6-1-2001

Ecophysiology of Schinus terebinthifolius contrasted with native species in two South Florida ecosystems

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ECOPHYSIOLOGY OF *SCHINUS TEREBINTHIFOLIUS* CONTRASTED WITH NATIVE SPECIES IN TWO SOUTH FLORIDA ECOSYSTEMS

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2001

TABLE OF CONTENTS

Page

Chapter 1. Literature review on plant invasions……1

Chapter 2. Water utilization patterns of the invasive exotic *Schinus terebinthifolius* and native species in two coastal plant communities…….22

Chapter 3. Seasonal water-use by the invasive exotic, *Schinus terebinthifolius*, in native and upland disturbed communities…….……..56

Chapter 4. Seasonal gas exchange by the invasive exotic *Schinus terebinthifolius* versus coastal native plant species in Florida..……..……..80

Chapter 5. Seasonal gas exchange characteristics of *Schinus terebinthifolius* in a native and disturbed upland community……..…102

Chapter 6. Growth and gas exchange of Brazilian pepper (*Schinus terebinthifolius*) and native South Florida species in response to salinity treatments……...121

Chapter 7. Growth and gas exchange responses of flooded *Schinus terebinthifolius* and native South Florida species……...…….……155

Chapter 8. Ecophysiology of *Schinus terebinthifolius* in South Florida --concluding remarks……...……..171

Appendix I……...…….……...175

Literature cited……...…….…….176

Chapter 1

Literature review on plant invasions

INTRODUCTION

Since the earliest days of human history, we have altered our environment to suit our needs (diCastri 1989). This has included transporting plants and animals for our own purposes. The introductions of non-native plants and animals into new communities, however, have been restricted by human mobility and in part our ability to transport organisms on a large-scale. However in today's globalized economy, the scale of introductions has increased tremendously (Carlton and Geller 1993, Jenkins 1999, McNeely 1999). The speed and volume of organisms being transported around the world in the last few centuries has allowed for far greater numbers of successful introductions than the last several thousand years put together (Brown 1989, diCastri 1989); and introductions, either intentional or accidental, have influenced our daily lives tremendously.

EFFECTS OF INVASIVES ON NATIVE COMMUNITIES

Not all organisms introduced into a new environment will successfully colonize the new habitat and of those that do colonize, only a small fraction will become invasive (see Apppendix I) (Williamson 1996). As early as 1837, Darwin (1839) had already observed cardoon (*Cynara cardunculus*) and fennel (*Foeniculum vulgare*) from Europe growing unchecked in parts of South America. However the impact of non-native species

was not formally documented until Elton's (1958) "Ecology of invasions by plants and animals". Despite Elton's book, there was a general lapse of scientific interest in biological invasions until the 1980's when it was brought to public and scientific attention that invasive plants and animals were causing significant ecological (e.g. Schmitz et al. 1997) and economic damage (e.g. Bright 1998, Pimentel et al. 2000). Since then, the history and dynamics of biological invasions have been documented in books such as those by Mooney and Drake (1986), Macdonald et al. (1986), Groves and Burdon (1986), Drake and Mooney (1989), diCastri et al. (1990), Cronk and Fuller (1995), Pysek et al. (1995a), Brock et al. (1997), Simberloff et al. (1997), Luken and Thieret (1997) and Sandlund et al. (1999a).

Not all plant and animal introductions have negative impacts. Beneficial introductions such as livestock and agricultural crops sustain large human populations around the world; more than 90% of the world's agricultural harvest is from 20 plant and 6 animal species (Sandlund et al. 1999b). Additionally, introductions of non-native species also have increased biodiversity in many parts of the world. For example, Britain now has 49 mammalian species, almost double the original number of native species present (Jarvis 1979). Locally, London has 2100 species of flowering plants and ferns compared to the 1500 species native to Britain, while Berlin has 839 native species and 593 non-native species, much higher than the surrounding countryside (Kowarik 1990).

On the other hand, some species introductions have caused significant ecological and economic damage. The single biggest human-induced loss of biodiversity because of an invasive species was from the introduction of the Nile perch (*Lates niloticus*) into Lake Victoria that exterminated at least 200 of the 300 species of endemic cichlids

(Ogutu-Ohwayo 1999). Today, almost 20% of the vertebrate species threatened by extinction are in that status because of invasive species (McNeely 1999).

Previous work on invasive exotic species has been largely descriptive. Work is still mainly focused on quantifying the impacts of invasive species on native communities. Below are some well-documented descriptions of the impacts of invasive exotic plants on the ecosystem and community:

a) Alteration of geomorphological processes

Coastal dune topography in California, Oregon, and Australia has been changed by the presence of the European grass, *Ammophila arenaria* that has stabilized the sandy foredunes (Macdonald and Richardson 1986, Wiedemann and Pickart 1996), changing the ecology of coastal ecosystems**.**

An Australian import into the United States, *Casuarina equisetifolia*, has made coastal shorelines steeper and more compact in parts of Florida thereby affecting loggerhead turtle (*Caretta caretta*) nesting success (Doren and Jones 1997). An Old World riparian species, *Tamarix ramosissima*, forms thickets that have stabilized stream channels, changing the Green River's (Utah) topography and causing flooding (Graf 1978). Additionally high *T. ramosissima* transpiration rates also have lowered water tables when they occur at high densities (Randall 1993), altering vegetation composition of the surrounding areas. In both the Pacific Northwest of the United States and the Atlantic Coast of Europe, *Spartina townsendii* and *S. anglica* are invading tidal mud flats, stabilizing these flats and collecting litter (Hubbard 1965,

Thom 1992), thereby changing coastal morphology by raising the level of the mud flats.

b) Alteration of biogeochemical cycles

Myrica faya and *Leucaena leucocephala* are nitrogen fixers. In Hawaii, they are invading volcanic areas and altering the belowground chemistry, speeding up primary succession by potentially allowing other non-native species to colonize these areas as well (Vitousek 1986). *Mesembryanthemum crystallinum*, the annual iceplant, grows in saline areas on the West Coast of the United States; it accumulates salt and deposits it into its surrounding areas when it dies at the end of the growing season (Vivrette and Muller 1977), excluding competing species from growing in its vicinity.

c) Alteration of hydrological cycles

Many plant species have been documented to reduce forest runoff. The species list includes *Hakea sericea, Acacia longifolia* and *A. mearnsii* (Macdonald et al. 1989, Macdonald and Richardson 1986, Versfeld and van Wilgen 1986), *Tamarix* spp. (Vitousek 1986), *Datura innoxia, Nicotiana glauca* and *Prosopsis* spp. (Macdonald and Nott 1987).

d) Alteration of fire regimes

The European cheatgrass, *Bromus tectorum,* burns readily and quickly in habitats it invades in the arid western United States (Klemmedson and

Smith 1964). Post-burn areas are often further invaded by other exotic species, altering burn patterns (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998). *Chromolaena odorata*, which occurs at savanna-forest ecotones, burns into forest margins, reducing forest patch sizes (Macdonald 1983). Others such as *Melaleuca quinquenervia* (Wade et al. 1980), *Schinus terebinthifolius* (Ewel et al. 1982), *Arundo donax* (Bell 1993), *Hakea sericea* (Van Wilgen and Richardson 1985) and *Acacia saligna* (Holmes and Cowling 1997) reduce the frequency and alter the mean intensity of fires, lowering plant species diversity.

HYPOTHESES ON SUCCESS OF INVASIVE SPECIES

After habitat destruction, biological invasion is the second greatest threat to biodiversity (Diamond and Case 1986). However, despite there being over 1000 studies on biological invasions (Pysek et al. 1995a), science has still found it hard to predict which species will become invasive. Many studies have attempted to explain the success of invasive exotic plants, by either studying the intrinsic plant traits or the extrinsic plant environment (Mack and D'Antonio 1998). A few of the currently widely accepted hypotheses are listed below:

a) Predator release hypotheses

Frequently when species are transported from their native habitats to a new environment, their predators and parasites are left behind (Elton 1958, Crawley 1989, Cox 1999). Studies have shown that species in their non-native habitat often have

higher reproductive success (Dingle 1980, Jain and Martins 1979), higher growth rates and form larger individuals (Blossey and Notzold 1995) than original populations in their native habitat. This could be because of decreased herbivory (Schierenbeck et al. 1994) and hence change in biomass allocation from defense to growth (Blossey and Notzold 1995).

b) Competitive release

A species introduced into a new range is sometimes freed from its native competitors. In areas of high plant diversity such as the tropics where there is a lot of competition for light and nutrients, a plant transported to another environment and released from competitive pressure will often grow faster and larger (Orians 1986, Blossey and Notzold 1995) than individuals in the original population, and often outcompetes native congeners in its new range.

A frequently suggested hypothesis as to why some communities are particularly invasible is that these communities have unoccupied niche-spaces (Elton 1958, Herbold and Moyle 1986). An early common hypothesis in the study of invasion biology was that invasive exotics mostly invaded disturbed ecosystems (e.g. Hobbs 1989). Disturbance was believed to create new microhabitats and hence new niches for invasive plant species (e.g. Kotanen 1997). However, studies in the past decade have shown that this hypothesis is not supported in all case studies. Invasive species are not only commonly found in disturbed areas but they also invade native undisturbed habitats (e.g. Wiser et al. 1998, Huenneke 1991, Lodge 1994, Stohlgren et al. 1999). Tilman and Pacala (1993) propose that as plants cannot completely

utilize all the available resources in their environment. So even if a habitat is undisturbed there will always be resources available to species that are able to extract these resources.

Unoccupied niches are believed to be found within geologically young communities where the available niche spaces have not been completely filled. Both Florida and the Hawaiian islands are geologically young; Florida has only attained its current biogeography in the last 5,000 years (Long 1974) while the island of Hawaii, over 3000 km from the North American continent, is less than 1 million years old (Carson and Clague 1995). Because of Florida's peninsular location and Hawaii's isolation from the continental United States, both geographic locations conform to island biogeography principles and hence are probably susceptible to invasive species.

c) Genetic change

A plant's release from selection pressure can also potentially contribute to its invasiveness. Both biotic and abiotic pressures within a plant's native environment are constantly selecting for particular characteristics (Gray 1986); introduction into a new environment might potentially be favorable to the invasive species by either releasing it from these pressures or allowing particular traits to dominate. A rangeland crop, the rose clover (*Trifolium hirtum*), is thought to have undergone subtle genetic changes since its introduction in 1946. Rose clover is reproductively more vigorous in disturbed roadside habitats than in the original range populations. The disturbed populations also have higher genetic variation than the original range populations

(Jain and Martins 1979, Martins and Jain 1979). On the contrary, low genetic variability has been shown in successful invasives such as slender wild oat (Clegg and Allard 1972), *Striga asiatica* (Werth et al. 1984) and cheatgrass (Novak et al. 1991, Novak and Mack 1993) that indicate the fixation of many loci.

Hybrid vigor has also been shown in many species. The hybrid of the exotic *Carpobrotus chilensis* and native *C. edulis* has been shown to have higher reproductive output and higher germination rates after gut passage than its native parent (Vilà and D'Antonio 1998). The salt marsh grass *Spartina anglica*, a fertile mutant hybrid of the native North American *S. patens* and the European *S. maritima*, is able to colonize lower intertidal areas than either parent (Thompson 1991) and is currently displacing *S. maritima* in many coastal areas of Europe. Hybrids also threaten native species via introgression that leads to either extinction or genetic assimilation of the parent species (Stohlgren et al. 1999).

It has also been suggested that characteristics such as a small genome size allow a species to become more invasive as it is strongly correlated to short generation times (Rejmanek and Richardson 1996). The finding that small nuclear DNA content (i.e. genome size) is correlated with small seed mass (Thompson 1991, Wakamiya et al. 1993) and short juvenile periods (Wakamiya et al. 1993), potentially indicates selection for short generation time.

d) Reproductive output

It has been proposed that invasive species are r-strategists (Rejmanek 1989); Rejmanek and Richardson (1996) showed that many invasive species have high

reproductive rates. Meskimen (1962) showed that mature adult *M. quinquenervia* could produce up to 20 million wind-borne seeds per plant. Lonsdale (1993) recorded over 9000 seeds m^{-2} (about 10 mg/seed) within a *Mimosa pigra* stand. Moreover invaders such as *Chrysanthemoides molinifera a*nd *Acacia longifolia* were often found to have higher seed outputs in their introduced environment than their native habitats (Noble 1989).

e) Physiology

Species that are able to utilize resources available in the environment more effectively tend to be able to compete better than native species. Polley et al. (1994) have shown that increasing atmospheric CO_2 levels could contribute to the physiological ability of *Prosopsis glandulata* (honey mesquite) to invade C_4 grasslands. Baruch and Goldstein (1999) have shown that the invasive exotic species in Hawaii tend to have higher photosynthetic-nitrogen-use-efficiency than natives, indicating more effective resource utilization. Similarly, *Bischofia javanica* has been shown to respond faster to light availability in gaps than native Japanese tree species, potentially outcompeting native species in gaps once it is present in the understory (Yamashita et al. 2000). *Tamarix ramosissima*, an invader of floodplains and riparian areas, has been shown to be more drought tolerant than native species, allowing it to outcompete the natives and form monospecific stands (Cleverly et al. 1997). *Mesembryanthemum crystallinum*, an invader of saline areas in the West Coast of the United States, not only tolerates high salt content within its cells but has also been shown to switch from C_3 to CAM metabolism when exposed to high salinity and low

water availability (Winter and Ziegler 1992). This metabolic switch allows it to tolerate conditions of extreme stress, potentially outcompeting native species. Shade tolerance (Jones and McLeod 1990) and stem photosynthesis (Bossard and Rejmanek 1992) also have been suggested as potential mechanisms of invader success.

The ability of science to make predictions on which exotic species will become invasive is still limited (Drake and Mooney 1989, Beerling 1995, Thompson et al. 1995). First, many success factors are species- or habitat-specific (Rejmanek 1999, Radford and Cousens 2000). Monterey pine (*Pinus radiata*) is innocuous within its home range in California but a serious pest plant in Chile where it was introduced for forestry (Bright 1998). Second, predictability is limited because of lag times (Kowarik 1995). The success of invaders is not an overnight process; Kowarik (1995) showed that invasion by exotics in Brandenburg, Germany accelerates after an average of 147 years after introduction. Lag times have been attributed to the nature of population growth, eventual change in environmental conditions to suit the invader and development of genetic fitness for the new environment (Crooks and Soule 1999).

Third, life history traits that allow one species to be invasive do not necessarily apply to other species with the same characteristics. Table 1.1 lists the potential life history characteristics that can allow a species to be invasive (Baker 1965). No single character can reliably predict the invasiveness of a species (Pysek et al. 1995b) and all invasive species need only to have a subset of these characteristics to be invasive. It is hard to come up with predictive rules for invasiveness as species success can vary from habitat to habitat. However, with large data sets on many species, one can come up with

generalizations for the taxa examined. A recent study of global data sets by Daehler (1998) showed that the plants that have the highest probabilities of becoming invasive are: aquatic or semi-aquatic plants, grasses, nitrogen-fixers, climbers and clonal trees. Orchids, bromeliads and gesneriads, despite having many of the characteristics outlined by Baker (1965) in Table 1.1 (e.g. high numbers of hybrids, small seed sizes and large reproductive outputs) had low probabilities of becoming invasive according to Daehler's analyses. Therefore, the knowledge that we have to date is not sufficient to predict invasiveness in plants. More research needs to be done on understanding how each plant functions before better substantive generalizations can be made.

INVASIVES IN SOUTH FLORIDA

Florida, after Hawaii, has the greatest number of exotic invasive species. The theories proposed for this high number of exotics are: 1) the relatively depauperate flora and fauna of peninsular Florida (Ewel 1986, Myers and Ewel 1992) which has vacant niches available for new species to colonize, 2) the large number of plants and animals that are transported through South Florida (U.S. Congress 1993), and 3) the high degree of human disturbance in the Florida landscape (Simberloff 1997).

Virtually every ecosystem in South Florida is plagued by invasives. The greatest threat originates from those species which tend to form non-successional monospecific canopies in the habitats that they invade, changing the ecology, hydrology and oftentimes the geomorphology of these habitats. Examples of such species include invasives such as *Schinus terebinthifolius*, *Melaleuca quinquenervia*, *Casuarina equisetifolia* and *Eichhornia crassipes. Schinus terebinthifolius* often forms dense monospecific stands that

do not readily burn (Doren and Whiteaker 1990) and been shown to lower plant species diversity (Loope and Dunevitz 1981, Krauss 1987) as well as reduce faunal residence in an area (Curnutt 1989). Stands of *M. quinquenervia* are generally found in wetland areas; the high transpiration rates of *M. quinquenervia* alter the hydrology of the local area and this fire-tolerant exotic persists through fires better than native species (Ewel 1986). A freshwater marsh can be a drained, monospecific stand when invaded by this exotic. *Casuarina equisetifolia* is often found in coastal areas where its roots often form a dense mat, preventing turtles from nesting. Vines such as the air potato (*Dioscorea bulbifera*) and kudzu (*Pueraria lobata*) blanket tree canopies (Horvitz 1997), displacing native species.

