rate (Odum and McIvor 1990). The decreased production of *Avicennia germinans* and *Laguncularia racemosa* is attributed to higher salinity stress (Odum and McIvor 1990).

As mangrove litter decays, it supplies dissolved organic carbon to estuarine systems, which invertebrates consume and initiate the detritus-based food web found in estuarine systems (Odum and McIvor 1990). The trunk and root systems serve as a substrate for algae and sessile invertebrates, which also contributes to net productivity of the mangrove ecosystem (Odum and McIvor 1990).

Mangrove ecosystems also act as sinks for various nutrients in the environment, including nitrogen, phosphorus, trace elements and heavy metals (Odum and McIvor 1990). The dense mat of roots and attached epiphytic flora and fauna filter these elements out of the water (Odum and McIvor 1990). These areas also serve as an area for nitrogen fixation, which is generally greatest where there is the highest rate of decaying mangrove leaves (Odum and McIvor 1990).
Communities of marine, estuarine and terrestrial fauna are frequently associated with mangroves (Lugo 1998). It is estimated Florida mangroves support 220 species of fishes, 24 species of reptiles and amphibians, 18 species of mammals, 181 species of birds and hundreds of species of invertebrates (Odum and McIvor 1990). Among the organisms supported by the mangrove ecosystem are many endangered species, including *Crocodylus acutus* (American crocodile), *Lepidochelys kempii* (Atlantic ridley sea turtle), *Trichechus manatus* (Florida manatee), *Haliaeetus leucocephalus* (bald eagle), and *Felis concolor* (Florida panther) (Odum and McIvor 1990). Threatened species or species of concern utilizing the mangrove ecosystem includes *Falco peregrinus* (peregrine falcon), *Pelecanus occidentalis* (brown pelican) and *Nerodia clarkia var. taeniata* (Atlantic salt marsh snake) (Odum and McIvor 1990). The trees provide roosting and nesting areas for the *Mycteria Americana* (wood stork), *Eudocimus albus* (white ibis), *Ajaia ajaja* (roseate spoonbill), *Phalacrocorax auritus* (cormorant), *Pelecanus occidentalis* (brown pelican), and multiple species of egrets and herons (Odum and McIvor 1990).

Prop roots of the mangroves may be as important to juvenile marine organisms as seagrass beds (Odum and McIvor 1990). Mumby et al. (2004) found an increase in adult biomass of fishes when mangrove habitat was connected to adult habitat on coral reefs. Mangroves were an intermediate habitat between the sea grass beds and coral reefs (Mumby et al. 2004). Prop roots provide nursery areas for commercially important fishes and invertebrates, such as the *Panulirus argus* (spiny lobster), *Mugil cephalus* (mullet), *Megalops atlanticus* (tarpon), and *Centropomus undecimalis* (snook) (Odum and McIvor 1990). In areas where the density of mangroves has declined, both the sport and commercial fisheries also have suffered declines (Odum and McIvor 1990).
Brazilian pepper, *Schinus terebinthifolius*

**Introduction of *Schinus terebinthifolius* to Florida**

*S. terebinthifolius*, commonly called Brazilian pepper (Anacardiaceae), is native to subtropical Brazil, Paraguay and Argentina (Jones and Doren 1997). It was brought to Florida in the 1800s as an ornamental in two separate introductions on the east and west coast of Florida (Williams et al. 2005). Its west coast introduction was facilitated by Dr. George Stone of Punta Gorda, who widely distributed the seedlings for use in landscaping (Jones and Doren 1997). Although present in Florida since the 1800s, *S. terebinthifolius* was not identified as a problem until the 1950s when vegetation surveys conducted in Everglades National Park found it to be increasing in abundance and recognized this exotic had the potential to create large scale changes in natural habitats (Ferriter 1997).

In its native habitat, *S. terebinthifolius* colonizes a wide range of habitats from sea level to elevations of 700 meters (Jones and Doren 1997). It grows as scattered individuals among other plant species and does not form the dense, monotypic stands in its native range as is seen in central and south Florida (Ferriter 1997). This evergreen shrub can reach heights of seven meters, has a multiple-stemmed trunk containing leaves made up of four or six lateral leaflets, and produces small flowers in fall (Figure 8a), followed by large quantities of small, bright red berries from November through January (Figure 8b) (Jones and Doren 1997).

Studies of microsatellite and chloroplast DNA suggest that the two strains of this exotic were introduced to Florida from separate source populations and have since hybridized (Williams et al. 2005). Hybrid vigor has been cited as one explanation for this
exotic’s successful invasion into almost every habitat in central and south Florida (Williams et al. 2005). The highly invasive behavior seen in Florida is not found within its native range in South America (Williams et al. 2005).

**Invasion of Florida Habitats**

In Florida’s sub-tropical climate, *S. terebinthifolius* flourished and spread throughout native habitats (Ferriter 1997). In the Everglades, a mapping project in 1987 estimated 105,000 acres of *S. terebinthifolius* within the Park boundaries (Jones and Doren 1997). More recent surveys completed by the South Florida Water Management District estimate this exotic now occupies over 700,000 acres throughout central and southern Florida and is the most widespread exotic plant in the state (Ferriter 1997). *Schinus 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). *Schinus terebinthifolius* colonizes a variety of habitats and soils in Florida and tolerates a wide range of abiotic conditions (Mytinger and Williamson 1987). For example, it 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).

Successful invaders tend to have characteristics that allow them to establish in new habitats (Rejmanek and Richardson 1996). These include high growth rates, high seed production, continuous growth, resprouting after damage, tolerance of a wide range of growing conditions, tolerance of shade, pollination by insects, and animal-dispersed seeds (e.g. Rejmanek and Richardson 1996, Morgan and Overholt 2005). All of these characteristics are possessed by *S. terebinthifolius*, which enable this exotic to out-
compete native vegetation and successfully invade new habitats in Florida (Jones and Doren 1997).

Studies have also shown possible inhibitory effects of *S. terebinthifolius* on surrounding vegetation due to the production of allelopathic compounds (Jones and Doren 1997). One study from the 1970s tested allelopathic properties of *S. terebinthifolius* on germination of native plants and results showed an extract from the fruits had the greatest negative effect on germination (Morgan and Overholt 2005). 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 species, *Bidens alba* (common beggar tick) and *Rivina humilis* (rougeplant). Although many publications have discussed the allelopathic properties of *S. terebinthifolius* (e.g. Jones and Doren 1997, Gordon 1998, Ferriter 1997), the effect on plants in the natural environment is still not well known (Morgan and Overholt 2005). *Schinus terebinthifolius* is not known to be allelopathic in its native range in South America, although, research has shown in other exotics that allelopathic chemicals may be more effective in an invaded area compared to the natural range (Morgan and Overholt 2005). Native flora may co-evolve adaptations which prevent them from being susceptible to the allelopathic chemicals (Morgan and Overholt 2005). When an exotic invades a new area, plants are not adapted to the exotics’ chemicals and may be more susceptible to the inhibitory effects (Morgan and Overholt 2005). Allelopathic chemicals may be another mechanism for the successful invasion of *S. terebinthifolius* into central and southern Florida habitats. However, additional research is needed to fully understand the allelopathic capabilities of Brazilian pepper (Morgan and Overholt 2005).
Seed dispersal by vertebrates increases the probability of a plant invading new habitats and is cited as the primary mechanism for invasion by exotics into undisturbed areas (Rejmanek and Richardson 1996). Despite the high concentrations of chemicals, including monoterpenes and triterpenes in the fruits, invasion by *S. terebinthifolius* was mediated by dispersal of seeds from digested fruits by birds and small mammals (Jones and Doren 1997). *Turdus migratorius* (American robin) is believed to be responsible for the spread of *S. terebinthifolius* seeds, but the fruit is also commonly eaten by *Dumettella carolinensis* (grey catbird), *Mimus polyglottos* (Northern mockingbird), *Pycnonotus jacocus* (red-whiskered bulbul), *Procyon lotor* (raccoon) and *Didelphis virginiana* (opossum) (Jones and Doren 1997). One cause for the high consumption rate of the fruit is the time of year when the fruits are available (Jones and Doren 1997). Fruits are produced between November and February and can be retained on the tree for approximately eight months (Jones and Doren 1997). Because the largest production of fruit occurs when other food sources are unavailable, species use the Brazilian pepper fruits as an alternative to native sources (Ferriter 1997). This has helped this plant invade almost every habitat in central and southern Florida (Jones and Doren 1997). A related plant native to South America of the same genus, *Schinus molle*, produces similar fruits to *S. terebinthifolius* and is used as an alternative food source for birds and small mammals when other foods are scarce (Silva et al. 2004). Research showed a rise in metabolic rate of the culpeo fox, *Pseudalopex culpaeus*, when its diet included these fruits (Silva et al. 2004). This suggests that the animals eating the fruits of *S. molle* pay a higher metabolic cost to compensate for the ingestion of the chemicals within the fruit (Silva et al. 2004).
Early successional communities and disturbed habitats are more susceptible to invasion than older, established communities because opportunistic invaders can take advantage of newly available resources (Jones and Doren 1997). *Schinus terebinthifolius* adapts quickly to an altered environment and often out-competes natives in the newly opened environment (Jones and Doren 1997). Once established, it can entirely replace native plants (Jones and Doren 1997). Although it is not fire adapted, vigorous resprouting of mature trees occurs from the root-crown after fire and *S. terebinthifolius* generally increases in an area after fire due to their rapid growth rate and ability to out-compete native hardwood species (Jones and Doren 1997).

A successful invader in an undisturbed habitat should be shade tolerant in order for the seedlings to establish themselves in the understory of the established vegetation, where they compete with native herbs and grasses for light resources (Gordon 1998). In open areas, *S. terebinthifolius* can grow at rates of 0.3 to 0.5 meters per year, which is one of the highest growth rates exhibited by a woody plant (Jones and Doren 1997). *Schinus terebinthifolius* seedlings are shade tolerant, but the rate of growth in partial light is slower than the high growth rate observed under full light conditions (Jones and Doren 1997). *Schinus terebinthifolius* seedlings were found out-competing native understory plants in the pine rockland habitat of south Florida (Gordon 1998). It was estimated that the species richness of these sites decreased by fifty percent due to competition with *S. terebinthifolius* (Gordon 1998). The adaptation for shade tolerance enables the seedlings to persist in the understory of mature trees, and, if a disturbance occurs that opens up the canopy, vigorous growth occurs under the newly available resources (Jones and Doren 1997).
Another important factor for the successful establishment of invasive species is its ability to change the habitat structure of the area that it invades (e.g. Rejmanek and Richardson 1996, Jones and Doren 1997, Gordon 1998). By changing the structure and composition of habitat, an invasive species can change the resources available to the native species, which may reduce species richness in an area and lead to new selective pressures (Gordon 1998). This change in flora was demonstrated by Herwitz et al. (1996) when they documented the changes in flora on a protected, barrier island in the Gulf of Mexico. During the fifteen-year time interval between plant surveys, *S. terebinthifolius* invaded the island of Cayo Costa and became one of its dominant species (Herwitz et al. 1996). Herwitz et al. (1996) cited the increased abundance of *S. terebinthifolius* and the exotic *Casuarina equisetifolia* (Australian pine) as the key factor in the decrease of species richness on the island. The dominance of the two exotic plants decreased the number of available niches on the island, causing a decrease in abundance of the native plants and altered the existing communities on the barrier island (Herwitz et al. 1996).

**Invasion of Mangrove Ecosystems by *Schinus terebinthifolius***

In order to evaluate the potential for *S. terebinthifolius* to invade mangrove ecosystems, Mytinger and Williamson (1987) designed an experiment to test germination and survival of *S. terebinthifolius* seedlings on soils of the Everglades National Park. Their experiments documented that viability of seeds decreased as salinity increased; 60% of seeds soaked in saltwater with salinity levels of 40 ppt remained viable. Germination also decreased with increases in soil salinities (Mytinger and Williamson 1987). The results led them to conclude that mangrove ecosystems were not at risk for invasion by *S. terebinthifolius*, unless the system was altered to change the environmental...
characteristics (Mytinger and Williamson 1987). However, with sixty percent of the seeds viable after submersion in 40 ppt saltwater, the potential for germination existed, particularly in estuarine environments with intermediate salinity levels. Ewe and Sternberg (2005) evaluated growth and gas exchange of *S. terebinthifolius* at different salinities and compared the results of *S. terebinthifolius* to the responses found in four native species, including two mangrove species, *Rhizophora mangle* and *Laguncularia racemosa*. The gas exchange response of *S. terebinthifolius* to increased salinity was most similar to that found in the native red mangrove *R. mangle* (Ewe and Sternberg 2005). Allocation of biomass in *S. terebinthifolius* changed in response to salinity, with the greatest increase in the shoot biomass (Ewe and Sternberg 2005). This resulted in taller plants compared to the native species (Ewe and Sternberg 2005). Ewe and Sternberg (2005) concluded that morphological and physiological changes in *S. terebinthifolius* in response to salinity indicated salt tolerance in Brazilian pepper.