This dissertation covers 3 years of study related to the invasive *Schinus terebinthifolius*. The Florida Exotic Pest Plant Council, a group of scientists and land managers interested in controlling exotic species, released its first List of Exotic Pest Plants in 1991; *Schinus* was classified in Category I. A plant in this category was determined to have the ability to significantly alter ecosystem structure and function (FLEPPC 2001). Attempts at *Schinus* control have been in the form of burning (Doren et al. 1991), various forms of mechanical removal (e.g. Koepp 1979, Ewel et al. 1982, Gioeli and Langeland 1997, Stees 1995, Workman 1979) and biocontrol (Habeck 1995, Krauss 1963, Marlatt and Ridings 1979, Medal et al. 1999).

Table 1.1. Characteristics of an ideal weed (adapted from Baker 1965).

1. Has no special environmental requirements for germination
2. Has discontinuous germination (self-controlled) and great longevity of seed.
3. Shows rapid seedling growth.
4. Spends only a short period of time in the vegetative condition before beginning to flower.
5. Maintains continuous seed production for as long as growing conditions permit.
6. Is self-compatible, but not obligatorily self-pollinated or apomictic.
7. Cross-pollination can be achieved by a nonspecialized flower visitor or wind.
8. Has very high seed output in favorable environmental circumstances.
9. Can produce some seed in a very wide range of environmental circumstances. Has high tolerance of (and often plasticity in the face of) climatic and edaphic variables.
10. Has special adaptation for both long-distance and short-distance dispersal.
11. If a perennial, has vigorous vegetative reproduction.
12. If a perennial, has brittleness at the lower nodes or of the rhizomes or rootstocks.
13. If a perennial, shows an ability to regenerate from severed portions of the root-stock.
14. Has ability to compete by special means: rosette formation, choking growth, exocrine production (but no fouling of soil for itself), etc.

PREVIOUS STUDIES ON *SCHINUS TEREBINTHIFOLIUS* BIOLOGY AND ECOLOGY

Barkley (1944, 1957) reviewed the taxonomy of the genus *Schinus* of which there are 17 species. *Schinus terebinthifolius* is reportedly found in tropical areas throughout the world (Barkley 1944, Horvitz et al. 1998). The first written record of *Schinus* in Florida was from Barkley (1944), after examination of an herbarium specimen of *Schinus* in the Missouri Botanical Garden Herbarium collection; this specimen had been collected from a cultivated individual growing in Florida between 1842 and 1849.

Nothing more is known about the status of this exotic until the 1890's when *Schinus* was reported as being actively distributed by Dr. George Stone to his community of Naples in Southwest Florida (Nehrling 1944). At that time, *Schinus* was viewed as a desirable ornamental because of the abundance of red berries found on the plant during Christmas time, earning it the local common name of "Christmas berry" and "Florida holly".

Between the 1890's and late 1970's, few studies were conducted on *Schinus terebinthifolius*. Kaistha and Kier (1962) carried out a chemical analysis on the terpenes in this species but mention of *Schinus* in the literature was mainly as part of descriptive work (Barrett 1956, Lemke 1992, Loope 1980, Tomlinson 1980). In the late 1970's interest in *Schinus* developed in part because of the increasing presence of *Schinus* in the Florida landscape including Everglades National Park. Within Everglades National Park, *Schinus* is found from the upland pinelands (Ewel et al. 1982) to the mangrove swamps (Olmsted and Loope 1985, Mytinger 1985, Mytinger and Wiliamson 1986). The largest stand of *Schinus* however, is found in a 2000 ha previously farmed area of Everglades

National Park known as the Hole-in-the-Donut. After abandonment of farming, this disturbed area did not revert back to native vegetation but instead became an end-succession forest predominantly composed of *Schinus* (Krauss 1987). *Schinus* was also observed spreading into adjacent pinelands from this disturbed area (Olmsted and Loope 1985).

In the early 1980's, scientific awareness that *Schinus* was invading disturbed habitats and native communities spurred interest in *Schinus* biology and ecology. *Schinus* biology has been documented by reports from Ewel et al. (1982) and Ferriter (1997). Additionally, there have been proceedings from two local symposia on exotic pest plants (Workman 1979, Center 1991). In addition to Morton's (1978) study of *Schinus* impact on humans, ecological studies also have been carried out. These include a study by Burch (1992), who examined the impact of the love vine, *Cassytha filiformis*, on *Schinus* growth and reproduction. He found that *C. filiformis* limited *Schinus* growth but under natural conditions, did not limit *Schinus* reproduction significantly. A study by Dunevitz and Ewel (1981) found that *Myrica cerifera* had alleleopathic effects on *Schinus* seedling growth. *Schinus* impact on animals has also been studied. Curnutt (1989) found that fewer breeding birds used *Schinus* in the Hole-in-the-Donut area than native plant communities; Panetta and McKee (1997) showed that frugivorous birds which passed *Schinus* seeds through their gut significantly aided *Schinus* germination. Two recent studies have examined arthropods within *Schinus* stands. Clouse (1999) examined leaf-litter inhabitants within a *Schinus* stand while Burckhardt and Basset (2000) studied the relationship of jumping plant-lice with *Schinus*. Ecophysiological studies, mainly focusing on seedling behavior also have been carried out. Nilsen and Muller (1980a,

1980b) compared *Schinus* with its congener (another exotic that is widely found in California), *Schinus molle.* They examined seedling germination and establishment under a variety of conditions. The conclusion from their studies was that, given their experimental conditions, *Schinus molle* seemed a better invader than *S. terebinthifolius*, as *S. molle* had higher germination rates and also grew better under drier conditions. In 1985, Mytinger completed a study on *Schinus* seedling responses to salinity; her findings indicated that *Schinus* did not germinate readily at salinities higher than 5 p.p.t. Recently, a study by Pattison et al. (1998) examined the gas exchange of a variety of native and exotic species in Hawaii. Their study, which included *Schinus*, showed that this exotic had higher relative growth rates and photosynthetic nitrogen-use efficiency than native Hawaiian rainforest species.

STUDY GOALS

The purpose of this study was to determine if: 1) *Schinus* ecophysiology (in terms of water uptake and gas exchange) was different from that of native species and 2) if ecophysiology of the exotic could help explain its widespread distribution in Florida. Biological studies have examined the phenology, ecology and physiology of invasive exotic species in attempt to understand what contributes to their invasiveness. *Schinus* has a wide tolerance for a large range of native habitats: it can be found growing on an almost bare rock substrate within the upland rock pinelands of Everglades National Park and in saline mangrove areas around South Florida. Although *Schinus* seedling ecophysiology has been examined by other workers (Nilsen and Muller 1980a and 1980b,

Mytinger 1985) few studies have been carried out to explain how, once established, *Schinus* is able to persist in such a variety of habitats.

Schinus shows many of Baker's characteristics, such as seeding under a wide range of environments, high seed output, rapid seedling growth and adaptation for long-distance dispersal. However, our understanding of *Schinus* characteristics does not explain the underlying mechanisms contributing to this species ecological success. This work addresses the physiological mechanisms this plant uses in water uptake and gas exchange. Ecological characteristics such as large numbers of seeds and wide dispersal do not necessarily indicate invisibility (Daehler 1998). If the large numbers of seedlings (e.g. in *Schinus*) were unable to physiologically tolerate the environmental conditions in the new habitat, this species would not be as widely distributed today in South Florida. Hence it is important to study the physiology of this species to further understand its behavior in the environment.

This work was carried out using both physiological and ecological techniques. To better determine *Schinus* physiological behavior over spatial and temporal scales, the exotic was compared against a suite of native species that were found together with *Schinus* within the plant communities it is invading. This study contributes to a greater understanding of the underlying physiological mechanisms that potentially allow the success of an invasive species.

Specifically, I compared certain physiological characteristics of *Schinus* against native species in two geographically distinct ecosystems where the exotic was found to

be invading, and I contrasted two communities within each ecosystem (Fig. 1.1). The goal of these comparisons was to find out what mechanisms, particularly as they related to water uptake and gas exchange, the exotic might utilize to cope with the abiotic environment, and if *Schinus*' characteristics were significantly different from native species. If differences were present, they will provide a basis for conjecture how *Schinus* physiology contributes to it being an invasive exotic in Florida.

HYPOTHESES ON *SCHINUS* SUCCESS

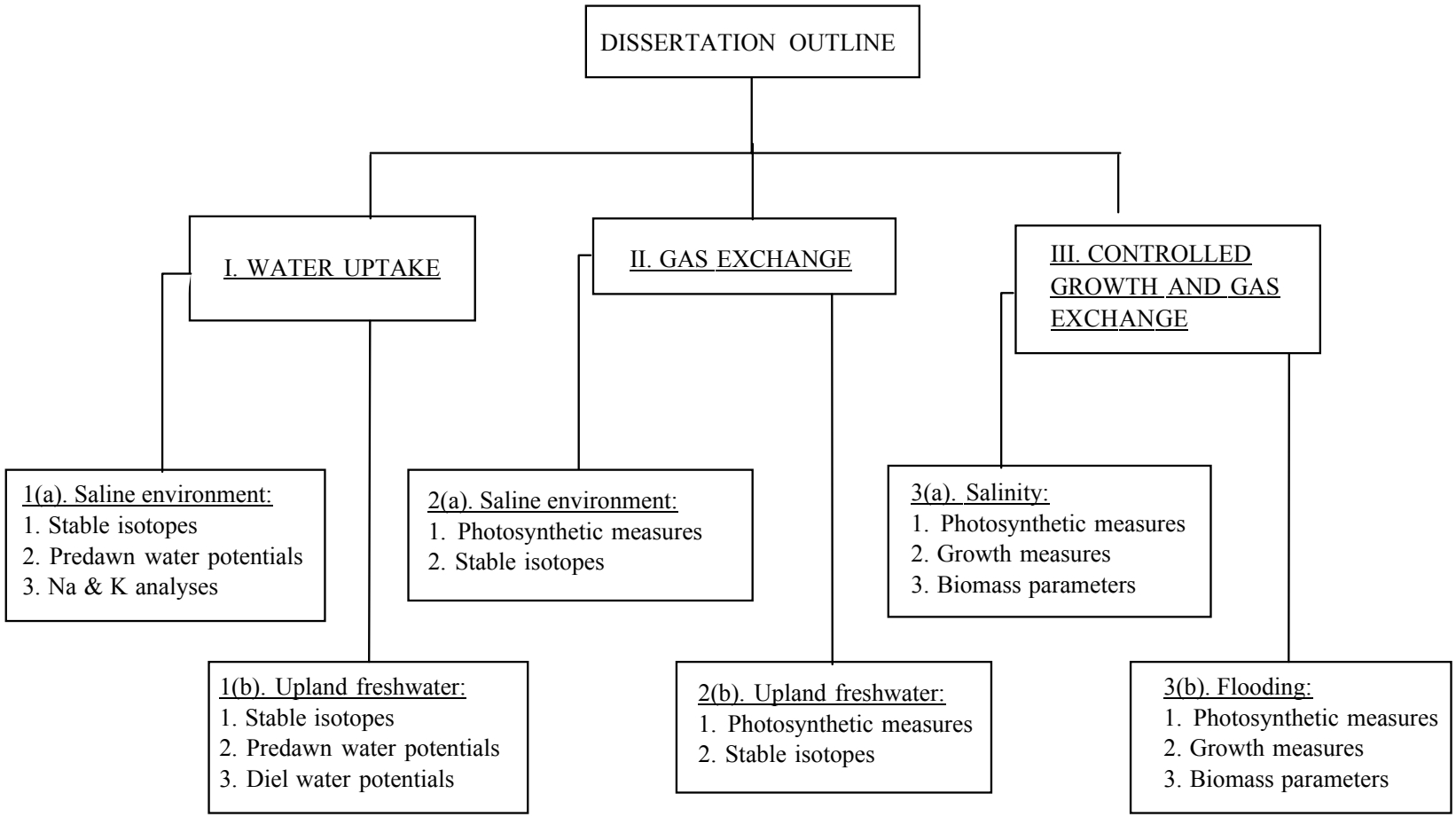
Schinus terebinthifolius and native species water uptake patterns and gas exchange were compared in field and glasshouse studies. Methods used to test each hypothesis are shown in Fig. 1.1. The specific hypotheses tested were:

Component 1. *Schinus* water uptake

Hypothesis 1a: *Schinus* is capable of preferentially tapping into fresher water than native species in the saline transition zone area.

I hypothesized that in a saline environment, *Schinus* would be able to preferentially exploit less saline pockets of water in areas of large horizontal and vertical salinity heterogeneity.

Figure 1.1. Components of the dissertation.



Component 2. *Schinus* gas exchange

Hypothesis 2a: *Schinus* assimilation, water-use efficiency (WUE) and photosynthetic nitrogen-use efficiency (PNUE) in an upland freshwater site within a saline environment is greater and less seasonally variable than those of native species.

I hypothesized that compared to native species, *Schinus* would not only have a greater assimilation, WUE and PNUE but also be physiologically less affected by seasonal fluctuations in water availability than native species.

Hypothesis 2b: *Schinus* assimilation, water-use efficiency (WUE) and photosynthetic nitrogen-use efficiency (PNUE) in an upland freshwater site is higher than native species both during the wet and dry season.

I hypothesized that *Schinus* would have higher assimilation rates and be less affected by seasonal fluctuations in water availability and groundwater levels than native species. It was also expected that *Schinus* would seasonally maintain its WUE and PNUE rates despite soil water fluxes whereas native species would be physiologically more affected by these hydrological fluxes.

Component 3. *Schinus* growth and gas exchange under controlled conditions

Hypothesis 3a: *Schinus* growth rate and photosynthesis, under controlled glasshouse conditions at 0, 8 and 15 parts per thousand salinity, would be greater than those of native species.

I hypothesized that *Schinus* would have higher growth rates, assimilation and PNUE than native species when high salinity treatments were imposed on the plants.

Hypothesis 3b: *Schinus* growth rates, assimilation and photosynthetic nitrogen-use efficiency would be higher than those of native species under controlled flooding.

I hypothesized that *Schinus* would have higher growth rates, assimilation and PNUE than native species when grown under drought or flooded conditions.

Chapter 2

Water utilization patterns of the invasive exotic *Schinus terebinthifolius* and native species in two coastal plant communities

INTRODUCTION

An invasive exotic is a non-indigenous species that is successfully reproducing outside of its native habitat, independent of human help. Although the majority of non-native plant species do not independently disperse into new habitats, those that do can sometimes pose a significant threat to the integrity of native communities. The ecological impacts of these invaders on native communities can be significant both economically and ecologically (Bright 1998, Pimentel et al. 2000). Invasive exotic species have been shown to cause changes such as alterations in soil conditions, hydrology, fire regimes and species diversity (e.g. see reviews in Vitousek 1986, Cronk and Fuller 1995).

Schinus terebinthifolius Raddi (hereafter *Schinus*) is an exotic plant species commonly known as Brazilian pepper, Florida holly, or Christmas berry. *Schinus* is found in approximately 280,000 ha in South Florida; it occupies the greatest acreage of all woody exotic plant species in South Florida, exceeding *Melaleuca quinquenervia* and *Casuarina equisetifolia* (1993 South Florida Water Management District Survey as cited in Schmitz et al. 1997). *Schinus* was imported from temperate South America over 100 years ago as an ornamental (Nehrling 1933). Since its escape from cultivation, it has been widely found in disturbed areas as well as in native habitats. It is a dioecious, shrubby evergreen perennial that grows up to a maximum height of 13 m in South Florida (Barrett

1956). It sprouts easily from the root base and is often multi-stemmed. *Schinus* has been found from upland pinelands (Loope et al. 1979) to coastal mangrove communities (Mytinger 1985, Mytinger and Williamson 1986) suggesting that it has physiological tolerance for a broad range of soil and hydrological conditions.

Schinus success within South Florida has been attributed to its ability to invade disturbed habitats. Studies have examined *Schinus* distribution (Barkley 1944, Lemke 1992), phenology (Barkley 1944, Tomlinson 1980, Ewel et al. 1982, Ferriter 1997), reproductive biology (Ewel et al. 1982) and plant-animal interactions (Curnutt 1989) within South Florida. Although studies have briefly described the physiology (Pattison et al. 1998) and ecological characteristics of *Schinus* (Horvitz et al. 1998), the question of whether there are underlying physiological mechanisms that allow *Schinus* persistence and tolerance of a variety of conditions have never been examined. In its native habitat, *Schinus* is often found in the landward fringes of coastal berms (Fabris et al. 1990) and may be adapted to high salinity. Therefore, salinity tolerance of *Schinus* could contribute to its success in South Florida saline communities such as transitional zones and mangrove forests. On the other hand, if there are freshwater pockets in these communities, *Schinus* might utilize water from these pockets more efficiently than native species and thereby co-exist in the same general area as salt-tolerant mangroves. To understand *Schinus* ecophysiology, it is important to characterize the horizontal and vertical heterogeneity of salinity in this coastal habitat.

The purpose of this study was to determine if the water uptake patterns of *Schinus* differ from those of native glycophytes, and approach those of salinity tolerant mangrove species in the coastal areas. I used the measurements of predawn water potentials, sodium

(Na^+) and potassium (K^+) concentrations of sap and soil water, and stable isotope techniques to determine if *Schinus* had the same water uptake patterns as native species in two coastal communities, a saline transition zone and an upland pineland.

METHODS AND MATERIALS

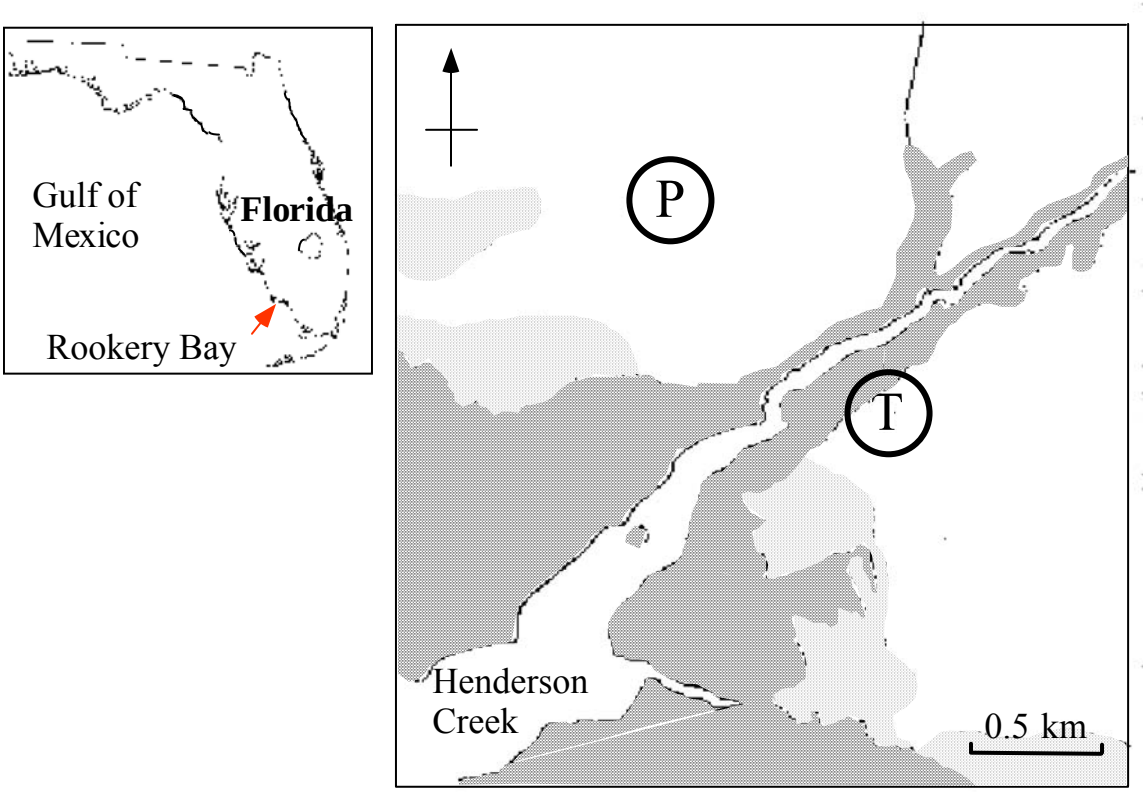
Study site

The study sites were located in southwest Florida (Fig. 2.1) within Rookery Bay National Estuarine Research Reserve. This 6,000 ha reserve is comprised predominantly mangrove and shallow marine communities; upland communities only occupy 5% of the reserve. The substrate in this area is composed of a mix of shell, quartz and calcium carbonate sand (Johnson and Barbour 1990).

Sites were chosen where *Schinus* was found to be one of the major components of the plant community. The first was a transition zone site (26°02.6'N, 81°42.6'W) located between an upland pineland and mangrove community. The second study site was an upland pineland (26°02.8'N, 81°43.1'W) with seasonally brackish groundwater (Fig. 2.1). In addition to *Schinus*, vegetation in the transition zone site was comprised of a mixture of both upland and salt-tolerant plant species. Plants typical of upland communities such as *Randia aculeata*, *Rapanea punctata*, and *Sabal palmetto* occurred alongside salt-tolerant species such as *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa* and *Conocarpus erectus.*

The transition zone site was located close to the estuary of Henderson Creek and hence exposed to belowground tidal effects (Fig. 2.1). Annually, groundwater depths ranged from 1.5 cm to over 50 cm deep. During the wet season, the groundwater was

Figure 2.1. Map of Florida (inset) indicating the location of Rookery Bay National Estuarine Research Reserve. The relative locations of the pineland (P) and transition zone (T) sites are indicated relative to Rookery Bay. The clear areas (□) are upland areas, usually sandy pinelands. On the north side of Henderson Creek, part of the uplands north of the study site has been converted to cattle-pasture. The stippled areas (▨) are salt marshes and the bricked patterns areas (▦) are mangrove forests.



predominantly freshwater runoff from upland areas. In the dry season, freshwater input was reduced, allowing greater seawater intrusion; hence the groundwater was a mixture of both water sources (Rookery Bay National Estuarine Research Reserve, unpublished data). A hypersaline soil surface exists because of the evaporation of water from the soil surface.

The upland pineland site was farther inland (Fig. 2.1) and hence less exposed to salinity fluxes than the transition zone site. Groundwater in this site was consistently deeper year-round than the transition zone; salinity ranged from 0 parts per thousand (p.p.t.) in the wet season to brackish (9 p.p.t) at the end of the dry season. This site had an open canopy of *Pinus elliottii* var. densa Little and Dorman with an understory shrub layer of *Sabal palmetto, Randia aculeata, Rapanea punctata* as well as *Schinus* and *Melaleuca quinquenervia* seedlings.

Southwest Florida receives an average of 1500 mm of rainfall annually (Snyder et al. 1990). Rainfall is strongly seasonal, and approximately 75% of annual precipitation is during the warm wet season (May - Nov). Dry, cool days characterize the dry season (Nov - May). Hurricanes occur during the wet season, making landfall in South Florida on average once every three years (Gentry 1974). The last major hurricane to pass through this area (Hurricane Irene; October 15, 1999) resulted in dry, windy local conditions but did not cause significant vegetation damage (Hopkins, pers. comm.).

Species studied

Five species were compared in this study. Water relations of *Schinus* were compared to native species widely found within the community. In the transition zone

site, *Schinus* was compared to two native salt-tolerant mangrove species and two native freshwater species. The mangrove species were *Rhizophora mangle* L. (Rhizophoraceae) and *Laguncularia racemosa* (L.) Gaertn. f. (Combretaceae). *Rhizophora mangle* (red mangrove) is the most widely occurring species in South Florida (Tomlinson 1986); this species reaches its northern extent in north-central Florida (Odum et al. 1985). *Laguncularia racemosa* (white mangrove) has an overlapping geographical distribution with *R. mangle,* but is generally found towards the landward fringe of a mangrove community, in disturbed or irregularly flooded areas (Ball 1980). The native freshwater species sampled were *Rapanea punctata* (Lam.) Lundell (Myrsinaceae) and *Randia aculeata* L. (Rubiaceae). *Rapanea punctata* (= *Myrsine floridana*) is a tropical species that is commonly found in pineland and hammock communities. *Randia aculeata* is a subtropical plant that is found commonly growing in pinelands. Both species attain the stature of either shrubs or small trees (Tomlinson 1980), and although they are usually commonly found in pineland communities, they also were major components in the transition zone site.

All five species sampled were major components of the transition zone community. The mangrove species, however, were absent from the pineland site. Hence, *Schinus* was only compared to the freshwater native species in the pineland site. Five individuals of each species within each site were tagged and sampled once each at the end of the wet and dry seasons. An attempt was made to track physiological changes in individuals. However, in the transition zone, two individuals of *R. punctata* and a single *R. aculeata* either died between sampling periods or had not regenerated sufficiently for

measurement. Thus measurements were taken on the nearest conspecific neighbor (< 1 m distant).

Water and soil measurements

Soil salinity and water content were sampled to determine the spatial and temporal heterogeneity in belowground hydrological conditions. To characterize horizontal salinity fluctuations and spatial heterogeneity within the transition zone site, a 10 m x 10 m grid was constructed within the area. Wells of PVC pipes (2.5 cm inner diameter) were established at 1 m intervals to 50 cm depth. Wells were capped between sampling periods to prevent evaporative loss of groundwater. Water was extracted from the water table and salinity measured using a refractometer from September 1997 - January 1998. Sampling was terminated in mid-February when groundwater levels dropped to below 50 cm. All salinity values were plotted using Microsoft Excel (Version 7.0) that linearly interpolated differences in salinity between adjacent soil cores.

To characterize the vertical heterogeneity of soil salinity and soil water isotope composition, three soil cores were randomly taken from each site every sampling period (18 April and 30 October 1998, 27 April 1999). Soil samples (12 cm diameter) were collected from the surface and at 15 cm depth intervals until groundwater was reached. Samples were individually stored in 50 mL borosilicate tubes, sealed with Parafilm, and were immediately taken back to the Stable Isotope Laboratory of the Department of Biology at the University of Miami. All soil samples were frozen until analysis. The samples were thawed prior to cryogenic water extraction; they were weighed before and after cryogenic extraction to determine water content. Percent water content was

determined by dividing soil water content by soil dry weight. Subsamples of the dried soils were rehydrated with known amounts of water for Na^+ and K^+ analyses (described below). A second batch of subsamples was ashed at 550ºC in a convection oven to determine organic content; percent soil organic content was determined as the weight of soil organic matter divided by soil dry weight.

Predawn water potentials (PDWP)

Plant xylem water potential was measured between 0200-0530 hrs at both sites. Sampling was carried out at the end of the wet and dry seasons for a total of four seasons (2 November 1997, 18 April and 30 October 1998, 27 April 1999) in the transition zone site and 3 seasons (no 2 November 1997 sampling) in the pineland site. Tips of plant stems 5 - 20 cm in length were collected, and water potential immediately measured in-situ using a Scholander pressure chamber (PMS 600, PMS Instruments, Corvallis, Oregon). Stems smaller than 0.8 cm in diameter were selected when possible, but in *R. mangle* the bark often had to be stripped from stems that were too large for the chamber aperture.

Na^+ and K^+ analyses

For each season, subsamples of soil cores (collected and dried as described above) were rehydrated by adding known amounts of distilled water in excess of saturation. The sample was then stirred with a glass rod and allowed to sit at room temperature for an hour. A small aliquot of the water was then used for determination of soil water Na^+ and

K^+ concentrations by flame photometer (IL 943, Instruments Laboratory, Lexington, MA). Soilwater salinity (in p.p.t.) was determined based on Na^+ concentration.

Stem samples were collected from plants in the transition zone site during the wet season (15 June 1997) and again during the 1999 dry season sampling (27 April 1999). Xylem water was expressed from plant samples using the Scholander pressure chamber and collected in 100μL glass micropipettes. Exposed ends of the micropipets were sealed with Cryto-Seal®. All samples were taken back to the laboratory and diluted with known amounts of distilled water for analysis using the flame photometer. Na^+ and K^+ concentrations (in mmols L^{-1}) of the original samples were calculated based on the dilution factor. Discrimination against Na^+ in plant xylem during water uptake was then calculated with the following equation:

$$\text{Discrimination} = (Na^+/K^+)_{std}/(Na^+/K^+)_{sam}$$

The $(Na^+/K^+)_{sam}$ was the Na^+/K^+ ratio (mmol L^{-1}/ mmol L^{-1}) of xylem water while $(Na^+/K^+)_{std}$ was the Na^+/K^+ ratio of full-strength sea water (= 47.3). Discrimination increases with greater selectivity against Na^+ uptake.

Stable isotope analysis

Fully suberized plant stem sections less than 1 cm in diameter were collected between 0900 – 1100 hrs on the sampling days (18 April and 30 October 1998, 27 April 1999). Live stem sections without leaves were selected where possible to minimize isotopic fractionation. The stem samples were stored similar to the soil cores. To determine oxygen stable isotope signatures, cryogenically extracted stem water was prepared according to the method described by Epstein and Mayeda (1953) before being

analyzed using an ion-ratio gas mass spectrometer (VG Isogas, Middlebury, England). I did not determine the hydrogen isotope ratio of plant water because a previous study by Lin and Sternberg (1992) indicated discrimination against deuterium during water uptake by some coastal species in South Florida. Isotopic abundance was expressed using the following equation:

$$\delta \text{‰} = [(R_{sample} / R_{standard}) - 1] 1000$$

where R_{sample} is the O^{18}/O^{16} ratio of the sample and $R_{standard}$ is the O^{18}/O^{16} ratio of standard mean ocean water (SMOW).

RESULTS

Soil and water measurements

Soilwater content was dependent on soil organic content for all seasons sampled (Fig. 2.2). Soil organic content, analyzed with a three-factor fixed-effects (Model I) analysis-of-variance (ANOVA), varied with site ($F_{1,46} = 95.22$, $P < 0.01$), season ($F_{2,46} = 128.42$, $P < 0.05$) and depth ($F_{3,46} = 582.19$, $P < 0.01$). There were also season x depth ($F_{6,46} = 4.68$, $P < 0.01$) and site x depth ($F_{3,46} = 2.89$, $P < 0.05$) interactions. Post-hoc Bonferroni comparisons of means determined that organic content was higher during the wet season at the soil surface than at depth for both sites. There was also more organic matter at the soil surface in the transition zone site compared to the pineland site. From 15 - 60 cm belowground, the unsaturated substrate in both sites was predominantly sand that had lower water and organic content than the substrate at the surface. As expected based on organic matter content, soil water content also varied with site x depth ($F_{3,46} = 6.87$, $P < 0.01$) (Table 2.1). There was more soil water in the transition zone compared to

Figure 2.2. Soilwater versus organic content in cores taken from the transition zone (◇) and freshwater (Δ) sites. Clear symbols represent individual cores from the 1998 dry season sampling while the dark symbols represent the 1998 wet season. For these two seasons, water contents were significantly related to soil organic content (% water = 19.775 + [3.956 x % organic]; r = 0.918; $P < 0.01$). For the third season, water contents were also significantly related to soil organic content. The asterisk (∗) and the cross (×) respectively represent the 1999 dry season values from the saline transition zone and the upland pineland.

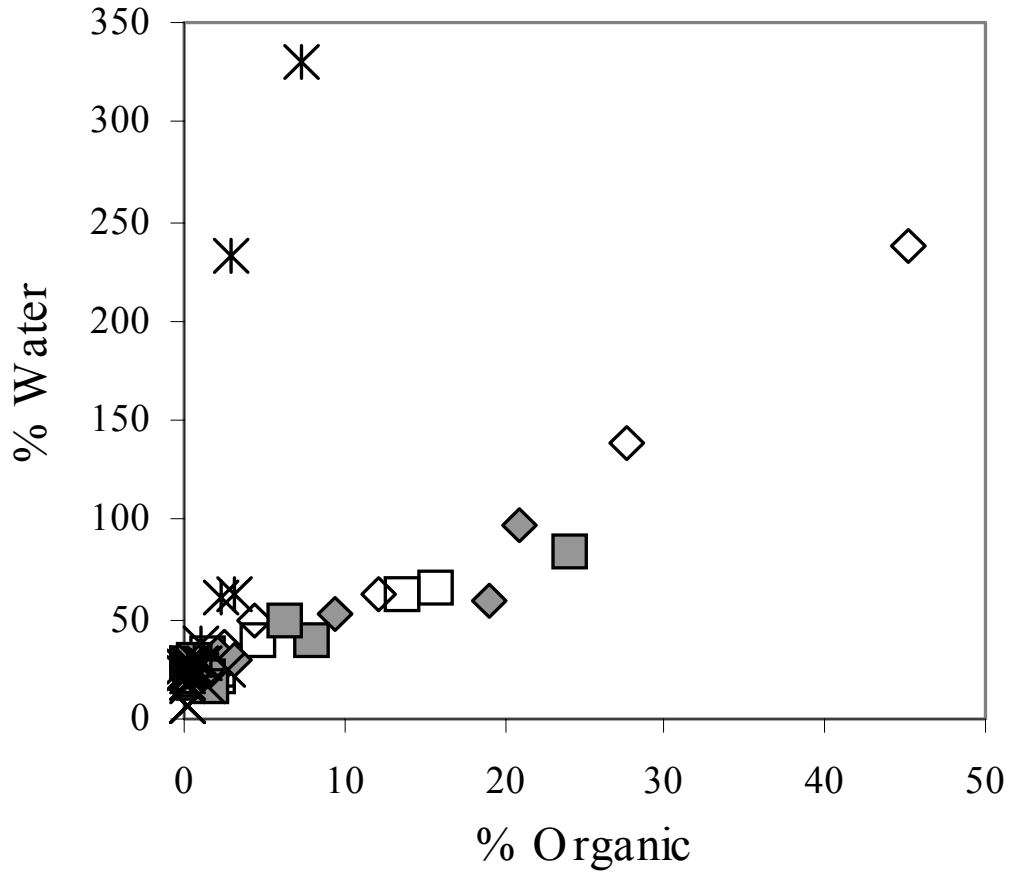


Table 2.1. A three-factor Model I ANOVA of soil water content sampled from both sites, over three seasons at four different depths.