In a study designed to evaluate litter fall of red mangroves by pruning, it was reported that after opening up the canopy created by the mangroves, *S. terebinthifolius* seedlings increased in experimental plots (Parkinson et al. 1999). Light transmission into the lower portion of the canopy increased by more than thirty percent after pruning (Parkinson et al. 1999). Pruning simulates the damage to the mangroves following a physical disturbance, such as a hurricane, freeze, or from homeowners pruning mangroves to allow them a better view from their home (Parkinson et al. 1999). The productivity of the red mangroves also decreased after pruning due to the loss of leaves, propagules and the apical buds, giving the *S. terebinthifolius* a competitive edge over the damaged mangroves (Parkinson et al. 1999). This aspect would become particularly
important in areas where mangroves are at their northern range for temperature tolerance or areas frequently experiencing hurricanes.

The purpose of my study is to evaluate competition between the invasive *S. terebinthifolius* and three native species of mangroves, *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*, in the coastal estuarine system along the east coast of Central Florida in Canaveral National Seashore. The effects of competition will be evaluated by testing the ability of *S. terebinthifolius* to: 1) chemically inhibit growth of mangrove propagules, 2) invade coastal habitats by dispersing seeds in the water, 3) alter species richness and abundance of the flora when present in a mangrove system, and 4) recruit and survive in mangrove habitat. By better understanding the invasibility and impact of *Schinus terebinthifolius* on mangroves, coastal resource managers will be able to develop the most effective management strategies to prevent this exotic from altering the structure and productivity of the mangrove ecosystem.
CHAPTER 2: SUCCESS OF WATER DISPERsal AS A SECONDARY DISPERsal VECTOR FOR BRAZILIAN PEPPER (SCHinus TEREBINThIFOLIUS) IN A FLORIDA ESTUARY

Introduction

In Florida’s estuaries, mangrove ecosystems have suffered significant losses due to natural and human disturbances (Odum and McIvor 1990); these disturbances potentially leave mangrove communities vulnerable to invasion by the opportunistic exotic, Schinus terebinthifolius (Brazilian pepper). Schinus terebinthifolius was introduced to Florida in the 1800s from South America as an ornamental in two separate introductions on the east and west coast of Florida (Williams et al. 2005). Although present in Florida for over one hundred years, S. terebinthifolius was not identified as a problem until the 1950s when vegetation surveys conducted in Everglades National Park found it to be increasing in abundance and recognized this exotic had the potential to create large-scale changes to natural habitats (Ferriter 1997). This opportunistic exotic has invaded nearly every habitat in central and south Florida and 1997 vegetation surveys estimated it occupied 700,000 acres throughout the state (Ferriter 1997). Schinus 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). Schinus terebinthifolius displaces native flora and forms monotypic stands, which alters the native structure and functions of the community (Jones and Doren 1997).

Seed dispersal by vertebrates increases the probability of a plant invading new habitats and is often the primary mechanism for invasion by exotics into undisturbed
areas (Rejmanek and Richardson 1996). The primary mode of dispersal for S. terebinthifolius seeds that has been documented is through consumption of fruits by birds and mammals (Ferriter 1997). Turdus migratorius (American robin) is believed to be responsible for the spread of S. terebinthifolius seeds, but the fruit is also commonly eaten by Dumettella carolinensis (grey catbird), Mimus polyglottos (Northern mockingbird), Pycnonotus jacosus (red-whiskered bulbul), Procyon lotor (raccoon) and Didelphis virginiana (opossum) (Jones and Doren 1997). Schinus terebinthifolius fruit is produced between November and February and can be retained on the tree for approximately eight months (Jones and Doren 1997). Because the largest production of fruit occurs when native food sources are unavailable, species use the Brazilian pepper fruits as an alternative food source (Ferriter 1997). The time of fruit production can increase the invasion potential of a plant, because it increases the likelihood of consumption by native seed dispersers when production occurs during times when native food sources are unavailable (Gosper et al. 2005). By producing fruits when native food is scarce, the potential for shifts in foraging behavior by native frugivores to include the exotic plant is increased (Gosper et al. 2005). This benefits the exotic by increasing dispersal of seeds into other habitats (Gosper et al. 2005).

Panetta and McKee (1997) documented that S. terebinthifolius seeds consumed by an Australian frugivore Zosterops lateralis (silveryeyes) had a higher germination rate than seeds planted within intact fruits. The increase in germination was attributed to the removal of the exocarp of the seeds, since there was no significant difference in the germination of seeds after consumption by the birds and seeds which had the exocarp removed manually (Panetta and McKee 1997). The exocarps of S. terebinthifolius may
contain inhibitory chemicals (Nilsen and Muller 1980). Laboratory trials found a decrease in germination of lettuce and *S. terebinthifolius* when exposed to extracts from exocarps of *S. terebinthifolius* seeds (Nilsen and Muller 1980). Consumption of fruits by birds and mammals appears to remove this exocarp and increase the probability of germination of *S. terebinthifolius* seeds (Panetta and McKee 1997).

The role of water in dispersing seeds of *S. terebinthifolius* has not been well studied (Ferriter 1997). Although individual fruits and fruit clusters of *S. terebinthifolius* have been observed in Mosquito Lagoon floating within the water currents, becoming stranded on oyster reefs, and settling in the intertidal region of the shoreline, it is unclear if this is an effective mode of dispersal in estuaries. The purpose of this study is to examine the ability of Brazilian pepper growing in an estuarine environment to invade new coastal habitats by dispersing seeds in water. Water dispersal requires seed characteristics to successfully disperse seeds to a new habitat, including buoyancy, movement with water currents, becoming stranded in suitable habitat and germination after dispersal (Poschlod et al. 2005). The potential for water dispersal in *S. terebinthifolius* was examined by: 1) determining the length of time fruits remain buoyant in different water salinities, 2) estimating the dispersal rate of fruits, 3) evaluating the role of boat wakes in moving floating fruits above the mean high water mark and into suitable habitat, and 4) estimating the viability of seeds after soaking in saltwater for up to fourteen days.
Methods

Study Area
All collection of seeds occurred in Mosquito Lagoon in Canaveral National Seashore, located on the east coast of Florida south of New Smyrna Beach (28° 56.04 N, 80°49.2 W) (Figure 9). Canaveral National Seashore was established in 1975 and includes a mix of habitats ranging from the ocean and beach dunes to salt marsh and coastal hammocks (Green 2002). Approximately two-thirds of Canaveral National Seashore consists of Mosquito Lagoon (Green 2002). Mosquito Lagoon is the northernmost portion of the Indian River Lagoon system, an estuary that extends 250 km along the east coast of Florida and supports an estimated 3000 species of animals and 1000 species of plants (Green 2002).

Study Species
Schinus 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 seven meters and has a multiple-stemmed trunk (Jones and Doren 1997). The compound leaves are made up of four or six lateral leaflets, which are oblong with toothed margins and are connected to the primary leaf axis by a small, red stalk (Ferriter 1997). Schinus terebinthifolius is dioecious and produces small flowers on branched inflorescences in the fall, usually from August-October (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 (drupes) containing individual seeds from November through February (Ferriter 1997). Schinus terebinthifolius colonizes a variety of habitats and soils in
Florida and tolerates a wide range of abiotic conditions (Mytinger and Williamson 1987). It has been identified in both disturbed and undisturbed areas of tropical hardwood forests, pine rocklands, sawgrass marshes, and mangrove swamps in central and south Florida (Jones and Doren 1997).

**Buoyancy of *Schinus terebinthifolius* fruits**

The buoyancy of *S. terebinthifolius* fruits was determined by placing fifty fruits in five-gallon buckets filled with 0 ppt, 15 ppt or 30 ppt salt water. The number of floating fruits was recorded daily until all fruits lost buoyancy and sank. The number of days fruits remain buoyant represents the length of time fruits could disperse in water. Fruits were gathered from a minimum of eight trees, mixed and randomly chosen for trials. A total of eight trials were conducted during winter 2004 and summer 2005, based on the availability of fruits. The length of time fruits remained buoyant in different salinities was compared using survival analysis (Wilcoxon statistic, SPSS 14.0).

**Dispersal rate of *Schinus terebinthifolius* fruits in Mosquito Lagoon**

Individual fruits of *S. terebinthifolius* (n = 30) or fruit clusters (n = 15) were released into Mosquito Lagoon waters and their movements were tracked for ten minutes on three dates: 3 October 2004, 21 June 2005, and 13 July 2005. After ten minutes, the total distance the fruit or fruit cluster traveled was measured from the starting position with a 100-m transect tape. This allowed us to estimate the rate of dispersal for fruits and fruit clusters once floating in the Lagoon. The overall mean dispersal rate of individual fruits was determined from all three trials and was combined with the highest mean number of days fruits retained buoyancy to estimate the potential dispersal distance of *S. terebinthifolius* through water dispersal. Wind speed was measured with a Kestrel 2000.
wind meter every thirty minutes on each trial date. Salinity and temperature were measured at the beginning of each trial date. A two-way ANOVA (trial date X type of fruit) was used to compare the distances moved by individual fruits and fruit clusters (SPSS 13.0 Student Version).

**Boat wake impacts on shoreward dispersal of *Schinus terebinthifolius* fruits**

Boat wakes may assist floating *S. terebinthifolius* fruits reach suitable habitat above the intertidal region. To determine the distance boat wakes move fruits of *S. terebinthifolius* stranded in the intertidal zone, 50 fruits were lined up along a transect tape parallel to shore at the water’s edge. A 17 ft. (5.1 m) Boston Whaler with a 40 hp motor was driven past the shore at maximum speed (approximately 45 km h\(^{-1}\)) to create wakes (15 trials, 3 days). For each trial the height of the boat wake was measured to the nearest centimeter with a stadia rod. The wind speed was measured with a Kestrel 2000 wind meter. The total distance fruits moved from the transect tape was measured in centimeters with a measuring tape. Fruits which moved from the starting point towards land were recorded as positive dispersal distance and those which moved from the starting point towards land and then back towards the water were recorded as negative dispersal distance.

The results from this experiment represent the total impact of boat wakes and wind-created waves on moving the fruits. To separate the impact of these two influences, the effect of wind created waves on moving *S. terebinthifolius* fruits deposited onshore was determined by measuring the distance fruits moved after 30 s of exposure to wind waves alone. The wind speed was monitored with a Kestrel 2000 wind meter in 30 s time intervals and then the maximum wind speed for each interval was recorded. Distances
fruits moved in boat wake and wind-created wave trials were compared using a two-way ANOVA (trial date X wave type) (SPSS 13.0 Student Version).

**Viability of Schinus terebinthifolius fruits after dispersing in salt water**

The maximum amount of time *S. terebinthifolius* fruits retain buoyancy and remains viable is not known. To test the viability of fruit-encased seeds after soaking in salt water, 325 *S. terebinthifolius* fruits were placed in 36 ppt salt water from Mosquito Lagoon. Twenty-five of these fruits were removed from the saltwater each day and planted in 3.8 L pots filled with top soil (Southland Topsoil) each day over the next thirteen days. Twenty-five fresh fruits not exposed to salt water were planted in a 3.8 L pot filled with top soil (Southland Topsoil) to serve as a control. These pots were monitored daily for four months for germination of fruits. This experiment was repeated three times, beginning on 6 May 2005, 25 May 2005 and 13 June 2005.

**Results**

**Buoyancy of Schinus terebinthifolius fruits**

*Schinus terebinthifolius* floated a maximum of 16 days in 0 ppt saltwater (Figures 10a, 11). The mean number of days (± SE) fruits remained buoyant in 0 ppt saltwater ranged from 3.4 ± 0.1 to 6.9 ± 0.4 days in the eight buoyancy trials (Table 1). In 18 ppt saltwater, fruits of *S. terebinthifolius* floated a maximum of 21 days (Figures 10b, 11). The mean number of days (± SE) fruits remained buoyant ranged from 3.7 ± 0.1 to 12.14 ± 0.6 days throughout the eight trials (Table 1). *Schinus terebinthifolius* fruits floated a maximum of 20 days in 36 ppt saltwater (Figures 10c, 11). The mean number of days (± SE) fruits remained buoyant in 36 ppt saltwater ranged from 4.4 ± 0.3 to 8.9 ± 0.5 days in the eight trials (Table 1). The overall mean number of days fruits remained buoyant from
all eight trials was 4.8 (± 0.1) days in 0 ppt saltwater, 6.3 (± 0.2) days in 18 ppt saltwater, and 6.4 (± 0.1) days in 36 ppt saltwater.

Survival analysis found a significant difference (p < 0.05) in the length of time fruits remained buoyant between salinity treatments of fruits in six of the eight trials (Table 2). Comparisons between the length of time fruits remain buoyant in 0 ppt saltwater compared to 18 ppt saltwater was significantly different in four of the eight trials. However, comparisons between the fruits floating in 36 ppt saltwater compared to 0 ppt saltwater found fruits in the 36 ppt saltwater remained buoyant significantly longer in six of the eight trials (Table 2). The length of time fruits remained buoyant in 36 ppt saltwater compared to 18 ppt saltwater was significantly greater in three of the eight trials (Table 2).