Factor	df	MS	F	*P*
Site	1	15744.396	12.931	.001
Season	2	1058.988	0.870	.426
Depth	3	20371.556	16.731	<.001
Site x Season	2	3444.994	2.829	.069
Site x Depth	3	8360.537	6.867	.001
Season x Depth	6	1068.117	0.877	.519
Site x Season x Depth	6	2475.967	2.034	.080
Error	46	1217.565		

the pineland site and as organic content decreased with depth, a corresponding decrease in soil water content was observed as well.

Within the transition zone site, groundwater (i.e. water table) salinity was horizontally (Fig. 2.3) and vertically (Fig. 2.4) heterogeneous over time. Groundwater salinity sampled at 50 cm decreased from the wet to dry season as groundwater levels dropped during the period monitored. At its most shallow point within the sampling grid, groundwater was 10 cm from the soil surface during the middle of the wet season (Sept 1997) but decreased to greater than 50 cm at the middle of the dry season (Feb 1998). This resulted in sampling progressively nearer to the surface of the groundwater table. During this period, pools of fresh water were found within the matrix of saline water (Fig. 2.3). Groundwater salinity ranged from 5 - 25 p.p.t. in October to 3 - 22 p.p.t. in January.

Vertical salinity within the unsaturated soil layer varied seasonally (Fig. 2.4). Salinity in the unsaturated soil varied by site ($F_{1,46} = 128.33$, $P < 0.01$) and season ($F_{2,46} = 12.50$, $P < 0.01$) but not at the different depths sampled ($F_{3,46} = 1.29$, $P > 0.10$). Soil salinity covaried with all three factors. Salinity was highest at the soil surface in the transition zone during the two dry seasons.

Predawn water potentials (PDWP)

Predawn water potentials within each site were analyzed separately with a two-factor fixed-effects (Model I) ANOVA (Table 2.2). Predawn water potentials of all species varied with season. Post-hoc Bonferroni comparisons of means showed that the only exception to this pattern was in *Schinus* ($P > 0.10$) growing in the transition zone.

Figure 2.3. Salinity (Sept. 1997 - Feb. 1998) within a 10 x 10 m grid sampled at 1 m intervals at 50 cm depth. The first sampling, during September 1997, was of an 8 m x 10 m grid. Sampling area was subsequently enlarged to 10 m x 10 m.

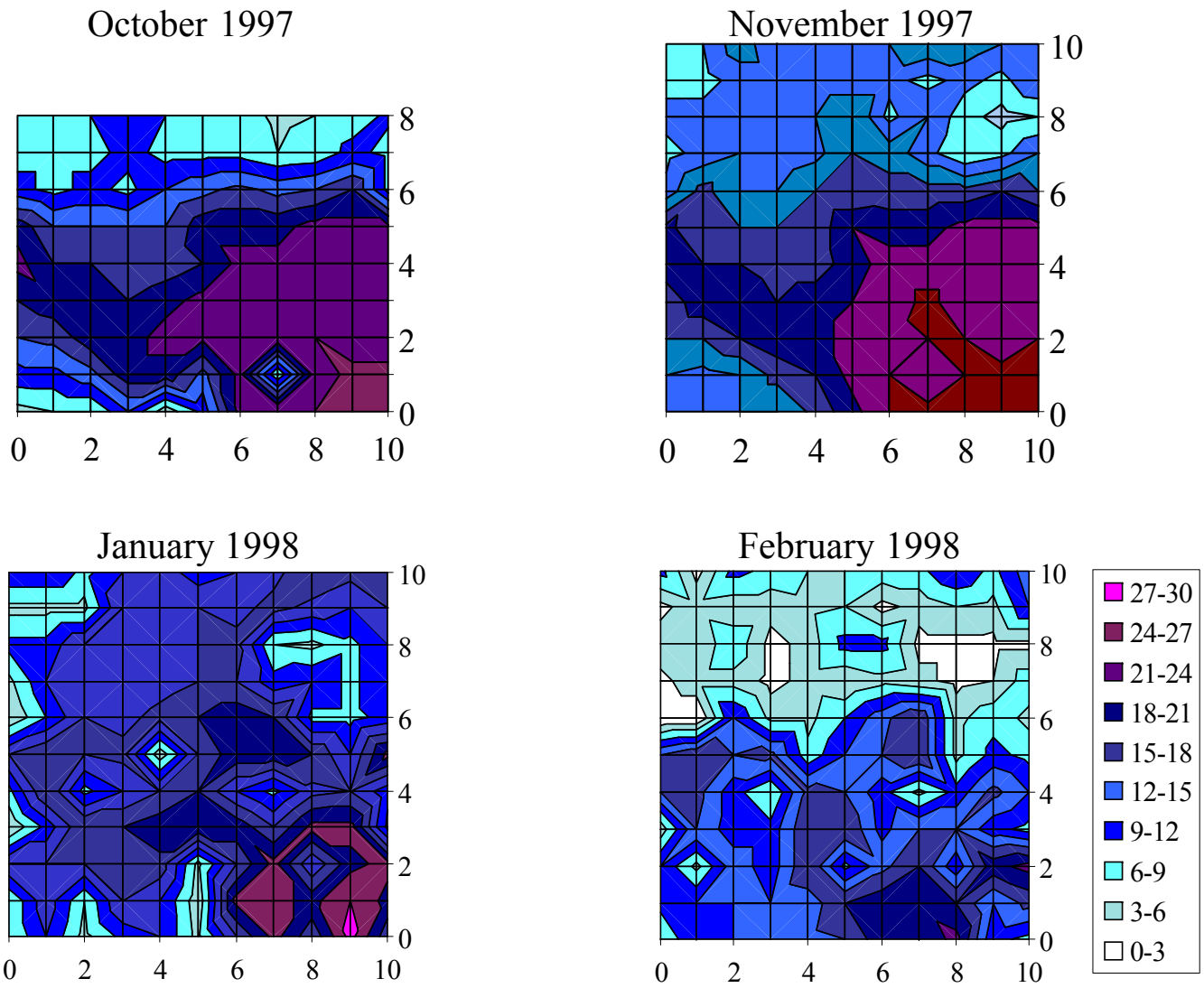
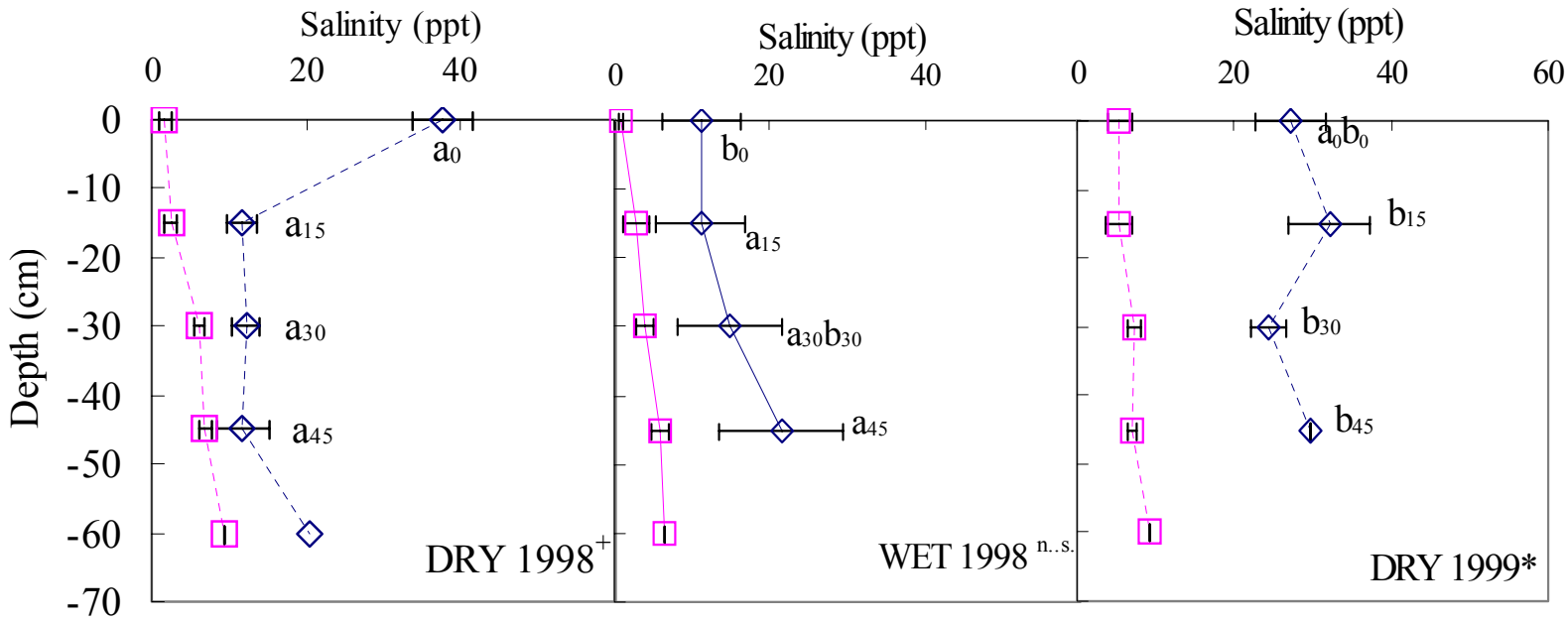

October 1997
November 1997
January 1998
February 1998
0
2
4
6
8
10
27-30
24-27
21-24
18-21
15-18
12-15
9-12
6-9
3-6
0-3

Figure 2.4. Salinity during the dry and wet seasons within both the transition and pineland sites. Three soil cores (± SEM) were taken from each site every sampling period to the depth of groundwater. Groundwater was reached from 45 - 60 cm belowground. The diamonds (◇) represent cores from the transition zone community; the squares (□) represent cores from the freshwater community. Four cores, one each from both sample sites during the 1998 dry season, a third from the 1998 wet season in the upland pineland and a last from the pineland site during the 1999 dry season had groundwater depths below 60 cm; hence values at this depth have no error bars. Depths labelled with the same letter do not differ significantly at the $P > 0.05$ level using a two-factor ANOVA.



\+ salinity between sites significantly different except at 45 cm

n.s. indicates non-significance between transition zone and pineland sites at that depth

* salinities between both sites within this season are significantly different at all depths

Table 2.2. Two-factor ANOVAs on plant predawn water potentials examining the effects of species and season in the transition zone and the pineland site.

	Transition zone				Pineland			
	df	MS	F	*P*	df	MS	F	*P*
Species	4	753.396	106.694	<0.001	2	0.263	0.113	0.893
Season	3	336.333	47.631	<0.001	2	71.404	30.785	<0.001
Species x Season	12	17.590	2.491	0.008	4	9.023	3.890	0.010
Error	80	7.061			36	2.319		

For all the native species at both sites and *Schinus* in the pineland, water potentials were higher during the wet season and lower during the dry season within species. Water potentials were significantly lower in the 1999 dry season than in the 1998 dry season for *R. mangle* and *R. punctata* at both sites. *Schinus* PDWP for the first three seasons in the transition zone (Fig. 2.5) were intermediate between those of native freshwater and mangrove species. In the last season, *Schinus* PDWP was higher than all of the native species in the transition zone. *Schinus* PDWP, however, did not differ from native species in the pineland site for all three seasons sampled (Fig. 2.5). When averaged over all seasons, native mangrove species in the transition zone had the lowest water potentials followed by *Schinus* and the freshwater species.

In the last three seasons when both sites were sampled, a three-factor Model I ANOVA was used to compare *Schinus*, *R. punctata* and *R. aculeata* sampled in both communities. There were significant differences in PDWP between sites, species, and seasons (Table 2.3). There was also an interaction of site x season and species x season (Table 2.3). Post-hoc Bonferroni pairwise comparisons of means showed that water potentials were lower in the transition zone than the pineland site during the dry season and both native species had lower water potentials compared to *Schinus* during the 1999 dry season (Fig. 2.5).

Salinity-stable isotope correlation

During the dry season, there was a relationship between soil water $\delta^{18}O$ values and salinity ($\delta^{18}O = -2.647 + [0.155 \text{ x (Seawater salinity)}]$; $r = 0.952$; $P < 0.01$) in the transition zone. Soil salinity (in p.p.t.) was extrapolated from the Na^+ ionic content based

Figure 2.5. Predawn water potentials (± SEM) of two dry and wet seasons in both the transition zone and upland pineland sites. Stippled bars represent the 1997 wet season (▨) clear bars (□) represent the 1998 dry season, the striped bars (▨) represent the 1998 wet season and the gray bars (■) represent the 1999 dry season. Asterisks (*) indicate the presence of significant seasonal differences within each species as analyzed with a two-factor ANOVA within each site; for each season within a site, a species' PDWP difference from *Schinus*, as indicated in a post-hoc Bonferroni comparison of pairs of means, is either indicated by a "less than"(<) or "greater than" (>) symbol. Within each season in the pineland site, PDWP of *Schinus* was not significantly different from native species except from *R. punctata* for the first sampling season in that site.

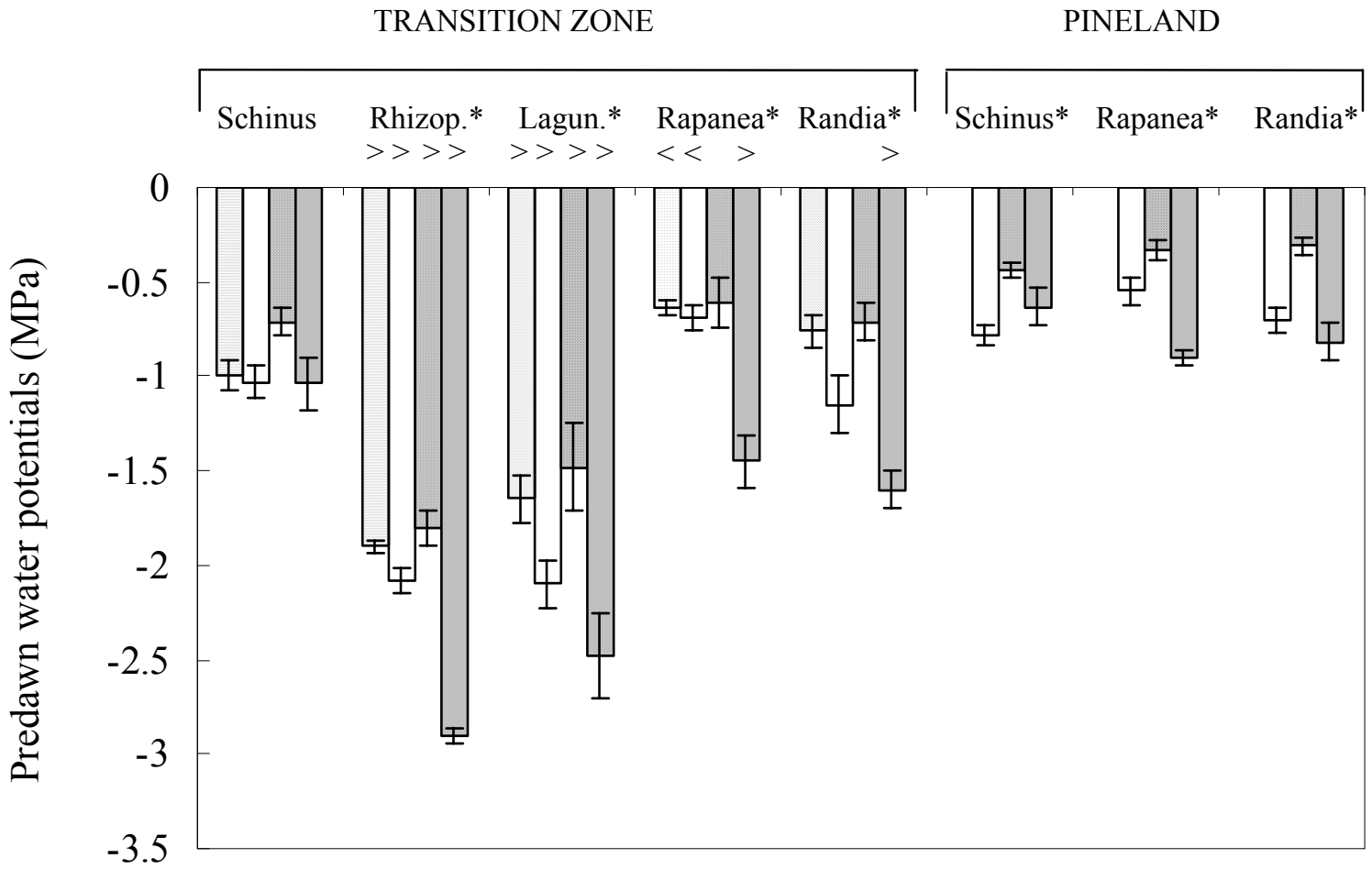

TRANSITION ZONE
PINELAND
Schinus
Rhizop.*
Lagun.*
Rapanea*
Randia*
Schinus*
Rapanea*
Randia*
> > > >
> > > >
< <
>
>
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
Predawn water potentials (MPa)

Table 2.3. A three-factor Model I ANOVA of *Schinus, Rapanea punctata* and *Randia aculeata* predawn water potentials for the two sites and three seasons sampled.

Source	df	MS	F	*P*
Site	1	348.1	77.379	<0.001
Species	2	14.8	3.285	0.043
Season	2	228.1	50.702	<0.001
Site x Species	2	12.4	2.765	0.070
Site x Season	2	21.33	4.730	0.012
Species x Season	4	29.6	6.582	<0.001
Site x Species x Season	4	1.745	0.388	0.817
Error	72	4.5		

on known seawater Na^+ concentrations. Soil surface water was more saline and isotopically enriched than samples at 15, 30 and 45 cm depth (Fig. 2.6).

Specific depth of water uptake by plants could not be determined because of the overlap of stable isotope signatures at the subsurface levels (Fig. 2.6); all plants are utilizing water from between 15 - 45 cm belowground or lower. Despite this, some general observations of plant stable isotope signatures were made. The order of average stem water isotopic enrichment from most depleted to most enriched was: *R. punctata*, *Schinus*, *R. aculeata*, *R. mangle* and *L. racemosa.* However, a single-factor ANOVA comparing $\delta^{18}O$ values of plant stem water from the transition zone during the dry season showed no significant differences among species ($F_{4,20} = 2.68$, $P > 0.05$).

Na^+ and K^+ analysis

Native species were pooled into their functional groupings as either mangrove or freshwater species for statistical analyses comparing seasonal differences because of the loss of several samples from the wet season. For Na^+/K^+ ratios, a two-factor Model I ANOVA of the pooled samples showed significant species ($F_{2,30} = 14.28$, $P < 0.01$), site ($F_{,30} = 18.91$, $P < 0.01$) as well as a species x season interaction ($F_{2,30} = 6.73$, $P < 0.01$). Post-hoc Bonferroni comparisons of means for the interaction effect showed that *Schinus* Na^+/K^+ ratios were higher in the dry (Fig. 2.7) than the wet season ($P < 0.05$) whereas similar analyses showed that significant seasonal shifts were not observed in either the mangrove ($P > 0.05$) or freshwater species ($P > 0.05$) (Table 2.4). *Schinus* and the mangrove species had significantly higher Na^+/K^+ ratios ($P < 0.05$) than freshwater species only during the dry season (Fig. 2.7).

Figure 2.6. Dry season $\delta^{18}O$ stable isotope values versus salinity (in p.p.t., based on Na^+ concentration) of soil water and plant samples in the transition zone site. Average stable isotope signatures (n = 5) in all plant species are shown with their standard error bars. Species names followed by the same letter/s do not differ significantly at the $\alpha = 0.05$ level using a post-hoc Bonferroni comparison of means after analysis with a single-factor ANOVA. Soilwater $\delta^{18}O$ signatures at different depths are represented as 0 cm (◇), 15 cm (□), 30 cm (Δ), 45 cm (○) and 60 cm (∗).

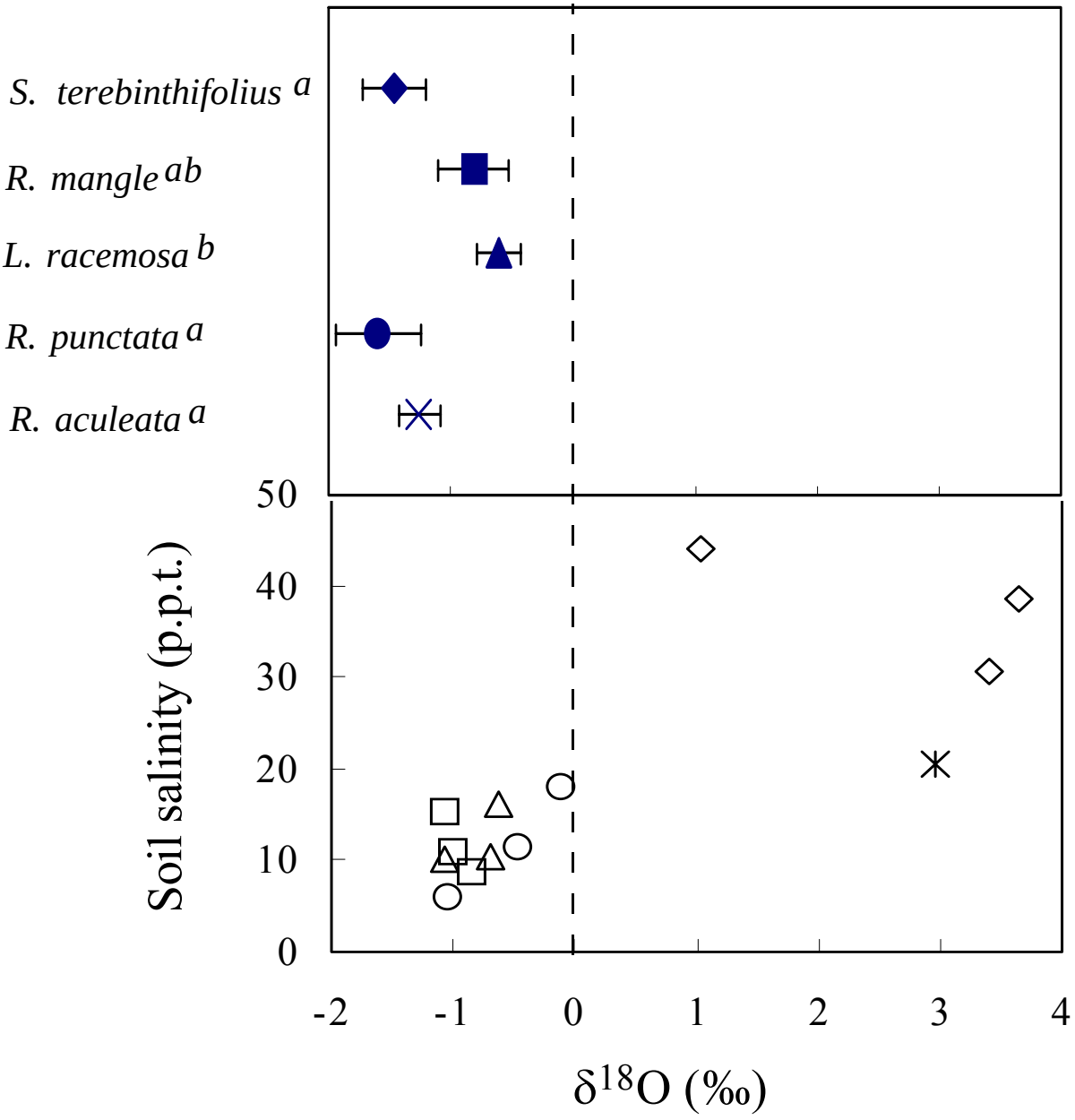

S. terebinthifolius a
R. mangle ab
L. racemosa b
R. punctata a
R. aculeata a
Soil salinity (p.p.t.)
0
10
20
30
40
50
-2
-1
0
1
2
3
4
δ18O (‰)

Figure 2.7. The Na^+/K^+ ratios (± SEM) of *Schinus* compared to the mangrove and freshwater species for a wet (dark bars) and dry (clear bars) season within the transition zone site.

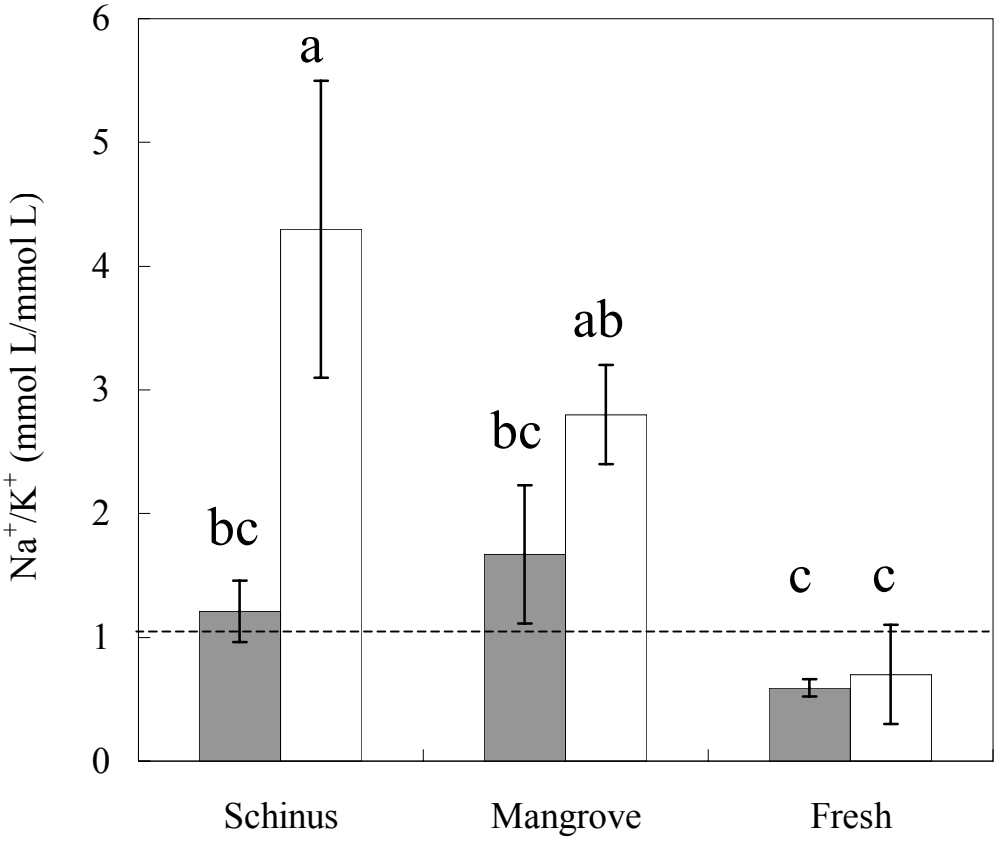


Table 2.4. Sodium (Na^+) and potassium (K^+) contents (in mmol L^{-1}) (± SEM) of plant xylem water in the transition zone during both wet and dry seasons. Because of the loss of some samples during the wet season, values for native species were pooled into their functional groupings. Values followed by the same letter do not differ significantly at the $P > 0.05$ level using a two-factor ANOVA.

	$Na^+ + K^+$			
	n	Wet season (June 1997)	n	Dry season (April 1999)
Schinus terebinthifolius	5	6.7 ± 0.3 [a]	5	211.9 ± 153.3 [b]
Mangrove species	3	38.2 ± 25.9 [a]	10	346.1 ± 30.6 [c]
Freshwater species	6	12.1 ± 5.5 [a]	7	280.5 ± 18.3 [bc]

Total $Na^+ + K^+$ contents of all groups (Table 2.4), analyzed with a two-factor Model I ANOVA showed significant species ($F_{2,30} = 9.55$, $P < 0.01$), season ($F_{1,30} = 282.46$, $P < 0.01$) as well as species x season interaction ($F_{2,30} = 3.72$, $P < 0.05$). Average total ionic content increased approximately 14 – 45 times from the wet to dry season in the different groups. A two-factor Model I ANOVA showed that discrimination against Na^+ uptake was species ($F_{2,30} = 14.26$, $P < 0.01$), season ($F_{1,30} = 18.83$, $P < 0.01$) and species-season dependent ($F_{2,30} = 6.81$, $P < 0.01$) (Fig. 2.8). Discrimination was similar in all species during the wet season and increased over seasons for the freshwater species. Discrimination against Na^+ was however lower in *Schinus* and the mangrove species during the dry season than the wet.

DISCUSSION

The transition zone site presents an extremely heterogeneous mosaic of different salinities that change through time (Fig. 2.3). The counter-intuitive decrease in salinity in this grid as the dry season progressed can be explained by the lowering of the water table during the dry season. If the groundwater is saline and overlain with a low salinity lens, then as the water table descends, samples will be progressively taken from upper less saline layers (Fig. 2.9). Evaporation may be responsible for the hypersalinity at the soil surface in the transition zone site during the dry season. This could potentially curtail water uptake by native freshwater species, in effect, creating physiological “drought” conditions despite high soil water content. Because soil water content during the 1998 dry season was similar to the previous wet season in the transition zone site (Fig. 2.2), a likely explanation for the decrease in dry season PDWP relative to their wet

Figure 2.8. Discrimination of Na^+ uptake (± SEM) by *Schinus*, the mangrove and freshwater species within the transition zone site. Dark bars represent the wet season while the dry season is shown with clear bars.

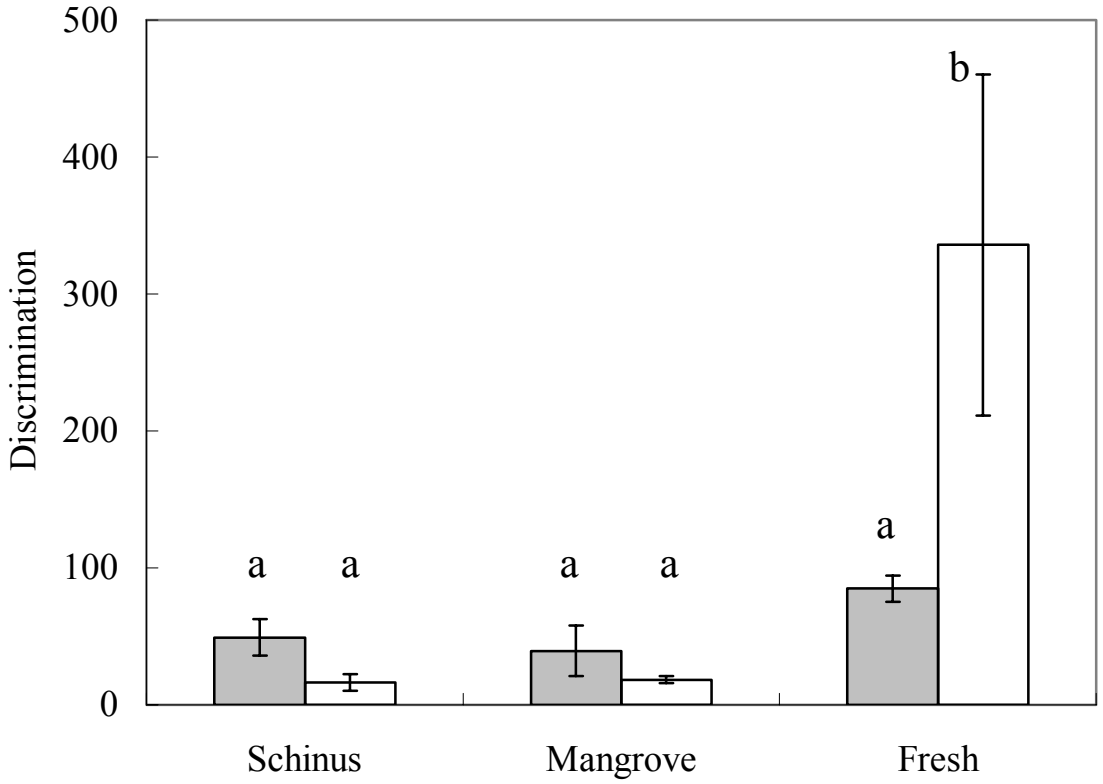
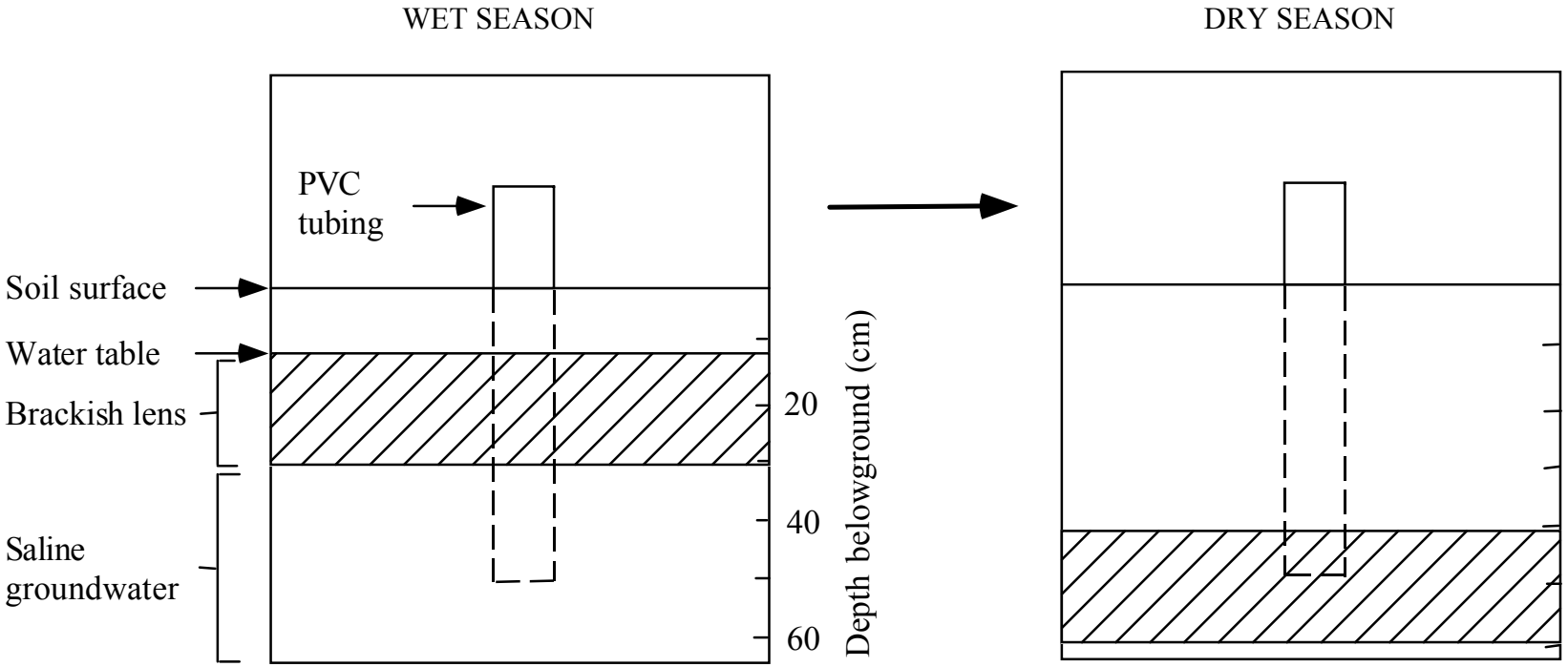


Figure 2.9. Cross-section example of a well within the 10 x 10 m grid that was cored in the saline transition zone. To assess temporal groundwater heterogeneity, wells were established at 50 cm depth. During the wet season, the well is tapping into saline groundwater. As the dry season progresses, groundwater levels drop and the well samples the brackish groundwater lens that overlies highly saline, deep water.



season values found in native freshwater species (Fig. 2.5) would be greater osmotic potentials induced by higher salinity in soil water during the dry season.