**Dispersal rate of *Schinus terebinthifolius* fruits in Mosquito Lagoon**

In trial 1, the mean distance (± SE) traveled in ten minutes for individual fruit was 12.8 ± 0.9 m and the mean dispersal rate was 0.02 ± 0.01 m s⁻¹ (Table 3). The mean distance traveled in ten minutes by the fruit clusters was 12.3 ± 2.0 m and the mean dispersal rate was 0.02 ± 0.01 m s⁻¹ (Table 3). The mean wind speed was 1.1 ± 0.3 m s⁻¹ and salinity was 25 ppt (Table 3).

In trial 2, the mean distance traveled by individual fruits in ten minutes was 40.4 ± 0.5 m and the mean dispersal rate was 0.06 ± 0.001 m s⁻¹ (Table 3). The mean distance traveled in ten minutes by fruit clusters was 21.7 ± 2.6 m and the mean dispersal rate was 0.04 ± 0.01 m s⁻¹ (Table 3). The mean wind speed was 1.2 ± 0.2 m s⁻¹ and salinity was 30 ppt (Table 3).
In trial 3, the mean distance individual fruit traveled in ten minutes was 19.7 ± 0.7 m and the mean dispersal rate was 0.03 ± 0.01 m s⁻¹ (Table 3). The mean distance traveled by fruit clusters in ten minutes was 22.30 ± 1.30 m and the mean dispersal rate was 0.04 ± 0.01 m s⁻¹ (Table 3). The mean wind speed was 0.80 ± 0.10 m s⁻¹ and salinity was 26 ppt (Table 3).

The overall mean dispersal rate (± SE) of individual fruits for all three trials combined was 0.04 ± 0.01 m s⁻¹ (Figure 12), with a range of dispersal rate between 0.01 m s⁻¹ to 0.07 m s⁻¹. The overall mean dispersal rate (± SE) of fruit clusters for all three trials combined was 0.03 ± 0.01 m s⁻¹ (Figure 12). Results of the two-way ANOVA found a significant interaction (F = 38.5, p< 0.01) between velocity of individual fruits and fruit clusters and trial date. Using the estimated dispersal rate of 0.04 m s⁻¹ and the overall mean number of days fruits remained buoyant in 36 ppt saltwater (6.4 days), the distance one fruit could travel before losing buoyancy was estimated to be 22.1 km in Mosquito Lagoon.

**Boat wake impacts on shoreward dispersal of Schinus terebinthifolius fruits**

The range of distances seeds moved when exposed to boat wakes was -10.7 cm to 120.5 cm in the first trial, -5.0 cm to 83.5 cm in the second trial, and -12.0 cm to 79.0 cm in the third trial. The mean distance individual fruit moved toward shore as a result of boat wakes was 23.1 ± 0.5 cm in the first trial, 49.1 ± 1.1 cm in the second trial and 18.4 ± 0.6 cm in the third trial (Table 4). The mean wind speed (± SE) during boat trials was 2.5 ± 0.2 m s⁻¹ for trial 1, 0.7 ± 0.1 m s⁻¹ for trial 2 and 2.6 ± 0.2 m s⁻¹ for trial 3 (Table 4). The mean wave height (± SE) was 0.2 ± 0.5 m, 0.2 ± 0.3 m and 0.2 ± 0.8 for trials 1, 2, and 3, respectively (Table 4).
In comparison, the mean distance fruits moved when exposed to wind created waves was 0.7 ± 0.1 cm in the first trial and 0.0 ± 0.0 cm in the second and third trials (Table 4). The mean wind speed (± SE) during wind trials were 4.2 ± 0.2 m s\(^{-1}\) for trial 1, 0.6 ± 0.04 m s\(^{-1}\) for trial 2 and 2.3 ± 0.2 m s\(^{-1}\) for trial 3 (Table 4). The mean wave height (± SE) was 0.0 ± 0.0 cm for all three trials (Table 4).

The overall mean distance (cm) (± SE) fruits moved for the three trials combined was 30.1 ± 1.2 cm and 0.2 ± 0.1 cm for the boat wake trials and wind trials, respectively (Figure 13). Results of the two-way ANOVA found a significant interaction (F = 457.5, p< 0.01) between the distance fruits moved by boat wake and wind wakes and trial date.

**Viability of *Schinus terebinthifolius* fruits after dispersing in salt water**

Germination was monitored until February 2006 and did not occur in any pots for all three trials, including the controls. All fruits visible on surface of soil had intact exterior coatings and had not opened to release seeds. Additional tests are currently being done using tetrazonium chloride to measure viability of seeds after soaking in saltwater.

**Discussion**

The results from this study support the hypothesis that water dispersal is an important dispersal mechanism for *Schinus terebinthifolius* seeds. Webb (1998) described the three major processes involved in seed dispersal. First, the seed must be released or removed from the tree (Webb 1998). In the case of *S. terebinthifolius* growing along the shore in Mosquito Lagoon, the mature trees are overhanging the water’s edge and fruits drop from the parent tree into the water. The second process is transport (Webb 1998). For water dispersal, this is a combination of the time seeds
remain buoyant and the rate of passive movement in the water currents (Poschlod et al. 2005). The third process is deposition into suitable habitats (Webb 1998). For *S. terebinthifolius*, this includes shoreward movement above the intertidal region, where it would have a greater chance of survival. Based on the results of this study, all three processes are occurring with water dispersal when *S. terebinthifolius* is in estuarine habitats.

The length of time a fruit remains buoyant is a major limiting factor to the distance floating seeds may disperse (Rabinowitz 1978). When dispersing in water currents, seeds must reach suitable habitat prior to losing buoyancy. Once buoyancy is lost, the seed will sink and lose any potential for survival unless it has reached suitable habitat. In this study, buoyancy was significantly longer in most trials for fruits floating in 36 ppt compared to 18 ppt and 0 ppt (Figure 10, Table 2). This suggests that increased dispersal distances are expected for fruits floating in high saline environments compared to areas of freshwater and brackish water. Increased buoyancy time may also increase the probability of settling in suitable habitat since it will float longer within water currents. If initial stranding occurs in an area unsuitable for establishment, the retention of buoyancy may allow the fruit to be dispersed multiple times if reintroduced to the water currents through wave action (Rabinowitz 1978). This could increase the probability of reaching a new habitat more suitable for establishment (Rabinowitz 1978).

The rate of movement determines the distance seeds will disperse during the buoyancy phase, however, it is dependant on multiple factors, including water currents and wind speed, and will be highly variable between local sites. This study estimated the mean dispersal distance of *S. terebinthifolius* seeds to be 30.8 km. Ozinga et al. (2004)
classified any vector which dispersed seeds greater than 100 m away from parent populations to be a long-distance dispersal vector. Based on this classification, water dispersal is an additional long-distance dispersal method of seeds from *S. terebinthifolius*.

After movement within the water currents, seeds need to be deposited into suitable habitat for germination prior to the loss of buoyancy. This is important in the case of *S. terebinthifolius*, which has low rates of survival in the saturated, high salinity soil found in the intertidal zone of estuaries (Mytinger and Williamson 1987). This is supported by field studies within Mosquito Lagoon that found *S. terebinthifolius* did not grow within 1 meter of the water’s edge (Donnelly, unpublished data). In order for water dispersal to be successful for *S. terebinthifolius*, seeds must be moved shoreward into drier and less saline soils. The results from the boat wake trials confirmed that *S. terebinthifolius* fruits moved by boat wakes were stranded over 1 meter shoreward, relocating them into a drier habitat more suitable for germination and increasing the probability that water-dispersed seeds could invade and establish in new habitats along the edges of estuaries.

Once stranded in suitable habitat, *S. terebinthifolius* seeds need to have retained germination capabilities during the dispersal period in order to colonize new habitat. The results from the viability trials were inconclusive since no seeds germinated in any treatment groups, including the control. One possible explanation for the absence of germination is that prolonged exposure to saltwater may decrease viability. Mytinger and Williamson (1987) found sixty percent of *S. terebinthifolius* seeds remained viable after submersion in 40 ppt saltwater for 72 hours, supporting the hypothesis that water dispersal is a viable secondary method for seed dispersal. Although viability and
germination decreased with increased salinities, the potential for germination exists, particularly in an estuarine environment with intermediate water salinities (Mytinger and Williamson 1987). Mytinger and Williamson (1987) removed seeds from the exocarps prior exposure to saltwater. It is currently unknown if seeds within the fruit (with an intact exocarp) would retain viability longer than those seeds directly exposed to saltwater.

Another possibility is that the seeds planted with intact exocarps are not capable of germination. In a study by Panetta and McKee (1997), seeds which had the exocarp removed had greater rates of germination than those planted within intact fruit. However, germination still occurred in seeds sown within the fruits, therefore, the seeds are not dependant on consumption and passage of vertebrates in order for germination to occur (Panetta and McKee 1997). More research is needed to understand the effect of saltwater on viability of S. terebinthifolius seeds after water dispersal.

*Schinus terebinthifolius* benefits from the consumption of fruits by frugivorous birds and mammals, which disperses seeds over long distances (Ferriter 1997). The consumption of fruits and subsequent spread of seeds by animal vectors has been attributed to the successful invasion of *S. terebinthifolius* into nearly every habitat in central and southern Florida (Jones and Doren 1997). By encasing the seed within a fleshy fruit, *S. terebinthifolius* successfully attracts frugivores to assist with seed dispersal. These characteristics also seem to increase the success of water dispersal, with the fruit acting as a buoyant dispersal vessel for the seed. The exterior coating of the fruit may also preserve the viability of the internal seeds by protecting the seed from damage by saltwater; however, this has not been demonstrated experimentally at this time.
The probability of survival of plant populations increases when the rates of long
distance dispersal and the number of long-distance dispersal vectors increase (Ozinga et
al. 2004). For exotic plants, the ability to invade increases significantly when multiple
dispersal vectors are employed by the species (Gosper et al. 2005). Long distance
dispersal may be particularly important for *S. terebinthifolius* because studies have shown
that this exotic contains allelopathic compounds which inhibit the establishment of some
plants, including conspecific plants (Nilsen and Muller 1980). Seeds of *S.
terebinthifolius* may have an increased chance of germination and survival when long
distance dispersal moves the seeds away from the parent population. By utilizing
multiple dispersal methods, *S. terebinthifolius* increases its chance for survival, spread
and establishment in estuarine environments. This emphasizes the need for management
of this exotic in coastal habitats, where the rate of spread and survival of *S.
terebinthifolius* may increase through the use of multiple dispersal pathways.
CHAPTER 3: ALLELOPATHIC PROPERTIES, RECRUITMENT AND IMPACT ON BIODIVERSITY OF SCHINUS TEREBINTHIFOLIUS IN MANGROVE SYSTEMS OF CENTRAL FLORIDA

Introduction

Mangroves establish themselves in an ecological niche unavailable to many other species due to the high salinity levels, tidal fluctuations, anaerobic substrates and the accumulation of toxins (e.g. Snedaker and Lahmann 1988, Lugo 1998). The environmental conditions of mangrove habitat inhibit the growth and survival of non-halophytic and terrestrial flora, which have not evolved the specialized adaptations found in the mangroves (Snedaker and Lahmann 1988, Lugo 1998). The abiotic conditions of mangrove ecosystems usually prevent invasions by native or exotic species (Snedaker and Lahmann 1988), unless the environmental conditions are changed due to natural or human mediated impacts (Mytinger and Williamson 1987, Lugo 1998). Recent natural and anthropogenic disturbances, such as hurricanes, habitat destruction and impoundment, have changed the natural conditions in many of the mangrove ecosystems in Florida (Odum and McIvor 1990, Lugo 1998). These alterations potentially leave them vulnerable to invasion by exotic plants, such as Schinus terebinthifolius (Brazilian pepper).

Schinus terebinthifolius is native to South America and was introduced to Florida for use as an ornamental in two separate introductions 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 and recognized this exotic had the potential to create large scale changes in natural habitats (Ferriter 1997). Surveys completed by the South Florida Water Management District in 1997 reported that *S. terebinthifolius* occupied an estimated 700,000 acres throughout Florida (Ferriter 1997).

Successful invaders tend to have certain characteristics that allow them to establish in new habitats, including high growth rates, high seed production, recovery after damage, tolerance of a range of environmental conditions, tolerance of shade, pollination by insects and animal-dispersed seeds (e.g. Rejmanek and Richardson 1996, Morgan and Overholt 2005). All of these characteristics are possessed by *S. terebinthifolius*, which enable this exotic to out-compete native vegetation and invade new habitats in Florida (Jones and Doren 1997). *Schinus terebinthifolius* colonizes in a variety of Florida habitats and tolerates a wide range of abiotic conditions (Mytinger and Williamson 1987). 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).