Higher $Na^+ + K^+$ contents of all species in dry compared to the wet season (Table 2.4) imply lower plant osmotic potentials during this dry season. Research has shown that high solute contents are correlated with low osmotic potentials (e.g. Levitt 1972, Suarez and Sobrado 1998). In the freshwater species however, the increase in xylem $Na^+ + K^+$ was because of a disproportionate increase in K^+ compared to Na^+ (Table 2.4). Although Na^+ is one of the most common ionic elements in seawater, high cellular Na^+ concentrations can disrupt cell function (Munns 1993), so plants regulate Na^+ uptake via mechanisms such as restricting salt intake, secreting, and excluding salts or storing excess Na^+ in specific organs (Salisbury and Ross 1992, Larcher 1995). Some glycophyte species have been shown to selectively exclude Na^+ while preferentially taking up K^+ against a large external gradient (e.g. Cheeseman and Wickens 1986, Busch and Smith 1995, Warwick and Bailey 1997). I observed this trend for the native freshwater species sampled (Table 2.4). *Schinus* and the mangrove species however discriminate the least against Na^+, indicating their tolerance of salinity. Glycophytic angiosperm dicotyledonous plants generally have Na^+/K^+ ratios less than 1 while halotolerant species can have $Na^+/K^+ > 1$ (Jeffries and Rudnik 1984, Flowers and Yeo 1986, Flowers et al. 1986, Larcher 1995). During the dry season when overall groundwater in the transition zone is probably at its most saline, *Schinus* Na^+/K^+ ratios are comparable to those of the mangrove species (Table 2.4) and significantly higher than those of the freshwater species, further indicating salinity exposure.

Predawn water potentials of *Schinus* however remain consistently higher than those of the mangrove species and are similar to or lower than those of the freshwater species (Fig. 2.5). The water potentials indicate that either: 1) *Schinus* is utilizing water similar to the freshwater species or 2) it takes up saline water without the exclusion of salts.

Schinus having high Na^+/K^+ and high water potentials indicates that this species does not discriminate against Na^+ uptake unlike many salt-tolerant species. It is possible that this species does not have ultrafiltration mechanisms that are found in mangroves (Tomlinson 1986). By not filtering out salts, there is less of a differential in water potential between *Schinus* and its surrounding soil. This would result in high water potential but low osmotic potentials (from high salt content).

Another invasive exotic, *Tamarix ramosissima*, has also been shown to have higher Na^+/K^+ contents compared to native species (Busch and Smith 1995). The relationship between salinity and isotope composition of soil water (Fig. 2.6), however, was not sufficiently high to predict the depth or salinity of the water taken up by *Schinus*.

Schinus was less affected by seasonality as its PDWP fluctuated less over the sampling period compared to the native species (Fig. 2.5). From the wet to the dry season of 1999, water potentials of all plant species decreased except in *Schinus* (Fig. 2.5). This lowering of water potentials was probably because of a decrease in the soil osmotic potential (Fig. 2.5) during this season. *Schinus* may be able to exploit fresh or brackish water pools in the heterogeneous transition zone environment (Fig. 2.3) more successfully than the natives, hence the lack of water potential fluctuations. *Schinus* may be tapping the fresh water pockets overlying saline groundwater during the dry season

more effectively than native species, possibly via opportunistic root growth. Such a strategy along with salinity tolerance may contribute to *Schinus*' success in coastal plant communities. *Schinus* capacity of tolerating high seasonal variability in salinity and persistence under high salinity during the dry season could allow this exotic to competitively exclude freshwater species from this community.

CONCLUSION

The transition zone where *Schinus* is found shows horizontal and vertical heterogeneity in salinity. Over time, patterns of heterogeneity, are amplified by seasonal changes in: 1) fresher waters occurring in pools overlying saline groundwater and 2) in the unsaturated soil water zone salinity is at its greatest at the surface where evaporation is occurring.

Schinus shows evidence of salt tolerance but the degree of tolerance, compared to native species, needs to be further explored. Water relations of *Schinus* in the transition zone, as evidenced by predawn water potentials, seem to be buffered from seasonal changes in soil matric or osmotic potential. Compared to native species, *Schinus* has the ability to better exploit freshwater pockets in this heterogeneous zone and like mangrove species, is able to tolerate salt during water uptake. These characteristics may offer an advantage for the establishment and persistence of *Schinus* in the mangrove transition zones.

The implications of these findings are important in predicting long-term community changes within coastal areas of Florida. Sea level rise (Ross et al. 1994) can potentially cause a decrease in coastal freshwater species and an increase in mangrove

forest acreage. The conversion from one native community to another, however, will not be continuous if *Schinus* is present and able to outcompete native species in the transition zone.

Chapter 3

Seasonal water-use by the invasive exotic, *Schinus terebinthifolius*, in native and upland disturbed communities.

INTRODUCTION

There are approximately 25,000 species of exotic plants in Florida, most of which have been imported for their ornamental value (Frank et al. 1997). Among these, 900 species potentially are invasive (Ward 1989). One of the areas most threatened by invasive exotic species is the Everglades National Park. A total of 217 introduced plant species have been recorded in Everglades National Park by Whiteaker and Doren (1989), comprising 26% of the recorded number of plant species present within park boundaries.

At 688,000 ha, Everglades National Park (ENP) is one of the largest national parks in the United States. This park, at the southern terminus of the Florida Peninsula is a unique subtropical biome that consists of a diverse range of marine and terrestrial ecosystems ranging from coral reefs and mangroves to sawgrass marshes, upland pineland, and closed canopy hammock communities. The maintenance of these ecosystems is strongly influenced by the seasonal precipitation received in the Florida peninsula; approximately 75% of annual rainfall occurs between the months of May – October (Chen and Gerber 1990).

Over 65% of the original 10,000 km^2 of the marshy Everglades ecosystem have been irreversibly drained (Stephens 1974) mainly for agriculture and development. Additionally, surface water-level manipulations for year-round human activities have

resulted in dry season groundwater levels lower than in historical times (Lodge 1994). Changes in hydrology potentially might contribute to the success of invasive exotics within the ENP if native species are unable to adjust to the changes or decrease in groundwater levels.

One of the most serious biological threats to the Everglades upland ecosystem is *Schinus terebinthifolius* Raddi (*Schinus*). *Schinus* is the most widely found exotic woody species in Florida (1993 South Florida Water Management District Survey as cited in Schmitz et al. 1997), and has been classified in Category I of the Florida Exotic Pest Plant Council's List of Invasive Species (FLEPPC 2001). A plant in that category is defined as being able to alter the structure and function of native communities. Within ENP, *Schinus* is found in such hydrologically distinct communities such as upland rock pinelands (Doren and Jones 1997), sawgrass marshes (deCoster et al. 1999), and even mangrove forests (Olmsted et al. 1981). Attempts to control *Schinus* have ranged from discing, through plant and substrate removal (Koepp 1979), to burning (Loope and Dunevitz 1981), and herbicide applications (Doren et al. 1991, Ewel et al. 1982). To date, the only effective method of controlling *Schinus* is by substrate removal (Doren et al. 1990).

Schinus ecophysiology has never been contrasted with that of native species in South Florida and only one study (Burch 1992) has briefly compared water potentials of *Schinus* with a native vine. Previous studies on water uptake patterns (Ewe et al. 1999) have shown that native plants in pinelands can access deeper groundwater than can closed-canopy hammock community species. In a coastal saline transition zone of southwest Florida, based on water potentials and sodium:potassium ratios, *Schinus*

showed some characteristics of salinity tolerance (Chapter 2). In this study, I compared water uptake patterns of *Schinus* and native species in a disturbed site (where human disturbance has resulted in *Schinus* being the canopy dominant) and in a fire-managed pineland community (containing an assemblage of primarily native species) where *Schinus* is invading. I hypothesized that *Schinus* would be less affected by seasonality than native species and thus would be less physiologically constrained by hydroperiod fluctuations.

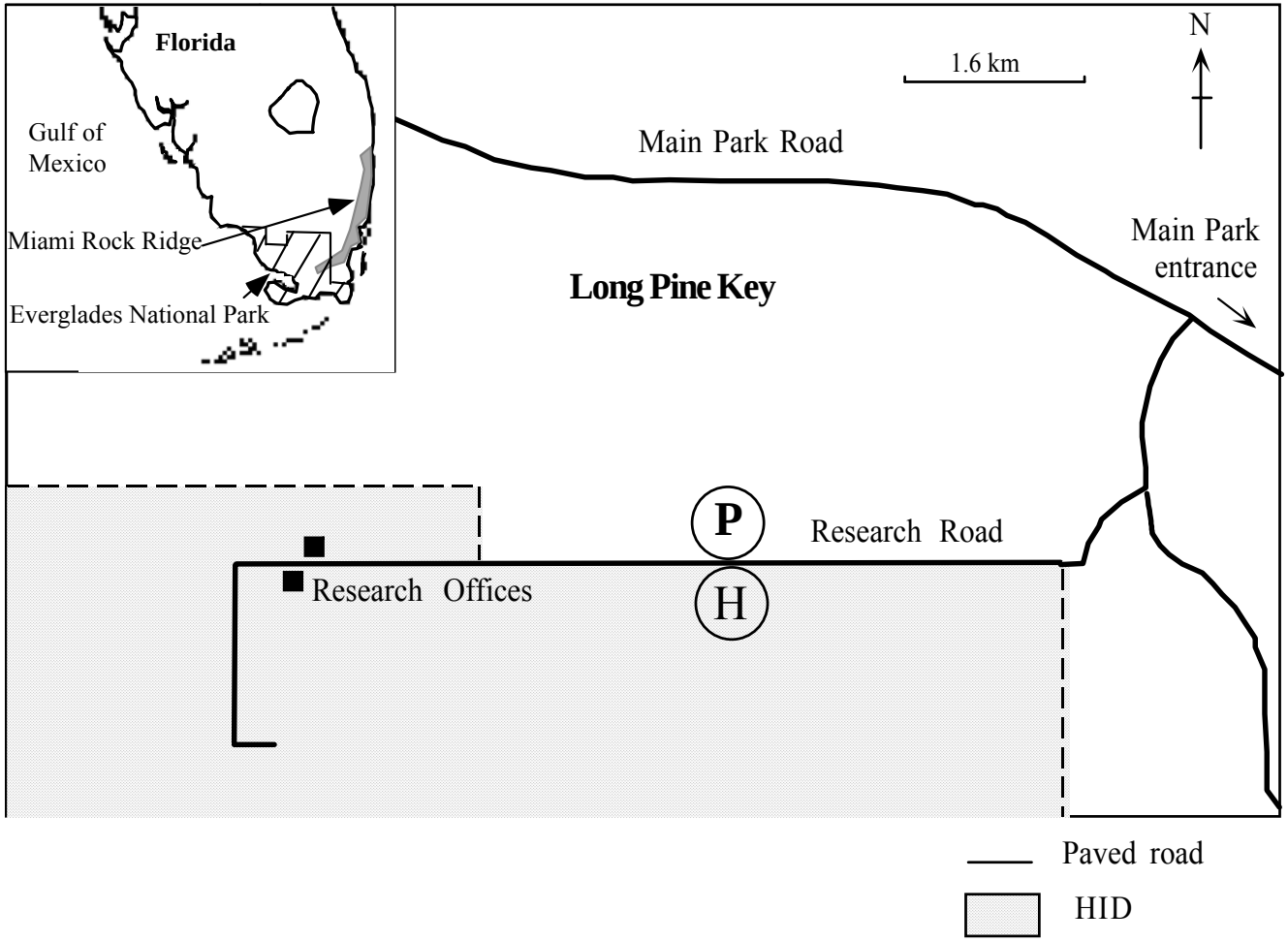
METHODS AND MATERIALS

Study site

Two adjacent study sites were selected within ENP. Both study sites are part of the Miami Rock Ridge, a rocky limestone outcrop that extends from the coast of east Florida into the Florida Everglades (Fig. 3.1, inset). The greatest elevation of the rock ridge exceeds 7.0 m at its northern terminus, but the ridge tapers to sea level at its westernmost edge (Snyder et al. 1990) within ENP. The average elevation at both study sites is about 1.0 m above sea level.

The first study site is a representative of a disturbed community, known as the Hole-in-the-Donut (HID; Fig. 3.1). The HID site, located on Long Pine Key, consists of 2,000 ha of previously farmed land that was rock-plowed early last century to provide a substrate for agriculture. This site has a mostly continuous layer of soil composed of a mix of organic matter and crushed limestone rock that ranges from less than 1 cm to over 30 cm in depth (Snyder et al. 1990). Change in substrate characteristic is believed to have prevented native plants from recolonizing this area (Olmsted and Loope 1985, Krauss

Figure 3.1. Study sites (P – pineland; H – Hole-in-the-Donut) located within the Long Pine Key (□) and Hole-in-the-Donut disturbed area (▨) in Everglades National Park. Inset: Everglades National Park (▨) on the Miami Rock Ridge (■) within Florida.



1987, Dalrymple et al. 1993). Instead of native plant succession after the cessation of farming, the area became a closed, relatively low canopy (4-5 m), dense forest of *Schinus* with an understory of *Ardisia elliptica* (Ewel et al. 1982, Dalrymple et al. 1993) and individuals of some weedy native species such as *Baccharis halimifolia*, *Myrica cerifera* and *Metopium toxiferum.* The HID site has relatively low vascular plant diversity compared to other plant communities within ENP (Olmsted et al. 1983). Currently the largest stand of *Schinus* within ENP is found in the HID.

The second study site (hereafter designated LPK) is a native rock pineland at Long Pine Key adjacent to the HID disturbed site (Fig. 3.1). Although the LPK site was farmed, it was not rock-plowed, and it has reverted to a native pineland community. The limestone stratum in the LPK site is pitted with holes and depressions. Soil, mostly of organic nature, is found only in limestone pockets and solution holes. The LPK site has an open monospecific canopy of *Pinus elliottii* var. *densa* Little and Dorman with a subcanopy of *Schinus* and several native species.

Species studied

Schinus is a dioecious shrubby evergreen perennial that grows up to about 5 m within the study sites. It is often multi-stemmed, and within the HID, forms a tangle of non-abscising branches. Within the LPK, *Schinus* water uptake pattern was compared to those of four native species − *Myrica cerifera* L. (Myricaceae), *Baccharis halimifolia* L. (Asteraceae), *Rapanea punctata* (Lam.) Lundell (Myrsinaceae) and *Randia aculeata* L. (Rubiaceae). All native species were multi-stemmed evergreen perennials commonly found in upland pineland areas. *Myrica cerifera* and *B. halimifolia* were also found in

disturbed habitats. Study species within the LPK were mostly small and shrubby because of park fire management practices; individuals of these species resprout after fires. Only two native species (*M. cerifera* and *B. halimifolia*) were compared to *Schinus* in the HID, as *R. punctata and R. aculeata* were not prevalent within this community. Five individuals of each species were labeled at each site, and water uptake measured for these same individuals every season.

Soil measurements

Five soil samples were collected from each site every sample period. Surface litter was removed before collecting the mineral soil. Single groundwater samples were collected from a well in a nearby pineland (< 2 km distant) at the end of the wet (2 May 1998) and dry (7 November 1998) season; groundwater depth was measured at time of sampling. After cryogenic extraction of water for stable isotope analysis, the dried soil samples were weighed before being ashed at 550°C over night. Soil water content was determined using the equation:

Water content (%) = [(Wet-Dry soil weight)/ Dry soil weight] x 100%

Soil organic content was determined by the following equation:

Organic content (%) = [1-(Soil weight post-ashing/Soil weight pre-ashing)] x 100%

Stable isotope analysis

Small (less than 1 cm in diameter), fully suberized plant stem sections were collected between 0900 - 1100 hrs on the sampling dates (2 May 1998, 7 Nov 1998). Where possible, plant sections proximal to the terminal tips but without leaves were

selected. Each plant or soil sample was stored individually in 50 ml Borosilicate tubes, sealed with Parafilm and taken to the Stable Isotope Laboratory of the Biology Department at the University of Miami where they were immediately frozen. Stem water was then cryogenically extracted. Oxygen stable isotope signatures of all samples were determined according to the methods of Epstein and Mayeda (1953); an isotope-ratio gas mass spectrometer (VG Prism, Micromass, Middlebury, England) was used to analyze the purified gas. Isotopic abundance was expressed in per mil units (‰) according to the following equation:

$$\delta^{18}O\ (‰) = [(R_{sample}/R_{standard}) - 1]\ 1000$$

where R_{sample} was the $^{18}O/^{16}O$ ratio of the sample and $R_{standard}$ was the $^{18}O/^{16}O$ ratio of standard mean ocean water (SMOW). Stable isotope values were then used to determine the fraction of deep groundwater usage versus shallow soil water using a modification of the end-member model (White et al. 1985), with the equation below:

$$\%\ \text{groundwater} = \frac{(\delta_{plant} - \delta_{soil})}{(\delta_{ground} - \delta_{soil})} \quad x\ 100\%$$

where δ_{plant} = isotope signature of the stem sample, δ_{soil} = isotope signature of soil water and δ_{ground} = isotope signature of groundwater.

Predawn water potentials

Predawn water potentials were measured at the end of three consecutive seasons, for two dry seasons (2 May 1998, 8 May 1999) and the intervening wet season (7 November 1998). The evening before sampling, each plant was individually tagged with electronic blinkers to facilitate plant identification during the predawn (0300 – 0600 hr) hours. To measure plant xylem water potentials, small (less than 15 cm in length) living

terminal stems were collected and immediately measured with a pressure chamber (PMS 600, PMS Instruments, Corvallis, Oregon).

Diel water potentials

Water potentials of plant stems were measured at approximately three hour intervals over a 24-hour period at the end of a dry (8-9 May 1998) and wet season (5-6 December 1998). Conspecific nearest neighbors of permanently tagged plants (usually < 1 m distant) were selected for sampling to prevent damage to marked individuals. Once again, small stems as collected for predawn water potentials were selected for measurement.

Statistical analyses

An analysis-of-covariance (ANCOVA) was used to examine the effect of season and site on soil water content with soil organic content as the covariate. For each season, plant percent groundwater usage based on isotopic signatures was compared to total groundwater (100%) by arcsine-transforming all values and using modified t-tests (Sokal and Rohlf 1998) to determine if significant amounts of soil water were utilized. For each site, PDWP differences among species and across seasons were analyzed with a two-factor Model I analysis-of-variance (ANOVA). For species common to both sites, differences among species, across sites, and between seasons were analyzed using three-factor ANOVA. A parallel set of analyses was carried out on diel water potential data. Parameters that were significant were further analyzed using post-hoc Bonferroni pairwise comparisons of means. All statistical analyses were carried out either using

SPSS 8.0.0 (SPSS Inc., Chicago, IL) or Statistix 7.0 (Analytical Software, Tallahassee, FL).

RESULTS

Soil measurements

The ANCOVA showed that soil water content was related to its organic content ($F_{1,15} = 18.96$, $P < 0.01$). The main effect of season was significant ($F_{1,15} = 37.10$, $P < 0.01$); soils had less water in the dry season than in the wet. No significance was observed, however, across sites ($F_{1,15} = 0.40$, $P > 0.10$) or for the interaction of site x season ($F_{1,15} = 0.21$, $P > 0.10$). Groundwater depths fluctuated with season, ranging from 0.12 m (7 Nov 1998) at the end-of-wet-season sampling to 1.54 m (2 May 1998) at the end-of-dry-season sampling.

Stable isotope analysis

Ground and soil water stable isotope signatures at both the LPK and HID sites were significantly different each season (Fig. 3.2). Groundwater was isotopically depleted compared to soil water. Soil water was more enriched in ^{18}O during the dry season than the wet season, and $\delta^{18}O$ ratios were consistently higher in the LPK site compared to the HID site.

Plant percent groundwater use analyses showed that in the dry season, all species at both sites relied predominantly on groundwater (Table 3.1, Fig. 3.2). In the wet season, most species, including *Schinus* at the HID site, shifted to using more soil water at both sites. The overall increase in soil water usage by all species in the HID site during the wet

Figure 3.2. Oxygen stable isotope ($\delta^{18}O$) signatures (± SEM) of plants from each site during the wet and dry seasons. The line within the rectangle represents the mean isotopic composition of soil water while the rectangle (□) represents the standard error of the mean. The solid thick line represents the groundwater stable isotope signature. Groundwater isotopic signatures are significantly different from those of soil water for both sites each sample season. Asterisks (*) indicate species that are utilizing significant ($P < 0.05$) amounts of soil water (see Table 3.1). Each species is denoted as such: *Schinus terebinthifolius* (○), *Myrica cerifera* (□), *Baccharis halimifolia* (◇), *Rapanea punctata* (△) and *Randia aculeata* (×).

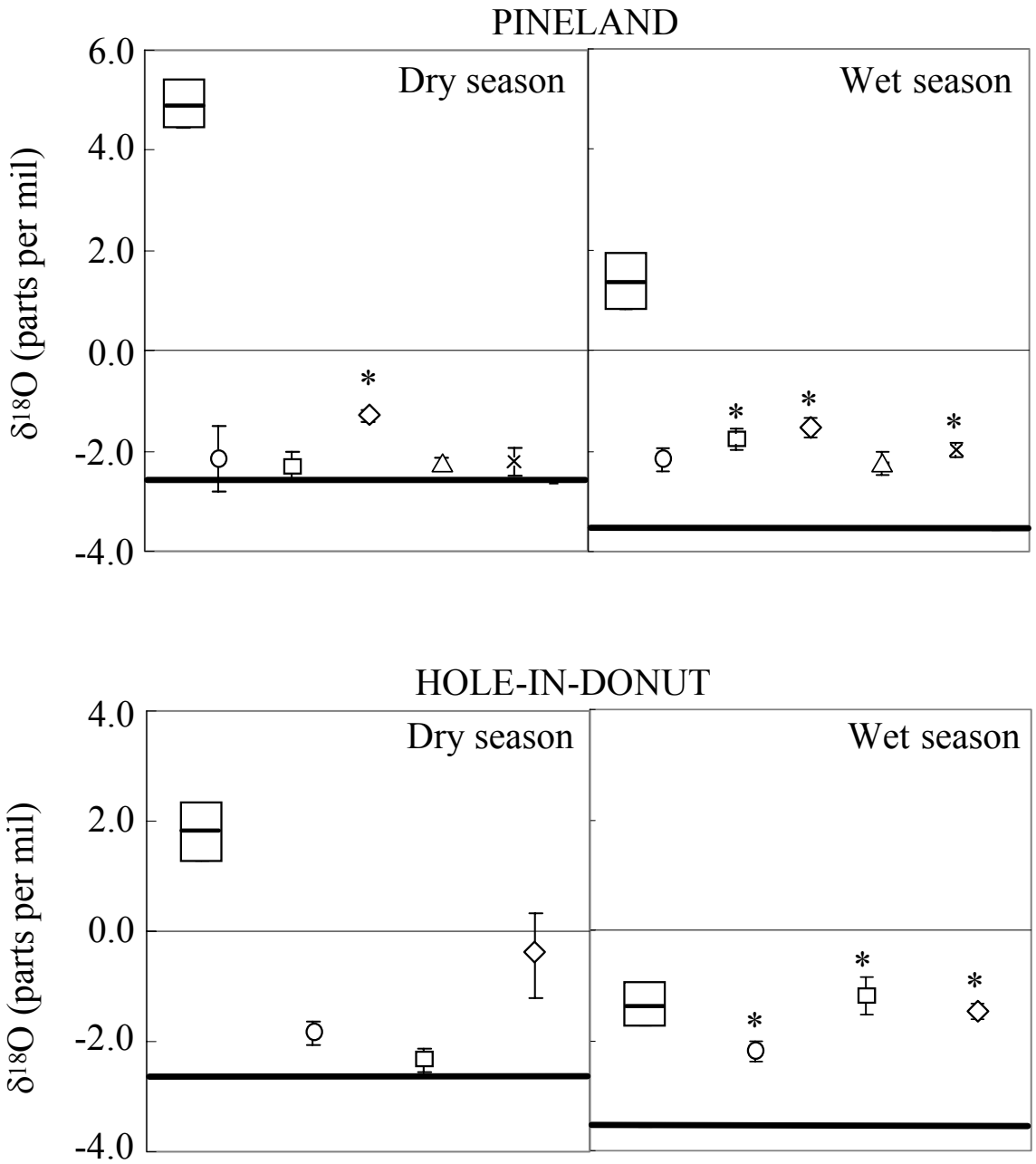

PINELAND
Dry season
Wet season
6.0
4.0
2.0
0.0
-2.0
-4.0
δ18O (parts per mil)
HOLE-IN-DONUT
Dry season
Wet season
4.0
2.0
0.0
-2.0
-4.0
δ18O (parts per mil)

Table 3.1. Percent groundwater usage (± SEM) by plant species in both study sites during the dry and wet seasons. Asterisks (*) indicate significant difference at the $P < 0.025$ level of the arcsine-transformed values from 100% groundwater usage using a modified one-tailed t-test (Sokal and Rohlf 1998).

Species	Dry season 1998		Wet season 1998	
	n	% groundwater usage	n	% groundwater usage
Pineland				
Schinus terebinthifolius	5	93.72 ± 19.29	5	72.03 ± 10.86
Myrica cerifera	5	95.56 ± 7.93	5	63.53 ± 9.38*
Baccharis halimifolia	5	82.41 ± 3.89	5	59.13 ± 8.88*
Rapanea punctata	5	95.16 ± 3.38	5	73.61 ± 10.16
Randia aculeata	4	94.65 ± 7.60	5	67.3 ± 5.90*
Hole-in-the-Donut				
Schinus terebinthifolius	5	82.28 ± 10.38	5	38.60 ± 18.73*
Myrica cerifera	5	93.76 ± 11.20	5	11.64 ± 16.07*
Baccharis halimifolia	5	50.44 ± 35.2	5	5.98 ± 10.01*

season was approximately 57% (Table 3.1). In the LPK site, only *Schinus* ($t_s = 2.351$, $P > 0.05$) and *R. punctata* ($t_s = 2.323$, $P > 0.05$) did not show significant seasonal shifts from ground to soil water uptake (Table 3.1, Fig. 3.2). At the end of the wet season, all native species use of soil water increased by an overall 26% in the LPK site compared to the dry season.

Predawn water potentials (PDWP)

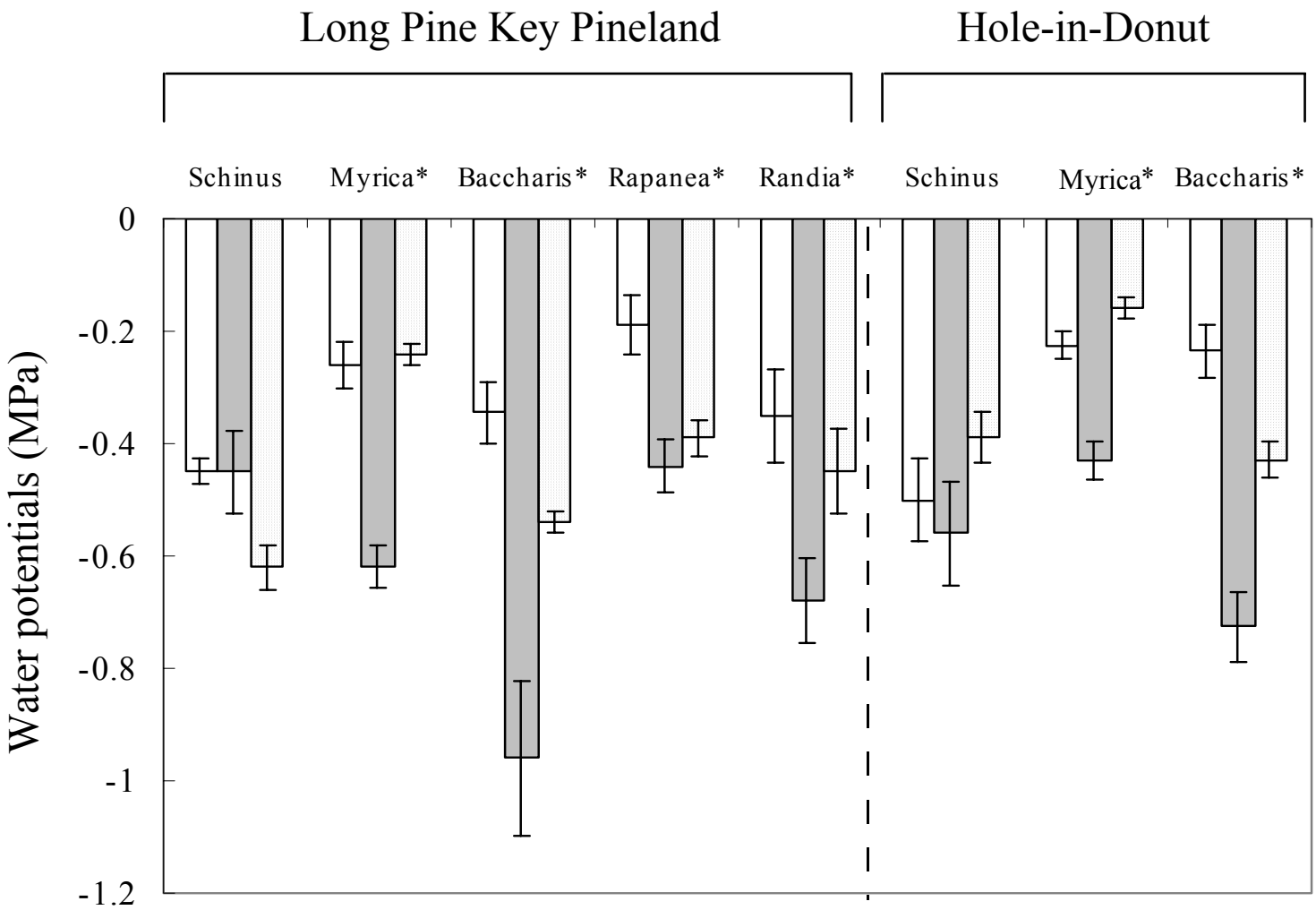
Within-site PDWP comparisons showed differences ($P < 0.05$) among species, across seasons as well as a significant interaction between species and season in both sites (Table 3.2). Post-hoc Bonferroni comparisons showed that significance of the interactions at both sites was attributable to higher PDWP during the 1998 and 1999 dry seasons than the wet season for native species (Fig. 3.3). This pattern was significant in *M. cerifera*, *B. halimifolia*, *R. punctata* and *R. aculeata* in the LPK site, and in both *R. punctata* and *R. aculeata* at the HID site. *Schinus* water potentials, however, remained constant over season at both sites. *Schinus* water potentials for both dry seasons were lower than those of native species (Fig. 3.3), but during the wet season, *Schinus* water potentials were similar to or higher than those of native species.

Predawn water potential of *Schinus, M. cerifera* and *B. halimifolia* in both sites when analyzed with a three-factor Model I ANOVA, showed significant ($P < 0.05$) species, site and seasonal differences (Table 3.3). In addition, there was an interaction of species with season as well as a significant interaction of all three factors. Post-hoc analyses showed that wet season PDWP values were lower than those of the dry season in the two native species but not *Schinus* at either site (Fig. 3.3). *Myrica cerifera* and *B.*

Table 3.2. Two-factor ANOVAs of predawn water potentials for plants in the: a) Long Pine Key pineland and b) Hole-in-the-Donut disturbed site.

	a) Long Pine Key pineland				b) Hole-in-the-Donut			
	df	Mean Squares	F	*P*	df	Mean Squares	F	*P*
Species	4	18.399	9.427	<0.001	2	20.456	14.653	<0.001
Season	2	61.036	31.274	<0.001	2	30.891	22.128	<0.001
Species x Season	8	9.775	5.009	<0.001	4	6.600	4.728	0.004
Error	60	1.952			36	1.396		

Figure 3.3. Predawn water potential (± SEM) in both study sites over three seasons. Clear bars (□) represent samples from the dry season of 1998, gray bars (■) represent samples from the wet season of 1998, and the dotted bars (▤), samples from the dry season of (1999). Two-factor ANOVAs were used to analyze seasonal differences across species within each site. Asterisks (*) indicate significant seasonal differences within species using post-hoc Bonferroni comparison of means.