*Schinus 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). By changing the structure and composition of habitat, an invasive species can change the resources available to native species, which may reduce species richness in an area and lead to new selective pressures (Gordon 1998). This change in flora was documented by Herwitz et al. (1996) on a protected, barrier island in the Gulf of Mexico. During the fifteen year time interval between plant surveys, *S. terebinthifolius* invaded the island of
Cayo Costa and became one of its dominant species (Herwitz et al. 1996). Herwitz et al. (1996) cited the increased abundance of *S. terebinthifolius* and *Casuarina equisetifolia* (Australian pine, another exotic tree species) as the key factors in the decrease of species richness on the island. The dominance of the two exotic plants decreased the abundance of native flora and altered the existing communities on the barrier island (Herwitz et al. 1996).

The impact of *S. terebinthifolius* on mangrove ecosystems has been contradictory in the literature (e.g. Mytinger and Williamson 1987, Parkinson et al. 1999, Ewe and Sternberg 2005). Mytinger and Williamson (1987) tested germination and survival of *S. terebinthifolius* seedlings on saline soils of Everglades National Park. The experiments documented that viability of seeds decreased as salinity increased; however, 60% of seeds soaked in saltwater with salinity levels of 40 ppt remained viable. Germination also decreased with increases in soil salinities (Mytinger and Williamson 1987). The results led them to conclude that mangrove ecosystems were not at risk for invasion by the *S. terebinthifolius* unless the system was altered to change the environmental characteristics (Mytinger and Williamson 1987).

Ewe and 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, *Rapanea punctata* (myrsine), *Randia aculeate* (white indiogberry), *Rhizophora mangle* (red mangrove) and *Laguncularia racemosa* (white mangrove). At high salinities, all species showed a decrease in gas exchange parameters, however, the gas exchange responses of *Schinus terebinthifolius* was most similar to the responses of the native red mangrove, *R. mangle* (Ewe and Sternberg
Allocation of biomass in *S. terebinthifolius* changed in response to salinity, with the greatest increase seen in the shoot biomass (Ewe and Sternberg 2005). This resulted in taller plants, giving *S. terebinthifolius* a competitive edge over the native plants when competing for space and light requirements (Ewe and Sternberg 2005). Ewe and Sternberg (2005) concluded that morphological and physiological changes in *S. terebinthifolius* in response to salinity indicate salt tolerance in Brazilian pepper.

A study evaluating litter fall of red mangroves after pruning reported an increase in *S. terebinthifolius* seedlings after creating openings in the mangrove canopy (Parkinson et al. 1999). Pruning simulated the damage to mangroves following an environmental disturbance, such as a hurricane or freeze, or from homeowners pruning mangroves to allow better views from their homes (Parkinson et al. 1999). The productivity of the red mangroves also decreased after pruning due to the loss of leaves, propagules and apical buds, giving *S. terebinthifolius* a competitive edge over the damaged mangroves and increasing the likelihood that *S. terebinthifolius* would increase in abundance in areas where mangroves are damaged (Parkinson et al. 1999). This is particularly important in areas where mangroves are at their northern range for temperature tolerance or areas frequently experiencing hurricanes.

Studies have also shown possible inhibitory effects of *S. terebinthifolius* on surrounding vegetation due to the production of allelopathic compounds (Jones and Doren 1997). *Schinus 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, coexisting with other flora (Ferriter 1997). One possible reason for this highly invasive behavior is that *S. terebinthifolius* produces
allelopathic compounds (Morgan and Overholt 2005). Allelopathy is a form of interference competition; one species releases toxic compounds and prevents the germination, growth and establishment of other plant species (Van Andel 2005). *Schinus terebinthifolius* is not known to be allelopathic in its native range in South America, although, research in other exotics has shown that allelopathic chemicals may be more effective in an invaded area (Morgan and Overholt 2005). Native flora may co-evolve adaptations which prevent them from being susceptible to allelopathic chemicals (Morgan and Overholt 2005). When an exotic invades a new area, plants are not adapted to the exotics’ chemicals and may be more susceptible to the inhibitory effects (Morgan and Overholt 2005). The production of allelopathic chemicals gives the exotic a competitive advantage over native flora and could lead to increases in abundance of the exotic in invaded habitats (Van Andel 2005).

One study from the 1970s tested allelopathic properties of *S. terebinthifolius* on germination of native plants and results showed the extract from the fruits had the greatest negative effect on germination (Morgan and Overholt 2005). The exocarps of *S. terebinthifolius* seeds may contain inhibitory chemicals (Nilsen and Muller 1980). Laboratory trials found a decrease in germination of lettuce and *S. terebinthifolius* when exposed to extracts from exocarps of *S. terebinthifolius* seeds (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 species, *Bidens alba* (common beggar tick) and *Rivina humilis* (rougeplant). Although many 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 purpose of this study is to evaluate ecosystem-level effects of *S. terebinthifolius* on invaded mangrove systems in the coastal estuarine system in Canaveral National Seashore along the east coast of Central Florida. This will be evaluated by testing the ability of *S. terebinthifolius* to: 1) chemically inhibit growth of mangrove seedlings, 2) alter species richness and abundance of the flora when present in a mangrove system, and 3) recruit and survive in mangrove habitat. By better understanding the invasibility and impact of *Schinus terebinthifolius* on mangroves, coastal resource managers will be able to develop the most effective management strategies to prevent this exotic from altering the structure and productivity of the mangrove ecosystem.

**Methods**

**Study Area**

All field work and collection of seeds occurred in Mosquito Lagoon in Canaveral National Seashore, located on the east coast of Florida directly south of New Smyrna Beach (28°56.0' N, 80°49.2' W) (Figure 9). Canaveral National Seashore was established in 1975 and includes a mix of habitats ranging from the ocean and beach dunes to salt marsh and coastal hammocks (Green 2002). Approximately two-thirds of Canaveral National Seashore consists of the estuary, Mosquito Lagoon (Green 2002). Mosquito Lagoon is the northernmost portion of the Indian River Lagoon system, which extends 250 km along the east coast of Florida and supports an estimated 3000 species of animals and 1000 species of plants (Green 2002). Mosquito Lagoon was designated an
Outstanding Florida Water and provides resources to a diverse group of terrestrial, marine and estuarine organisms (Green 2002).

**Study Species**

*Schinus terebinthifolius*

*Schinus 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 seven meters and has a multiple-stemmed trunk (Jones and Doren 1997). The compound leaves are made up of four or six lateral leaflets, which are oblong with toothed margins and are connected to the primary leaf axis by a small, red stalk (Ferriter 1997). *Schinus terebinthifolius* is dioecious and produces small flowers on branched inflorescences in the fall, usually from August-October (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 (drupes) containing individual seeds from November through February (Ferriter 1997). Seeds are primarily dispersed by birds and small mammals, which consume the fruits at high rates because fruit production occurs when less native food is available in Florida (Ferriter 1997).

*Rhizophora mangle*

*Rhizophora 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 allow oxygen to diffuse into the aerenchyma (Odum and McIvor 1990). *Rhizophora mangle* can reach heights up to twenty-five meters and has deep green leaves which are
paler green on the underside of the leaves (Tomlinson 1994). *Rhizophora mangle* flowers year round (Fernandes 1999) and flowers are wind-pollinated and self-compatible (Tomlinson 1994). After flowering and pollination occur, long, buoyant propagules grow up thirty centimeters before leaving the parent tree (Odum and McIvor 1990). These buoyant propagules disperse by water and are viviparous, with the growth of the embryo continuing throughout the dispersal stage (Rabinowitz 1978).

*Avicennia germinans*

*Avicennia germinans* (Avicenniaceae), the black mangrove, is characterized by a shallow system of laterally extending roots emerging from the substrate, known as cable roots (Tomlinson 1994). The cable roots contain pneumatophores with lenticels on the exposed portion that can extend up to twenty centimeters above the substrate (Odum and McIvor 1990). *Avicennia germinans* reaches heights of twenty meters and has narrow, elliptical leaves which are deep green on the upper surfaces and white on the lower surfaces (Tomlinson 1994). The leaves of *Avicennia germinans* are encrusted with secreted salt (Odum and McIvor 1990). White flowers form in the early summer months in Florida and are the largest in this genus at ten to thirteen millimeters (Tomlinson 1994). The flowers are pollinated by short-tongued insects, particularly honeybees (Tomlinson 1994). Its propagules are small, measuring two to three centimeters. These ovoid-shaped propagules are viviparous, with the embryo germinating immediately after release from the parent tree (Tomlinson 1994).

*Laguncularia racemosa*

*Laguncularia racemosa* (Combretaceae), the white mangrove, lacks prop or cable roots, but contains lenticels on the lower portion of the trunk (Odum and McIvor
Laguncularia racemosa can reach heights of fifteen meters or more and have flat, oval shaped leaves that are up to seven centimeters long (Odum and McIvor 1990). This species is usually dioecious; however, there is some evidence of monoecious trees and self-fertilizing flowers (Tomlinson 1994). The flowers are four to five millimeters in diameter, have a greenish-yellow color and form in the summer months in Florida (Tomlinson 1994). Flowers are pollinated by insect vectors, mostly bees (Tomlinson 1994). The small, ovoid-shaped propagules measure approximately two centimeters and are viviparous (e.g. Odum and McIvor 1990, Tomlinson 1994).

**Inhibitory effects of Schinus terebinthifolius**

Mangrove propagules were planted in August 2004 (*Rhizophora mangle*) and October 2004 (*Avicennia germinans* and *Laguncularia racemosa*). Each propagule was individually planted in a 3.8 L plastic pot containing top soil (Southland Topsoil) without additives or fertilizers (n = 250/species). Pots with propagules were kept in rectangular holding trays (24 m x 24 m) lined with 6 mm thick plastic sheets and filled with either 15 ppt or 30 ppt salt water (n = 125 for each species x salinity combination).

Each pot initially received 150 ml of 15 ppt or 30 ppt saltwater to saturate the soil. 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 watering holes in the bottom of each pot. Salinity of water in holding trays was monitored every two days with an optical refractometer. Water depth was monitored every two days with a meter stick. Salts (Instant Ocean Sea Salts) and tap water was added as needed to maintain depth and salinity.
Height from surface of soil to apical meristem was measured with a ruler after the emergence of the first leaves one week after planting for *R. mangle*, and two to three weeks after planting for *A. germinans* and *L. racemosa*. The total number of leaves was recorded for each plant at time of height measurement. Monitoring of the growth and survival of the mangrove seedlings continued until August 2005. Survival of *L. racemosa* was low and was not included in the following experimental trials.

In August 2005, intact Brazilian pepper 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 treatment groups (n = 20): 3 fruit densities of *Schinus terebinthifolius* x 2 water salinities. The total number of leaves and height from surface of soil to apical meristem was measured with a ruler every two weeks after the addition of the Brazilian pepper fruits until December 2005. Final heights and number of leaves were then recorded and all above ground biomass for each plant was removed, dried at 70ºC for 24 hours and weighed. Two-factor ANOVAs (density x salinity) were used to compare the mean growth rate, biomass and increase in number of leaves for each mangrove species (SPSS 13.0).

**Effect of *Schinus terebinthifolius* on biodiversity**

To estimate species richness and abundance of sites with and without *Schinus terebinthifolius*, 3 line transects (30 m) from the lagoon shoreline into the mangrove-upland ecotone were surveyed at 14 sites within Mosquito Lagoon (Figure 14a). Sites were chosen based on the presence or absence of a reproductive Brazilian pepper tree within 30 m of shoreline (n = 7 sites with Brazilian pepper and n = 7 for sites without Brazilian pepper). Initial starting points of transects were randomly chosen along a 60 m
transect tape run parallel to the shoreline. Plants in contact with the line were recorded at 1-m intervals to estimate species richness and abundance of native and exotic flora. Locations along transect line which did not touch any plant were recorded as empty patches. Soil salinity and moisture were recorded at 10-m intervals with an Aquaterr EC-300 soil probe along all transects. All transects were surveyed during a one week period in August 2005. Species richness was compared between sites using a two-factor nested ANOVA (SPSS 13.0). Correlation analysis (Pearson’s correlation) was used to determine the relationship between species richness, number of *Schinus terebinthifolius*, % soil moisture, soil salinity, and number of empty patches at each site (SPSS 13.0). Contigency tables and the Pearson Chi-Square statistic were used to further investigate the relationship between these variables and species richness (SPSS 13.0).

**Recruitment and survival of *Schinus terebinthifolius* in a mangrove ecosystem**

Ten of the fourteen transect sites (n = 6 sites with Brazilian pepper and n = 4 for sites without Brazilian pepper) were monitored monthly for recruitment of native mangroves and *S. terebinthifolius* (Figure 14b). Ten 0.25 m² quadrats, 3 m apart and parallel to shoreline, were marked in the following zones: 1) within the intertidal zone, 2) ten meters above the intertidal region and 3) twenty meters above the intertidal region at each of the ten sites. All flora was identified, counted and recorded within each quadrat. Monitoring occurred monthly for sixteen months, starting in August 2004 and continuing through December 2005 (monitoring did not occur during September 2004 due to hurricane). Three hurricanes impacted this region during the monitoring period, Hurricane Charley (13 August 2004), Hurricane Frances (5 September 2004), and Hurricane Jeanne (25 September 2004).
In February 2005, Volusia County Mosquito Control chemically treated *S. terebinthifolius* at sites 2, 6, and 9. Monitoring continued in order to evaluate the effectiveness of the chemical treatment and the subsequent development of flora following treatment at the above sites. For analysis purposes, sites were divided into three groups: 1) sites without Brazilian pepper (Site 1, 7, 8, 10), 2) sites with Brazilian pepper without chemical treatment (Sites 3, 4, 5), and 3) sites with Brazilian pepper with chemical treatment (Sites 2, 6, 9). The mean change in abundance during the hurricane season (August 2004- October 2004) and post-hurricane (November 2004- January 2006) at each type of site was estimated by calculating the difference in number of plants m$^{-2}$ between the first monitoring date and final monitoring date for each species of mangrove and *S. terebinthifolius*. Comparisons of mean change in abundance post-hurricane were made using a two-factor ANOVA (site X zone) for the three species of mangroves and *S. terebinthifolius* (SPSS 13.0).

**Results**

**Inhibitory effects of Schinus terebinthifolius**

Survival for all mangrove seedlings of *R. mangle* and *A. germinans* was 100% for all seed density treatments and salinities. The mean growth rate (± SE) (cm day$^{-1}$) for *R. mangle* was 0.02 ± 0.01 cm day$^{-1}$ with 0 fruits, 0.02 ± 0.01 cm day$^{-1}$ with 25 intact fruits, and 0.02 ± 0.02 cm day$^{-1}$ with 50 intact fruits for seedlings grown in 15 ppt saltwater (Figure 15a). *Rhizophora mangle* seedlings grown in 30 ppt saltwater had a mean growth rate (± SE) (cm day$^{-1}$) of 0.02 ± 0.01 cm day$^{-1}$ with 0 fruits, 0.02 ± 0.01 cm day$^{-1}$ with 25 fruits, and 0.02 ± 0.01 cm day$^{-1}$ with 50 fruits (Figure 15a). There was not a significant
difference ($F = 1.51, p = 0.22$) in the growth rate of *R. mangle* in the two salinities or three fruit densities (Table 5).

The mean growth rate ($± SE$) ($\text{cm day}^{-1}$) for *A. germinans* seedlings grown in 15 ppt saltwater was $0.03 ± 0.01 \text{ cm day}^{-1}$ with 0 fruits, $0.04 ± 0.01 \text{ cm day}^{-1}$ with 25 fruits, and $0.05 ± 0.01 \text{ cm day}^{-1}$ with 50 fruits (Figure 15b). *Avicennia germinans* seedlings grown in 30 ppt saltwater had a mean growth rate ($± SE$) ($\text{cm day}^{-1}$) of $0.06 ± 0.01 \text{ cm day}^{-1}$ with 0 fruits, $0.06 ± 0.01 \text{ cm day}^{-1}$ with 25 fruits, and $0.04 ± 0.01 \text{ cm day}^{-1}$ with 50 fruits (Figure 15b). There was a significant interaction ($F = 4.85, p = 0.01$) between salinity and fruit density on the growth rate of *A. germinans* (Table 6).

The mean total above ground biomass ($± SE$) ($\text{g}$) for *R. mangle* seedlings grown in 15 ppt saltwater was $9.2 ± 0.4 \text{ g}$ with 0 fruits, $11.2 ± 0.4 \text{ g}$ with 25 fruits, and $9.1 ± 0.5 \text{ g}$ with 50 fruits (Figure 16a). The mean total biomass ($± SE$) ($\text{g}$) for *R. mangle* seedlings grown in 30 ppt saltwater was $8.6 ± 0.71 \text{ g}$ with 0 fruits, $9.2 ± 1.00 \text{ g}$ with 25 fruits, and $9.2 ± 0.78 \text{ g}$ with 50 fruits (Figure 16a). There was not a significant difference ($F = 1.26, p = 0.29$) in the biomass of *R. mangle* in the two salinities or three fruit densities (Table 7).

*Avicennia germinans* seedlings grown in 15 ppt saltwater had a mean total biomass ($± SE$) ($\text{g}$) of $1.63 ± 0.13 \text{ g}$ with 0 fruits, $2.13 ± 0.14 \text{ g}$ with 25 fruits and $2.38 ± 0.23 \text{ g}$ with 50 fruits (Figure 16b). *Avicennia germinans* seedlings grown in 30 ppt saltwater had a mean total biomass ($± SE$) ($\text{g}$) of $2.63 ± 0.31 \text{ g}$ with 0 fruits, $3.66 ± 0.41 \text{ g}$ with 25 fruits and $2.14 ± 0.21 \text{ g}$ with 50 fruits (Figure 16b). There was a significant interaction ($F = 6.03, p < 0.01$) between salinity and fruit density for the biomass of *A. germinans* (Table 8).
The mean increase in number of leaves (± SE) of *R. mangle* seedlings during the four month period was 8.15 ± 1.24 leaves with 0 fruits, 11.10 ± 1.14 leaves with 25 fruits, and 5.35 ± 1.37 leaves with 50 fruits for seedlings grown in 15 ppt saltwater (Figure 17a). *Rhizophora mangle* seedlings grown in 30 ppt saltwater had a mean increase in number of leaves (± SE) of 5.05 ± 2.36 leaves with 0 fruits, 7.30 ± 1.53 leaves with 25 fruits, and 6.60 ± 1.46 leaves with 50 fruits (Figure 17a). There was not a significant difference (F = 1.51, p = 0.22) in the increase in number of leaves of *R. mangle* in the two salinities or three fruit densities (Table 9).

*Avicennia germinans* seedlings grown in 15 ppt saltwater had a mean increase in number of leaves (± SE) of 1.95 ± 1.99 leaves with 0 fruits, 5.05 ± 2.45 leaves with 25 fruits, and 7.60 ± 2.35 leaves with 50 fruits (Figure 17b). The mean increase in number of leaves (± SE) for *A. germinans* seedlings grown in 30 ppt saltwater was 4.10 ± 3.46 leaves with 0 fruits, 7.35 ± 2.89 leaves with 25 fruits, and 2.15 ± 0.78 leaves with 50 fruits (Figure 17b). There was a not significant interaction (F = 1.61, p = 0.20) between salinity and fruit density on the increase in number of leaves of *A. germinans* (Table 10), most likely due to high variance between treatments.

**Effect of *Schinus terebinthifolius* on biodiversity**

The total number of plant species in sites with adult Brazilian pepper was 24 species, compared to only 8 species at sites without an adult Brazilian pepper tree (Table 11). Sites without Brazilian pepper were dominated by native mangroves and halophytic plants, whereas the sites with Brazilian pepper had a more diverse flora with mangroves, halophytic plants and numerous upland hammock species (Table 11). Sites with Brazilian pepper had a range of mean species richness per site (± SE) of 7.00 ± 1.00 to
9.66 ± 1.20 species per site. Sites without Brazilian pepper had a range of mean species richness per site (± SE) of 2.67 ± 0.33 to 4.67 ± 0.33 species per site. The overall mean number of plant species per site (± SE) was significantly higher (t-test, p < 0.001) at sites with Brazilian pepper (7.95 ± 0.30 species), compared to sites without Brazilian pepper (3.76 ± 0.21 species) (Table 12, Figure 18). The results of the ANOVA found a significant difference in species richness (F = 11.39, p< 0.01).

The mean number of bare or empty patches (± SE) was 5.33 ± 0.83 at sites at sites with Brazilian pepper and 0.57 ± 0.20 at sites without Brazilian pepper. The number of empty or bare patches was significantly greater (t-test, p < 0.001) at sites with Brazilian pepper compared to sites without Brazilian pepper.

The mean relative abundance (%) (± SE) of Brazilian pepper was 8.82 ± 2.13 % at sites where it was present (Figure 19). Mean relative abundance (± SE) (%) of *Laguncularia racemosa* (white mangrove) was 7.57 ± 2.38 % and 5.41 ± 3.40 % at sites with Brazilian pepper and without Brazilian pepper, respectively (Figure 19); it was significantly different among sites (F = 2.70, p = 0.01). *Rhizophora mangle* (red mangrove) was in low abundance at both types of sites, with a mean relative abundance (%) (± SE) of 1.50 ± 0.51 % at sites with Brazilian pepper and 0.61 ± 0.36 % at sites without Brazilian pepper (Figure 19). This difference was significant between habitat types (F = 9.60, p< 0.01). *Avicennia germinans*, the black mangrove, was the most abundant mangrove species, with a mean relative abundance (± SE) (%) of 10.99 ± 2.51 % at sites with Brazilian pepper and 21.44 ± 2.99 % at sites without Brazilian pepper (Figure 19). This was significantly different among sites (F = 6.91, p< 0.01).

Other dominant halophytes were *Batis maritima* (saltwort), with a mean relative
abundance (%) (± SE) of 2.39 ± 1.09% and 58.34 ± 3.76% for sites with and without Brazilian pepper, respectively, and Salicornia perennis (perennial glasswort), with a mean relative abundance (%) (± SE) of 0.83 ± 0.40% and 6.05 ± 1.75% for sites with and without Brazilian pepper, respectively (Figure 19). The mean relative abundance was significantly different among sites for B. maritima (F = 35.65, p< 0.01) and S. perennis (F = 3.32, p< 0.01).

Soil moisture was significantly higher (t-test, p< 0.01) at sites without Brazilian pepper than at sites with Brazilian pepper, with a mean soil moisture (%) (± SE) of 88.03 ± 2.59% at sites without Brazilian pepper compared to 72.36 ± 4.37% at sites with Brazilian pepper (Table 12). Soil salinity was not significantly different (t-test, p = 0.41) at sites with and without Brazilian pepper, with a mean soil salinity of 1.30 ± 0.01 for sites with and without Brazilian pepper (Table 12).

A scatterplot matrix comparing the relationship between species richness, number of Brazilian pepper individuals, soil salinity, soil moisture and number of empty patches is shown in Figure 20. A positive relationship is suggested between species richness and number of empty patches, species richness and number of S. terebinthifolius, and number of Brazilian pepper and number of empty patches. A negative relationship is suggested for species richness and soil moisture, number of empty patches and soil moisture, and number of Brazilian pepper and soil moisture. Correlation analysis (Pearson’s correlation) found significant correlations between number of Brazilian pepper plants with species richness (p = 0.001) and number of empty patches (p = 0.006) (Table 7). There was also a significant correlation between the number of empty patches with soil moisture (p = 0.01) and species richness (p< 0.001) (Table 7). The affect of these
variables on species richness were further investigated by analyzing contingency tables with the Chi-Square statistic. Results found a significant effect of number of empty patches (p< 0.01) on species richness at transect sites.

**Recruitment of *Schinus terebinthifolius* and three native mangroves in Canaveral National Seashore**

Monthly changes in abundance of *Schinus terebinthifolius* was highest in the zones 10 m and 20 m above the intertidal region for sites that were chemically treated during the seventeen-month monitoring period (type BP2) (Figure 21a). An initial reduction was seen in *S. terebinthifolius* from August 2004 to November 2004 due to high mortality following hurricanes. The mean change in abundance (change in # plants m$^{-2}$) of *S. terebinthifolius* from August 2004 (before hurricanes) to October 2004 (after third hurricane) was negative in all zones and sites and ranged from -0.13 ± 0.13 plants m$^{-2}$ in the 0 m zone at site type BP2 to -22.93 ± 17.50 plants m$^{-2}$ in the 20 m zone at site type BP2 (Figure 22).

Monthly changes in abundance of *S. terebinthifolius* increased at BP2 sites in the 10 m and 20 m above the intertidal region after chemical treatment in February 2005. Although there was some fluctuation in numbers of *S. terebinthifolius* at sites without treatment (BP1), monthly changes in abundance was less at BP1 than at BP2 sites (Figure 21a). Monthly changes in abundance of *S. terebinthifolius* were low in the intertidal region at both types of sites. The mean change in abundance post-hurricanes was positive for the 0 m zone at BP1 sites and negative at BP2 sites (Figure 23a). In the 10 m and 20 m zone, mean change in abundance post-hurricanes was positive for both types of sites, with a greater increase seen at the sites that were chemically treated (Figure 23b,
23c). The mean change in abundance post-hurricanes was significantly different (F = 4.32, p = 0.02) between types of sites, but no interaction was found between zone and site type (F = 1.8, p = 0.16) (Table 15).

Monthly changes in abundance of *R. mangle* were highest in the intertidal region of all site types (Figure 21b). Monthly changes in abundance were less than 1 plant m$^{-2}$ or did not occur in the zones 10 m and 20 m at all site types. The mean change in abundance of *R. mangle* during hurricanes (August 2004 to October 2004) in the 0 m zone was positive at BP1 and BP2 sites, but was negative at sites without *S. terebinthifolius* (Figure 22a). The mean change in abundance post-hurricanes was negative in all zones and site types (Figure 23). The mean change in abundance was significantly different (F = 3.53, p = 0.04) among zones, however, no interaction between zones and site types was found (F=0.71, p = 0.58) (Table 16).

The monthly changes in abundance of *Avicennia germinans* had the greatest amount of monthly fluctuation in the 20 m zone at BP1 sites (Figure 21c). Monthly changes in abundance were highest in the fall months of 2004 following the hurricanes, with survival decreasing through the following months for most zones and types of sites (Figure 21c). *Avicennia germinans* had positive mean change in abundance during the hurricane months for all zones and site types except the 0 m zone at BP2 sites (Figure 22). These sites had a large amount of debris, which covered many seedlings, potentially causing higher rates of mortality for *Avicennia germinans* at these sites. The mean change in abundance post-hurricanes was negative in the 0 m zone at all site types (Figure 23a) and in zones 10 m (Figure 23b) and 20 m (Figure 23c) at site types BP1 and BP2. Sites without *S. terebinthifolius* had positive changes in abundance for *A.*
germinans in the zones 10 m and 20 m (Figures 23b, c). The mean change in abundance of A. germinans post-hurricanes was not significantly different among types of sites (F = 1.98, p = 0.16) or zones (F = 0.23, p = 0.79) (Table 17).

Monthly changes in abundance of Laguncularia racemosa were highest in zones 10 m and 20 m sites without S. terebinthifolius and at BP1 sites (Figure 21d). Low monthly changes in abundance were observed in the 0 m zone at all sites and in all zones of BP1 sites. The mean change in abundance during hurricane months was positive in 0 m zones at BP2 sites and negative for other site types in the 0 m zone (Figure 22a). Laguncularia racemosa had positive mean change in abundance during hurricane months for the 10 m and 20 m zones at all three types of sites (Figures 22b, c). The mean change in abundance post-hurricanes was positive in the 0 m zone at sites without S. terebinthifolius and at BP1 sites, but was negative in the zones 10 m and 20 m at sites without S. terebinthifolius (Figure 23). The mean change in abundance was not significantly different among site types (F = 0.61, p = 0.55) or zones (F = 0.38, p = 0.68) (Table 18).

Discussion

Schinus terebinthifolius has invaded many habitats in central and south Florida and has the ability to change natural community structure and functioning of the invaded systems (Williams et al. 2005). Schinus terebinthifolius is a successful colonizer in disturbed habitats due its high growth rate and tolerance for a wide range of abiotic conditions (Jones and Doren 1997). It is one of the most widespread exotic plant species in Florida and represents a serious biological threat to native Florida systems (Ferriter 1997). This study documented the successful invasion and establishment of S.
*terebinthifolius* in a disturbed mangrove habitat on the east coast of Florida, which may be facilitated by the production of allelopathic chemicals by *S. terebinthifolius*.

**Allelopathic properties of Schinus terebinthifolius**

Past studies have documented allelopathic properties of *S. terebinthifolius* negatively impacting the growth of native flora (Nilsen and Muller 1980, Morgan and Overholt 2005). In this study, *Avicennia germinans* had a reduction in growth rate and biomass when exposed to the highest density of *S. terebinthifolius* fruits growing in 30 ppt saltwater. Growth in higher salinities is more physiologically stressful to the plant (Ewe and Sternberg 2005) and may make the plant more susceptible to inhibitory compounds in high concentrations. *Rhizophora mangle* did not show a depression in growth or biomass when exposed to *S. terebinthifolius* fruits. The fruits used in this trial were intact when added to pots containing mangrove seedlings and the concentration of chemicals may not have been high enough to cause a depression in growth of *Rhizophora mangle*. Additional studies with crushed seeds would be useful to further test the effect of allelopathic chemicals on *Rhizophora mangle*.

The finding that growth of *A. germinans* was depressed by *S. terebinthifolius* fruits (Figure 15b) is ecologically significant because both *A. germinans* and *S. terebinthifolius* are usually found in the landward portion of mangrove habitat where 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 and *A. germinans* may be excluded due to the chemical compounds produced by *S. terebinthifolius*. *Rhizophora mangle* tends to grow in the saturated soil of the intertidal region (Odum and McIvor 1990), where it
would have less contact with *S. terebinthifolius*. Regular tidal flushing in the intertidal region may also prevent the build-up of toxic concentrations of allelopathic chemicals produced by *S. terebinthifolius*, decreasing the effect of the inhibitory chemicals. Allelopathic chemicals may be another mechanism for the successful invasion of *S. terebinthifolius* into central and southern Florida habitats; however, more research is needed to fully understand the allelopathic capabilities of *S. terebinthifolius* (see Morgan and Overholt 2005).

**Impact of Schinus terebinthifolius on mangrove ecosystems**

The presence of *S. terebinthifolius* in Florida ecosystems has led to a decrease in biodiversity in many invaded areas (Herwitz et al. 1996, Jones and Doren 1997, Ferriter 1997). However, my study found higher species richness in areas where *S. terebinthifolius* was present, compared to areas without this exotic. Species richness was correlated with the number of *S. terebinthifolius* at each site; increased species richness was related to higher numbers of *S. terebinthifolius*. Researchers have argued that species rich communities were more resistant to invasion and indicated greater ecosystem health; however, many diverse systems tend to have greater numbers of exotics and may be more susceptible to invasion because more diverse habitat can provide more opportunities for the exotic species (Myers and Brazely 2003).

High species richness in mangrove systems may suggest a degradation of habitat rather than a healthier system. Mangrove ecosystems are typically species poor in terms of flora, due to the specialized niche in which mangroves and a few other halophytic species inhabit (Lugo 1998). Compared to the diverse floral structure of most tropical forests, mangrove systems tend to have low species richness and do not have a true
understory (Alongi 2002). The number of native floral species endemic to mangrove ecosystems is expected to be low in mangrove habitats and is one reason why exotics are usually not a threat to undisturbed mangrove systems (Lugo 1998). In the mangrove habitat of Canaveral National Seashore, undisturbed mangrove sites had a mean species richness of less than four species per site. These species were limited to the three native species of mangroves and halophytic flora adapted to growing in saline, saturated soils, including *Batis maritme, Borrichia frutescens, Salicornia perrenis, Salicornia bigelorii,* and *Spartina alternifolia* (Table 11). These areas had a low number of empty patches, which prevented the invasion of *S. terebinthifolius* or other plant species. This is supported by the low monthly and mean changes in abundance of mangroves observed at these sites; the amount of available habitat for recruitment was less in undisturbed mangrove sites than in disturbed sites. Mangrove sites where *S. terebinthifolius* was present had mean species richness greater than seven species per site. These species included mangroves and halophytic plants, as well as upland hammock species, including *Ilex vomitoria, Baccharis halmifolia, Forestieria segregate* and *Myrica cerifa* (Table 5). In addition, sites with *S. terebinthifolius* had a greater number of weedy species, which are often the first plant species to colonize empty patches within disturbed sites (Myers and Brazely 2003). The increased occurrence of weedy species in addition to the terrestrial species supports the conclusion that sites with *S. terebinthifolius* are disturbed mangrove habitats.

The number of *S. terebinthifolius* was positively correlated with the number of empty patches at sites in Canaveral National Seashore (Table 13), supporting the hypothesis that *S. terebinthifolius* is a successful invader into disturbed mangrove habitat.
Past studies have shown disturbed habitats to be more vulnerable to invasion by *S. terebinthifolius* because of its high growth rate and prolific seed production, which allows this exotic to out-compete native plants once established in the disturbed area (Jones and Doren 1997). Disturbances increase the invasibility of a site by increasing the availability of suitable sites for exotic species (Hobbs and Huenneke 1992). Disturbed mangrove habitat is more vulnerable to invasion by exotic and native terrestrial flora because the abiotic conditions which limit the available niches are often altered, allowing for a more diverse flora to inhabit the area and increasing competition from other flora. Disturbances can change the plant structure of a community by shifting environmental characteristics which increases the potential of exotics invading an area (Hobbs and Huenneke 1992). Alterations to the physical environment in mangrove habitat of Canaveral National Seashore are increasing the competitive interactions between mangroves and other flora, resulting in decreased abundances of mangroves at disturbed sites and an increase in overall floral diversity.

Although mangroves are facultative halophytes, they usually dominate only in saline, saturated habitats due to increased competition from other flora when growing in lower saline or drier soils (Odum and McIvor 1990). Mangroves also tend to be shade intolerant due to the high stress of living within the marine environment, which limits their ability to compete in areas with a dense canopy structure (Snedaker and Lahmann 1988). In sites without *S. terebinthifolius*, the abundance of mangroves species and halophytic plants was significantly greater compared to sites with *S. terebinthifolius*. This was a result of the increased species richness of sites with *S. terebinthifolius*, which decreased the available niches for mangroves and increased the competitive interactions
between mangroves and other plants species. In the disturbed mangrove habitat, mangroves only dominate in the intertidal region, where they have the competitive advantage over other plant species.

Monthly changes of abundance at sites chemically treated for *S. terebinthifolius* was greater following treatment compared to sites where *S. terebinthifolius* was not treated. Chemical treatment kills mature *S. terebinthifolius*, resulting in increased canopy gaps and empty patches following treatment. This was followed by increased germination of seeds and growth of seedlings in the understory (Figure 21a), as observed by Parkinson et al. (1999) when gaps in the mangrove canopy led to an increase in *S. terebinthifolius* seedlings. Chemical treatment led to an overall increase in the abundance of *S. terebinthifolius* since the mean change in abundance was positive for *S. terebinthifolius* at sites which were chemically treated in the zones 10 m and 20 m above the intertidal region (Figure 23). Negative changes in abundance was found for *L. racemosa*, *R. mangle* and *A. germinans* at sites that were chemically treated for *S. terebinthifolius*, suggesting that the increase in canopy gaps did not facilitate the recruitment of native mangroves after the removal of mature *S. terebinthifolius* trees (Figure 23).

In Canaveral National Seashore, alterations to mangrove habitat increase the elevation of the substrate, which decreases the frequency of tidal inundation. This is supported by the lower mean soil moisture at disturbed sites with *S. terebinthifolius* compared to undisturbed areas without *S. terebinthifolius* (Table 12). Disturbed sites also had a greater number of empty patches, providing open space for recruitment of *S. terebinthifolius* and other non-halophytic plants. Soil moisture was correlated with the
number of empty patches; areas that had higher numbers of empty patches had lower soil moisture (Table 13). Empty patches would have higher evaporation rates of water from the soil than those shaded by plants; therefore the empty patches would be more favorable to terrestrial species rather than mangrove or saltmarsh plants, which dominate in saturated soils.

In the fall of 2004, Canaveral National Seashore was affected by three hurricanes, Hurricane Charley (August 2004), Hurricane Francis (September 2004) and Hurricane Jeanne (September 2004). Seedlings of *S. terebinthifolius* were lost because of smothering by debris; uprooting killed many medium and large Brazilian pepper trees. These results suggest *S. terebinthifolius* is not well adapted to withstanding hurricanes when growing in mangrove habitat. However, an overall increase in the number of mangroves was found at all sites in all three zones (Figures 22a, b, c). Mangrove ecosystems experience large-scale disturbances like hurricanes regularly and are adapted for withstanding high winds and prolonged flooding experienced during hurricanes (Alongi 2002). The timing of the three hurricanes corresponded to the dispersal season of propagules of the three mangrove species. This combined with an increase in the number of available patches due to damage and mortality of other tree species led to increased mangrove recruitment following the hurricanes. This is supported by the higher monthly recruitment observed during fall 2004 compared to fall 2005 for *L. racemosa* and *A. germinans* (Figures 21c, d).

**Conclusions**

This study documents that the invasion of *Schinus terebinthifolius* in mangrove systems is facilitated by disturbances altering the abiotic conditions of mangrove habitat.
In this case, the presence of *S. terebinthifolius* is an indicator of a larger problem facing mangrove ecosystems in Florida. Most management strategies for controlling the spread of *S. terebinthifolius* and other exotic species focus only on the exotic and not on the entire ecosystem (Hobbs and Humphries 1995). By considering the invaded ecosystem and related causes that increase the invasion potential of an ecosystem, more successful management practices can be implemented (Hobbs and Humphries 1995). The results from this study show that disturbances changing the environmental characteristics increase the invasibility of mangrove systems and management of the exotic species is only a small part in restoring systems to healthier states. Chemical treatment of adult *S. terebinthifolius* was not effective in decreasing the total number of *S. terebinthifolius* and led to an increased recruitment of this exotic at treated sites. Removal of adult *S. terebinthifolius* did not change the physical characteristics which allowed it to invade or prevent the reoccurrence of this exotic in mangrove systems. In addition, killing the mature trees may not reduce the allelopathic impact on neighboring vegetation since stem, leaf and seed matter remain to decompose. If allelopathic chemicals are present in the soil after treatment, recovery of native vegetation may be limited and canopy gaps may facilitate the recruitment of additional *S. terebinthifolius*. To prevent future increases in the abundance of this exotic, equal attention must be given to restoring and maintaining the integrity of mangrove ecosystems and to the development of management strategies for *S. terebinthifolius*. 
APPENDIX A: TABLES
Table 1. The mean number of days (± SE) fruits floated in 0 ppt, 18 ppt, and 36 ppt saltwater in eight independent trials.

<table>
<thead>
<tr>
<th>Trial</th>
<th>0 ppt</th>
<th>18 ppt</th>
<th>36 ppt</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.44 (0.19)</td>
<td>4.58 (0.29)</td>
<td>5.46 (0.28)</td>
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<tr>
<td>2</td>
<td>3.42 (0.09)</td>
<td>3.68 (0.13)</td>
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<td>3</td>
<td>5.98 (0.35)</td>
<td>6.44 (0.41)</td>
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<tr>
<td>4</td>
<td>3.56 (0.16)</td>
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<td>5.38 (0.27)</td>
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<td>4.24 (0.23)</td>
<td>6.08 (0.25)</td>
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<td>7</td>
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<td>5.24 (0.26)</td>
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</tr>
<tr>
<td>8</td>
<td>6.92 (0.39)</td>
<td>12.14 (0.62)</td>
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</table>

Table 2. The results of survival analysis comparing the length of times seeds remain buoyant when floating in 0 ppt, 18 ppt and 36 ppt saltwater.

<table>
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<tr>
<th>Trial</th>
<th>Overall</th>
<th>0 ppt- 18 ppt</th>
<th>0 ppt- 36 ppt</th>
<th>18 ppt- 36 ppt</th>
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</thead>
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<td>Wilcoxon Statistic</td>
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<td>Wilcoxon Statistic</td>
<td>p</td>
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<tr>
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<td>&lt;0.01</td>
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</tr>
<tr>
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<td>0.37</td>
<td>1.3</td>
<td>0.25</td>
</tr>
<tr>
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<td>&lt;0.01</td>
<td>8.3</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>5</td>
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<td>&lt;0.01</td>
<td>5.6</td>
<td>0.02</td>
</tr>
<tr>
<td>6</td>
<td>40.0</td>
<td>&lt;0.01</td>
<td>24.4</td>
<td>&lt;0.01</td>
</tr>
<tr>
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<td>0.23</td>
<td>0.4</td>
<td>0.54</td>
</tr>
<tr>
<td>8</td>
<td>32.9</td>
<td>&lt;0.01</td>
<td>27.7</td>
<td>&lt;0.01</td>
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</table>
Table 3. The mean wind speed (m/s) (± SE), water salinity (ppt), mean dispersal distance (m) (± SE) and mean dispersal rate (m/s) (± SE) of *Schinus terebinthifolius* fruits and fruit clusters during dispersal trials.

<table>
<thead>
<tr>
<th></th>
<th>Mean Wind Speed (m/s) (± SE)</th>
<th>Water Salinity (ppt)</th>
<th>Mean Dispersal Distance (m) (± SE)</th>
<th>Mean Dispersal Rate (m/s) (± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Trial 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruits</td>
<td>1.1 (± 0.30)</td>
<td>25</td>
<td>12.8 (± 0.90)</td>
<td>0.02 (± 0.01)</td>
</tr>
<tr>
<td>Clusters</td>
<td>1.1 (± 0.30)</td>
<td>25</td>
<td>12.3 (± 2.00)</td>
<td>0.02 (± 0.01)</td>
</tr>
<tr>
<td><strong>Trial 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruits</td>
<td>1.2 (± 0.20)</td>
<td>30</td>
<td>40.4 (± 0.50)</td>
<td>0.06 (± 0.01)</td>
</tr>
<tr>
<td>Clusters</td>
<td>1.2 (± 0.20)</td>
<td>30</td>
<td>21.7 (± 2.60)</td>
<td>0.04 (± 0.01)</td>
</tr>
<tr>
<td><strong>Trial 3</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruits</td>
<td>0.8 (± 0.10)</td>
<td>26</td>
<td>19.7 (± 0.70)</td>
<td>0.03 (± 0.01)</td>
</tr>
<tr>
<td>Clusters</td>
<td>0.8 (± 0.10)</td>
<td>26</td>
<td>22.3 (± 1.30)</td>
<td>0.04 (± 0.01)</td>
</tr>
</tbody>
</table>

Table 4. The mean wind speed (m/s) (± SE), mean wake height (cm) (± SE) and mean dispersal distance (cm) (± SE) for *Schinus terebinthifolius* fruits when exposed to boat wakes and wind waves.

<table>
<thead>
<tr>
<th></th>
<th>Mean Wind Speed (m/s) (± SE)</th>
<th>Mean Wake Height (cm) (± SE)</th>
<th>Mean Dispersal Distance (cm) (± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Trial 1</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>4.2 (± 0.17)</td>
<td>0</td>
<td>0.7 (± 0.12)</td>
</tr>
<tr>
<td>Boat</td>
<td>2.5 (± 0.24)</td>
<td>23.0 (± 0.52)</td>
<td>23.1 (± 0.54)</td>
</tr>
<tr>
<td><strong>Trial 2</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>0.6 (± 0.04)</td>
<td>0</td>
<td>0.0 (± 0.00)</td>
</tr>
<tr>
<td>Boat</td>
<td>0.7 (± 0.08)</td>
<td>20.2 (± 0.36)</td>
<td>49.1 (±1.06)</td>
</tr>
<tr>
<td><strong>Trial 3</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>2.3 (± 0.20)</td>
<td>0</td>
<td>0.0 (± 0.00)</td>
</tr>
<tr>
<td>Boat</td>
<td>2.6 (± 0.20)</td>
<td>22.8 (± 0.81)</td>
<td>18.4 (± 0.61)</td>
</tr>
</tbody>
</table>
Table 5. Results of two-factor ANOVA (salinity X seed density) comparing growth rate among treatments of *Rhizophora mangle*.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>0.000</td>
<td>1</td>
<td>0.000</td>
<td>16.236</td>
<td>0.056</td>
</tr>
<tr>
<td>Seed Density</td>
<td>0.000</td>
<td>2</td>
<td>0.000</td>
<td>5.808</td>
<td>0.147</td>
</tr>
<tr>
<td>Salinity*Seed Density</td>
<td>3.455E-05</td>
<td>2</td>
<td>1.728E-05</td>
<td>0.048</td>
<td>0.954</td>
</tr>
<tr>
<td>Error</td>
<td>0.041</td>
<td>114</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 6. Results of two-factor ANOVA (salinity X seed density) comparing growth rate among treatments of *Avicennia germinans*.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>0.003</td>
<td>1</td>
<td>0.003</td>
<td>0.659</td>
<td>0.502</td>
</tr>
<tr>
<td>Seed Density</td>
<td>0.002</td>
<td>2</td>
<td>0.001</td>
<td>0.182</td>
<td>0.846</td>
</tr>
<tr>
<td>Salinity * Seed Density</td>
<td>0.009</td>
<td>2</td>
<td>0.004</td>
<td>4.849</td>
<td>0.010</td>
</tr>
<tr>
<td>Error</td>
<td>0.101</td>
<td>114</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 7. Results of two-factor ANOVA (salinity X seed density) comparing biomass among treatments of *Rhizophora mangle*.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>19.660</td>
<td>1</td>
<td>19.660</td>
<td>1.646</td>
<td>0.328</td>
</tr>
<tr>
<td>Seed Density</td>
<td>36.855</td>
<td>2</td>
<td>18.427</td>
<td>1.543</td>
<td>0.393</td>
</tr>
<tr>
<td>Salinity * Seed Density</td>
<td>23.890</td>
<td>2</td>
<td>11.945</td>
<td>1.269</td>
<td>0.285</td>
</tr>
<tr>
<td>Error</td>
<td>1073.426</td>
<td>114</td>
<td>9.416</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 8. Results of two-factor ANOVA (salinity X seed density) comparing biomass among treatments of *Avicennia germinans*.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>17.385</td>
<td>1</td>
<td>17.385</td>
<td>2.104</td>
<td>0.284</td>
</tr>
<tr>
<td>Seed Density</td>
<td>13.385</td>
<td>2</td>
<td>6.693</td>
<td>0.810</td>
<td>0.553</td>
</tr>
<tr>
<td>Salinity * Seed Density</td>
<td>16.528</td>
<td>2</td>
<td>8.264</td>
<td>6.039</td>
<td>0.003</td>
</tr>
<tr>
<td>Error</td>
<td>156.008</td>
<td>114</td>
<td>1.368</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 9. Results of two-factor ANOVA (salinity X seed density) comparing the increase in number of leaves among treatments of *Rhizophora mangle*.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>106.408</td>
<td>1</td>
<td>106.408</td>
<td>1.421</td>
<td>0.355</td>
</tr>
<tr>
<td>Seed Density</td>
<td>234.017</td>
<td>2</td>
<td>117.008</td>
<td>1.563</td>
<td>0.390</td>
</tr>
<tr>
<td>Salinity * Seed Density</td>
<td>149.717</td>
<td>2</td>
<td>74.858</td>
<td>1.512</td>
<td>0.225</td>
</tr>
<tr>
<td>Error</td>
<td>5644.850</td>
<td>114</td>
<td>49.516</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 10. Results of two-factor ANOVA (salinity X seed density) comparing the increase in number of leaves among treatments of *Avicennia germinans*.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>3.333</td>
<td>1</td>
<td>3.333</td>
<td>0.017</td>
<td>0.908</td>
</tr>
<tr>
<td>Seed Density</td>
<td>203.450</td>
<td>2</td>
<td>101.725</td>
<td>0.518</td>
<td>0.659</td>
</tr>
<tr>
<td>Salinity * Seed Density</td>
<td>392.817</td>
<td>2</td>
<td>196.408</td>
<td>1.613</td>
<td>0.204</td>
</tr>
<tr>
<td>Error</td>
<td>13881.600</td>
<td>114</td>
<td>121.768</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 11. Flora identified at sites with Brazilian pepper (1) and sites without Brazilian pepper (2).

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
<th>1</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual Glasswort</td>
<td><em>Salicornia bigelovii</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Black Mangrove</td>
<td><em>Avicennia germinans</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Buttonwood</td>
<td><em>Conocarpus erectus</em></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Christmasberry</td>
<td><em>Lycium carolinianum</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Cordgrass</td>
<td><em>Spartina alternifolia</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Cowpea</td>
<td><em>Vigna luteola</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Florida Privet</td>
<td><em>Forestiera segregate</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Christmasberry</td>
<td><em>Lycium carolinianum</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Cordgrass</td>
<td><em>Spartina alternifolia</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Cowpea</td>
<td><em>Vigna luteola</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Florida Privet</td>
<td><em>Forestiera segregate</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Perennial Glasswort</td>
<td><em>Salicornia perennis</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Marsh Elder</td>
<td><em>Iva frutescens</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Prickly-pear Cactus</td>
<td><em>Opuntia humifusa</em></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Red Mangrove</td>
<td><em>Rhizophora mangle</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Sabal Palm</td>
<td><em>Sabal palmetto</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Saltgrass</td>
<td><em>Distichilis spicata</em></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Saltmarsh Fleabane</td>
<td><em>Pluchea odorata</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Saltwort</td>
<td><em>Batis maritima</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Saw Palmetto</td>
<td><em>Serenoa repens</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Sea Grape</td>
<td><em>Coccoloba uvifera</em></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Sea Myrtle</td>
<td><em>Baccharis halimifolia</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Sea Oxeye</td>
<td><em>Borrichia frutescens</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Sea Purslane</td>
<td><em>Sesuvium portulacastum</em></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Snowberry</td>
<td><em>Chiococca alba</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Southern Cedar</td>
<td><em>Juniperus virginica</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Wax Myrtle</td>
<td><em>Myrica cerifia</em></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>White Mangrove</td>
<td><em>Laguncularia racemosa</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Yaupon Holly</td>
<td><em>Ilex vomitoria</em></td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>

Total Number of Plant Species 24 8
Table 12. Mean species richness (± SE), mean soil salinity (± SE), and mean soil moisture (± SE) of sites with and without Brazilian pepper, *Schinus terebinthifolius*. Means of each variable were compared between sites with and without Brazilian pepper with a t-test.

<table>
<thead>
<tr>
<th></th>
<th>Mean Species Richness (± SE)</th>
<th>Mean Soil Salinity (ppt) (± SE)</th>
<th>Mean Soil Moisture (%) (± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sites w/ Brazilian Pepper</td>
<td>7.95 (± 0.30)</td>
<td>1.30 (± 0.01)</td>
<td>72.36 (± 4.37)</td>
</tr>
<tr>
<td>Sites w/o Brazilian pepper</td>
<td>3.76 (± 0.20)</td>
<td>1.30 (± 0.01)</td>
<td>88.03 (± 2.59)</td>
</tr>
<tr>
<td>t-test</td>
<td>t = 13.7</td>
<td>t = 0.59</td>
<td>t = -3.08</td>
</tr>
<tr>
<td></td>
<td>p&lt; 0.01</td>
<td>p = 0.27</td>
<td>p&lt; 0.01</td>
</tr>
</tbody>
</table>
Table 13. The Pearson correlation statistic comparing relationships between number of Brazilian pepper, soil salinity (ppt), soil moisture (%), species richness and number of empty patches at transects from study sites (n = 14).

<table>
<thead>
<tr>
<th></th>
<th># of Brazilian pepper</th>
<th>Soil Salinity (ppt)</th>
<th>Soil Moisture (%)</th>
<th>Species Richness</th>
<th># of Empty Patches</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sig. (2-tailed)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pearson Correlation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td># of Brazilian pepper</td>
<td></td>
<td>.048</td>
<td>-.202</td>
<td>.493(**)</td>
<td>.415(**)</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td>42</td>
<td>42</td>
<td>42</td>
<td>42</td>
</tr>
<tr>
<td>Soil Salinity (ppt)</td>
<td></td>
<td>.760</td>
<td>.201</td>
<td>.001</td>
<td>.006</td>
</tr>
<tr>
<td>Sig. (2-tailed)</td>
<td></td>
<td>42</td>
<td>42</td>
<td>42</td>
<td>42</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td>42</td>
<td>42</td>
<td>42</td>
<td>42</td>
</tr>
<tr>
<td>Species Richness</td>
<td></td>
<td>-.202</td>
<td>.230</td>
<td>-.006</td>
<td>.075</td>
</tr>
<tr>
<td>Sig. (2-tailed)</td>
<td></td>
<td>.760</td>
<td>.142</td>
<td>.971</td>
<td>.636</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td>42</td>
<td>42</td>
<td>42</td>
<td>42</td>
</tr>
<tr>
<td>Soil Moisture (%)</td>
<td></td>
<td>-.202</td>
<td>1</td>
<td>-.226</td>
<td>-.381(*)</td>
</tr>
<tr>
<td>Sig. (2-tailed)</td>
<td></td>
<td>.201</td>
<td>.142</td>
<td>.151</td>
<td>.013</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td>42</td>
<td>42</td>
<td>42</td>
<td>42</td>
</tr>
<tr>
<td>Species Richness</td>
<td></td>
<td>.493(**)</td>
<td>-.006</td>
<td>-.226</td>
<td>1</td>
</tr>
<tr>
<td>Sig. (2-tailed)</td>
<td></td>
<td>.001</td>
<td>.971</td>
<td>.151</td>
<td>.000</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td>42</td>
<td>42</td>
<td>42</td>
<td>42</td>
</tr>
<tr>
<td># of Empty Patches</td>
<td></td>
<td>.415(**)</td>
<td>-.381(*)</td>
<td>.634(**)</td>
<td>1</td>
</tr>
<tr>
<td>Sig. (2-tailed)</td>
<td></td>
<td>.006</td>
<td>.636</td>
<td>.013</td>
<td>.000</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td>42</td>
<td>42</td>
<td>42</td>
<td>42</td>
</tr>
</tbody>
</table>

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

Table 14. The Pearson Chi-Square statistic comparing the relationship between number of Brazilian pepper plants, soil salinity (ppt), soil moisture (%), and number of empty patches on species richness from study sites (n = 14).

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Pearson Chi-Square</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Brazilian pepper*Species Richness</td>
<td>69.77</td>
<td>0.07</td>
</tr>
<tr>
<td>Soil Salinity*Species Richness</td>
<td>234.21</td>
<td>0.32</td>
</tr>
<tr>
<td>Soil Moisture*Species Richness</td>
<td>338.00</td>
<td>0.29</td>
</tr>
<tr>
<td>Number of Empty Patches*Species Richness</td>
<td>153.75</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>
Table 15. The results of two-factor ANOVA comparing the post-hurricane change in abundance of \textit{S. terebinthifolius} among types of sites (No BP, BP1, and BP2) and zones (0 m, 10 m, and 20 m above the intertidal zone).

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type</td>
<td>17.159</td>
<td>2</td>
<td>8.580</td>
<td>4.320</td>
<td>.027</td>
</tr>
<tr>
<td>Zone</td>
<td>8.081</td>
<td>2</td>
<td>4.040</td>
<td>2.034</td>
<td>.156</td>
</tr>
<tr>
<td>Type * Zone</td>
<td>14.382</td>
<td>4</td>
<td>3.596</td>
<td>1.810</td>
<td>.165</td>
</tr>
<tr>
<td>Error</td>
<td>41.707</td>
<td>21</td>
<td>1.986</td>
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<td></td>
</tr>
</tbody>
</table>

Table 16. The results of two-factor ANOVA comparing the post-hurricane change in abundance of \textit{R. mangle} among types of sites (No BP, BP1, and BP2) and zones (0 m, 10 m, and 20 m above the intertidal zone).

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type</td>
<td>.636</td>
<td>2</td>
<td>.318</td>
<td>.757</td>
<td>.481</td>
</tr>
<tr>
<td>Zone</td>
<td>2.963</td>
<td>2</td>
<td>1.482</td>
<td>3.530</td>
<td>.048</td>
</tr>
<tr>
<td>Type * Zone</td>
<td>1.207</td>
<td>4</td>
<td>.302</td>
<td>.719</td>
<td>.588</td>
</tr>
<tr>
<td>Error</td>
<td>8.813</td>
<td>21</td>
<td>.420</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 17. The results of two-factor ANOVA comparing the post-hurricane change in abundance of \textit{A. germinans} among types of sites (No BP, BP1, and BP2) and zones (0 m, 10 m, and 20 m above the intertidal zone).

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type</td>
<td>20.524</td>
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<td>10.262</td>
<td>.617</td>
<td>.549</td>
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<tr>
<td>Zone</td>
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<td>2</td>
<td>6.385</td>
<td>.384</td>
<td>.686</td>
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<tr>
<td>Type * Zone</td>
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<td>4.823</td>
<td>.290</td>
<td>.881</td>
</tr>
<tr>
<td>Error</td>
<td>349.480</td>
<td>21</td>
<td>16.642</td>
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<td></td>
</tr>
</tbody>
</table>
Table 18. The results of two-factor ANOVA comparing the post-hurricane change in abundance of *L. racemosa* among types of sites (No BP, BP1, and BP2) and zones (0 m, 10 m, and 20 m above the intertidal zone).

<table>
<thead>
<tr>
<th>Source</th>
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<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
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<td>41.216</td>
<td>1.998</td>
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<tr>
<td>Zone</td>
<td>9.690</td>
<td>2</td>
<td>4.845</td>
<td>0.235</td>
<td>.793</td>
</tr>
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<td>Type * Zone</td>
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<td>15.649</td>
<td>0.758</td>
<td>.564</td>
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<tr>
<td>Error</td>
<td>433.307</td>
<td>21</td>
<td>20.634</td>
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<td></td>
</tr>
</tbody>
</table>
APPENDIX B: FIGURES
Figure 1. *Schinus terebinthifolius* (Brazilian pepper) growing along the shoreline of Mosquito Lagoon, New Smyrna Beach, Florida.

Figure 2. *Laguncularia racemosa* (white mangrove) and *Schinus terebinthifolius* (Brazilian pepper) growing together in Canaveral National Seashore.

Figure 3. *Schinus terebinthifolius* (Brazilian pepper) growing behind *Rhizophora mangle* (red mangrove) in Canaveral National Seashore.
Figure 4. The northern limits for *Rhizophora mangle* (R), *Laguncularia racemosa* (W) and *Avicennia germinans* (B) in Florida (Odum and McIvor 1990). *Avicennia germinans* extends into the panhandle on the west coast.

Figure 5. Prop roots (a), flowers (b) and propagules (c) of the red mangrove, *Rhizophora mangle*.
Figure 6. Cable roots (a), flowers (b), and propagules (c) of the black mangrove, *Avicennia germinans*.

Figure 7. The white mangrove, *Laguncularia racemosa*, (a) produces small white flowers (b) and propagules (c).

Figure 8. *Schinus terebinthifolius* (Brazilian pepper) produces flowers (a) in fall months and fruits (b) from November through February each year.
Figure 9. Canaveral National Seashore is located on the east coast of Florida, south of New Smyrna Beach (mangrove data from FWRI 2004, seagrass data from FWRI 2003).
Figure 10. The number of fruits floating each day in (a) 0 ppt saltwater, (b) 18 ppt saltwater, and (c) 36 ppt saltwater.
Figure 11. The mean number of fruits floating each day for all eight trials combined in 0 ppt, 18 ppt and 36 ppt salt water.
Figure 12. Mean dispersal rate (m s\(^{-1}\)) (+ SE) of *Schinus terebinthifolius* individual fruits and fruit clusters in Mosquito Lagoon. Two-way ANOVA found a significant interaction (F = 38.5, p< 0.01) between velocity of individual fruits and fruit clusters and trial date.

Figure 13. The mean dispersal distance (+ SE) (cm) of *Schinus terebinthifolius* fruits after exposure to wind waves and boat wakes. Two-way ANOVA found a significant interaction (F = 457.5, p< 0.01) between the distance fruits moved by boat wake and wind wakes and trial date.
Figure 14. The location of sites for (a) biodiversity transects (n = 7 sites with Brazilian pepper and n = 7 sites without Brazilian pepper) and (b) recruitment quadrats (n = 6 sites with Brazilian pepper and n = 4 sites without Brazilian pepper) in Canaveral National Seashore, Florida (mangrove data from FWRI 2004).
Figure 15. The mean growth rate (cm day\(^{-1}\)) (+ SE) of (a) *Rhizophora mangle* and (b) *Avicennia germinans* grown in 15 ppt and 30 ppt saltwater with three densities of *Schinus terebinthifolius* fruits: 0 (control), 25 or 50.

Figure 16. The mean above ground biomass (g) (+ SE) of (a) *Rhizophora mangle* and (b) *Avicennia germinans* grown in 15 ppt and 30 ppt saltwater with three densities of *Schinus terebinthifolius* fruits: 0 (control), 25 or 50.
Figure 17. The mean increase in number of leaves (+ SE) of (a) *Rhizophora mangle*, red mangrove, and (b) *Avicennia germinans*, black mangrove, grown in 15 ppt and 30 ppt saltwater with three densities of *Schinus terebinthifolius* fruits, 0 (control), 25 or 50.

Figure 18. Mean species richness (+ SE) at sites with Brazilian pepper and sites without Brazilian pepper. Species richness was significantly different at these two types of sites when compared using a 2-way ANOVA (F = 11.39, p < 0.01).
Figure 19. Mean relative abundance (%) (+ SE) of native mangroves and halophytic plants at sites with and without Brazilian pepper.
### Figure 20

Scatterplot matrix comparing the total number of *S. terebinthifolius* plants (Brazilian pepper), mean salinity (ppt), mean moisture (%), number of empty patches and species richness along transects at the fourteen sampling sites (n = 7 sites with Brazilian pepper, n = 7 sites without Brazilian pepper).
Figure 21. The monthly mean number m-2 (± SE) of (a) *Schinus terebinthifolius* (Brazilian pepper), (b) *Rhizophora mangle* (red mangrove), (c) *Avicennia germinans*
(black mangrove), and (d) *Laguncularia racemosa* (white mangrove) in the intertidal zone (0 m), 10 m and 20 m above intertidal zone at quadrat sites without *S. terebinthifolius* (No BP), sites with *S. terebinthifolius* that were not chemically treated (BP1) and sites with *S. terebinthifolius* that were treated (BP2). The y-axis of each chart is different in the above graphs.
Figure 22. The mean change in abundance (change in # plants m\(^{-2}\)) (± SE) during hurricanes in Fall 2004 (August 2004 - October 2004) of *Laguncularia racemosa* (white mangrove), *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), and *Schinus terebinthifolius* (Brazilian pepper) in the intertidal zone (a), 10 m (b) and 20 m (c) above the intertidal zone at sites without *S. terebinthifolius* (No BP), sites with *S. terebinthifolius* that were not chemically treated (BP1), and sites with *S. terebinthifolius* that were chemically treated (BP2).
Figure 23. The mean change in abundance (change in # plants m\(^{-2}\)) (± SE) post-hurricanes in Fall 2004 (November 2004 - January 2006) of *Laguncularia racemosa* (white mangrove), *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), and *Schinus terebinthifolius* (Brazilian pepper) in the intertidal zone (a), 10 m (b) and 20 m (c) above the intertidal zone at sites without *S. terebinthifolius* (No BP), sites with *S. terebinthifolius* that were not chemically treated (BP1), and sites with *S. terebinthifolius* that were chemically treated (BP2).
REFERENCES