Long Pine Key Pineland
Hole-in-Donut
Schinus
Myrica*
Baccharis*
Rapanea*
Randia*
Schinus
Myrica*
Baccharis*
Water potentials (MPa)
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2

halimifolia in the HID had higher dry season water potential compared to LPK plants; no site differences were observed for *Schinus* (Fig. 3.3).

Diel water potentials

For all species, water potential decreased during the daytime hours and increased at night, peaking during the predawn hours; this pattern was consistent for all species measured over both sites for the two seasons sampled. Daily extremes (i.e. predawn – midday) of water potentials were calculated to determine the degree of diel change (Fig. 3.4). Within each study site, two-factor Model I ANOVAs showed differences among species ($P < 0.05$); seasonal differences were only found in the HID ($P < 0.05$) (Table 3.4). Post-hoc comparisons revealed that in the LPK, significance among species was because of differences between *Schinus* and *R. aculeata*, while in the HID it was because of differences between *Schinus* and *B. halimifolia* (Fig. 3.4). In the HID, overall wet season daily extremes were greater than in the dry season.

For the three species sampled in both sites (*Schinus, M. cerifera* and *B. halimifolia*), a three-factor Model I ANOVA (Table 3.3) showed a significant difference in daily extremes of water potential for species, but not between sites or season. The species difference was in part because of smaller daily extremes in the water potentials of *Schinus* than those of *M. cerifera* and *B. halimifolia* at either site for both seasons sampled. *Schinus* changes differed significantly from those of native species, however, only in the HID in both wet and dry seasons (Fig. 3.4).

Figure 3.4. Wet and dry season predawn-noontime water potential differences (± SEM) of *Schinus terebinthifolius* (□), *Myrica cerifera* (▫), *Baccharis halimifolia* (■), *Rapanea punctata* (▨) and *Randia aculeata* (▧) in the Long Pine Key pineland (LPK) and Hole-in-the-Donut (HID) sites. Values followed by the same letter within a site do not differ significantly at the $\alpha = 0.05$ level using a post-hoc Bonferroni comparison of means after analysis with a two-factor ANOVA.

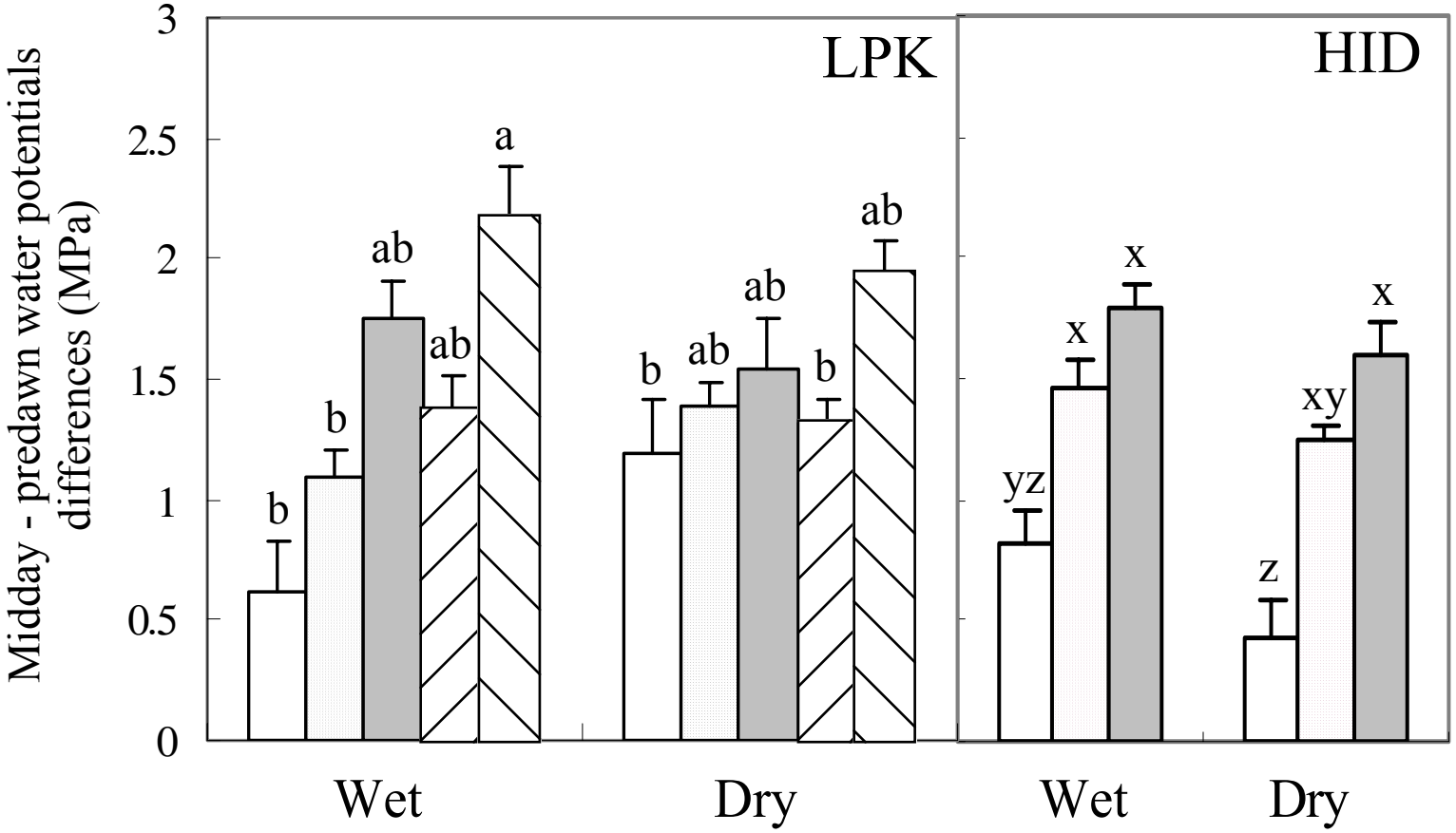

Midday - predawn water potentials differences (MPa)
3
2.5
2
1.5
1
0.5
0
LPK
HID
b
b
ab
ab
a
b
ab
ab
b
ab
yz
x
x
z
xy
x
Wet
Dry
Wet
Dry

Table 3.3. Results of three-factor Model I ANOVAs showing differences in predawn (3 seasons) and diel (2 seasons) water potential among species, site, and season.

	Predawn water potentials (MPa)				Diel water potentials (MPa)			
	df	Mean Squares	F	*P*	df	Mean Squares	F	*P*
Species	2	39.282	23.876	<0.001	2	4.198	35.960	<0.001
Site	1	19.182	11.659	0.001	1	0.023	0.197	0.659
Season	2	69.324	42.136	<0.001	1	0.008	0.065	0.800
Species x Site	2	3.153	1.916	0.155	2	0.227	1.947	0.154h
Species x Season	4	20.362	12.376	<0.001	2	0.135	1.159	0.322
Site x Season	2	2.304	1.401	0.253	1	0.907	7.765	0.008
Species x Site x Season	4	4.405	2.678	0.038	2	0.291	2.495	0.093
Error	72	1.645			48	0.117		

Table 3.4. Two-factor ANOVAs of species and season differences in daily extremes of diel water potentials at the: a) Long Pine Key pineland site and b) Hole-in-the-Donut disturbed site.

	a) Long Pine Key				b) Hole-in-the-Donut			
	df	Mean Squares	F	*P*	df	Mean Squares	F	*P*
Species	4	1.871	13.128	<0.001	2	3.034	39.934	<0.001
Season	1	0.068	0.480	0.492	1	0.540	7.107	0.014
Species x Season	4	0.318	2.228	0.083	2	0.026	0.336	0.718
Error	40	0.143			24	0.086		

DISCUSSION

Soil water availability fluctuated with season, with greater water availability in the soil during the wet season than in the dry season at both sites. For both seasons, soil water was isotopically more enriched in the LPK site than in the HID site (Fig. 3.2), probably because of greater evaporative rates under the open canopy of the pineland. Although there was no aboveground flooding at either site, soils at both sites appeared to be saturated during the wet season. Seasonal changes in water uptake based on stable isotope data of the LPK (Fig. 3.2) agree with the findings of Ewe et al. (1999) from a nearby pineland. Inferring from stable isotope data, three of the four native species sampled (*M. cerifera*, *B. halimifolia* and *R. aculeata*) in the LPK site shifted from deep groundwater to shallow soil water usage in the wet season, but this shift was not significant in *Schinus*. In the HID site, all species including the exotic exhibited a significant degree of ground to soil water use shift compared to the pineland species. At the end of the wet season, soil water usage increased from 43 to 82% in the HID site. Seasonal soil water usage shift in the HID site compared to the LPK site was most likely because of more soil development at the HID than LPK site. The disturbed HID site had a deeper and more continuous soil layer than the pineland in which soil was mostly found only in limestone pockets.

Unlike the Ewe et al. (1999) study, plant PDWP in the wet season at the LPK site did not reflect increased water availability by a reduction of PDWP (Fig. 3.3). Instead, despite greater soil water content during the wet season, all native species actually showed a decrease in predawn water potentials (Fig. 3.3) from the 1998 dry to wet season. Similar to native species in the LPK site, natives in the HID site also had

decreased water potentials during the wet season despite utilizing shallow soil water. This counterintuitive water potential response of LPK and HID native species to greater soil water availability than in the dry season could be because of intolerance to root flooding. The sites studied here are at slightly lower elevations than those studied by Ewe et al. (1999). Therefore, plants in this study may have been exposed to root flooding during the wet season. Although the plants sampled in this study did not appear to have physical symptoms of flood stress (e.g. wilting, leaf abscission, chlorosis), studies (e.g. Kozlowski and Pallardy 1984, Reid and Bradford 1984) have shown that sometimes, despite no outward aboveground morphological damage, physiological alterations and root dieback can occur when plant roots are submerged for prolonged periods. Flood-intolerant plants also have been shown to have decreased gas exchange capacity and low water potentials when plant roots are flooded (Naidoo 1983 and 1985, Kozlowski and Pallardy 1984). Thus, it is likely that native species from both sites are adversely affected by the abundance of water in and around their roots during the wet season.

Unlike native species in the LPK and HID sites, *Schinus* does not have significantly different predawn water potentials (Fig. 3.3) between seasons. If the above hypothesis of flood-induced water stress is correct, then the lack of PDWP response to increased amounts of observed soil water during the wet season by *Schinus* indicates that the exotic is more tolerant of root flooding than native species. It is possible that this exotic could have adaptations to flooding such as the internal maintenance of aeration via aerenchyma cells and presence of soil roots (Hook 1984). Soil roots, as defined by Hook (1984) are roots tolerant of flooding that regenerate after death of original root system. During the wet season, *Schinus* also had the smallest diel differences of all species at both

sites (Fig. 3.4). This finding is consistent with the hypothesis that *Schinus* is less affected by flooding than native species.

Contrary to expectation, these plant water potential data demonstrate that the wet season may stress native species more than the dry season in our two study sites. Findings from this study support the hypothesis that *Schinus* water relations are less affected by seasonality than native species, as observed in the saline transition zone of coastal southwest Florida (Chapter 2). Invasion of exotics into the Long Pine Key pinelands of Everglades National Park may have been facilitated inadvertently by human manipulation of water levels in South Florida. The water uptake patterns observed in native and exotic plants sampled suggest that the exotic may be favored over native species that are being physiologically stressed by root flooding during the wet season.

Chapter 4

Seasonal gas exchange by the invasive exotic *Schinus terebinthifolius* versus coastal native coastal plant species in Florida.

INTRODUCTION

Schinus terebinthifolius Raddi (*Schinus*) is an invasive exotic widely found in Florida. Introduced from South America over a hundred years ago as an ornamental, this species is now found throughout subtropical North America. It is an aggressive invader of both native and disturbed habitats (Doren et al. 1991). *Schinus* is the most widely found invasive exotic woody species in South Florida. This exotic occurs in over 280,000 ha of both disturbed and native plant communities of Florida (1993 South Florida Water Management District Survey as cited in Schmitz et al. 1997), ranging from upland pinelands (Ewel et al. 1982, Olmsted and Loope 1985, Doren et al. 1990) to coastal mangrove habitats (Mytinger 1985, Mytinger and Williamson 1986).

Many reasons (e.g. life history, reproductive biology, lack of herbivory, genetics, dispersal) have been cited as explanation for invasive species success (Cronk and Fuller 1995, Luken and Thieret 1997). Plant ecophysiology, explaining the underlying physiological mechanisms for observed ecological responses, has also been proposed as a possible explanation to plant success. Ecophysiological studies (e.g. Schierenbeck and Marshall 1993**,** Polley et al. 1994, Yamashita et al. 2000) have shown that gas exchange patterns often can potentially contribute to an invasive species' success. Plant gas exchange has been shown to be often related to its growth and biomass allocation

(Lambers and Poorter 1992). For example, a plant with high net CO_2 uptake (*A*) has the potential to assimilate carbon at a higher rate than a species with low *A* (Lambers et al. 1998). With limited water availability, a plant with high water-use efficiency (WUE) has the capacity to assimilate carbon with a lower rate of water loss, indicative of more efficient resource use. Carbon isotope signatures ($\delta^{13}C$) have been used in ecological studies (e.g. Sun et al. 1996, Damesin et al. 1998, Nativ et al. 1999) as they are positively related to a plant's long-term water-use efficiency (integrated WUE) (Farquhar et al. 1982a, Goldstein et al. 1989). Photosynthetic nitrogen-use efficiency (PNUE) is another parameter often used to assess plant function as it is positively correlated with growth (e.g. Mooney et al. 1978, Lambers and Poorter 1992).

This study was carried out in an ecosystem where *Schinus* was a co-dominant species. The two communities compared were a saline transition zone (between mangroves and pineland) and an upland seasonally brackish pineland. The goal of this study was to contrast gas exchange patterns of *Schinus* with native species in these two communities. In South Florida, seasonal rainfall causes fluctuating soil salinity (Chapter 2). In the wet season, high rainfall results in low soil salinity but in the dry season salinity increases due to evaporation. Salinity is an external stress to plants living in arid or coastal areas. Plant gas-exchange responses to salinity have included reduced gas exchange capacity and decreased nutrient uptake (Ball and Farquhar 1984, Huang et al. 1996, Ma et al. 1997, Sohan et al. 1999).

I hypothesized that *Schinus* gas exchange could potentially contribute to its success in a coastal environment. The specific hypotheses I tested were:

1. *Schinus* has higher *A*, WUE, and PNUE than native species in both study sites, and

2. *Schinus* gas exchange, WUE, and PNUE in the transition zone are less affected by seasonality compared to those of native freshwater species (i.e. low dry-wet season flux).

If the findings supported the hypotheses the implications are that *Schinus*, being less affected by seasonality, could potentially outcompete native species and dominate this coastal environment. If the findings did not support the hypotheses, it is likely that *Schinus* gas exchange and PNUE do not confer an advantage for the exotic's ability to invade coastal ecosystems.

METHODS AND MATERIALS

Study sites

The two study sites were located on the southwest coast of Florida (Fig. 2.1, inset) in Rookery Bay National Estuarine Research Reserve. This reserve is approximately 6,000 ha in size and is composed of both upland and shallow marine habitats. The two study sites are located near Henderson Creek that empties into Rookery Bay (Fig. 2.1). South Florida rainfall is strongly seasonal (Chen and Gerber 1990); approximately 75% of the annual rainfall (average = 1450 mm) occurs during the wet season (May-October). In the wet season, belowground runoff from inland areas result in significant belowground freshwater inputs to both study sites but during the dry season this freshwater source is depleted resulting in seawater mixing with groundwater

The first study site is in a coastal transition zone between mangroves and an upland pineland. This transition zone (26°02.6'N, 81°42.6'W) is exposed to belowground salinity from the fluctuating groundwater table, resulting in groundwater that reaches 25

parts per thousand (p.p.t.). Despite seasonal exposure to salinity this transition zone has both mangroves and pineland species, probably because of the spatial heterogeneity of pore water salinity (See Chapter 2 for more a complete description). In addition to *Schinus*, other co-dominant species include *Rhizophora mangle L.* (Rhizophoraceae), *Laguncularia racemosa* (L.) Gaertn. f. (Combretaceae), *Rapanea punctata* (Lam.) Lundell (Myrsinaceae) and *Randia aculeata* L. (Rubiaceae).

The second study site is an upland sandy pineland (26°02.8'N, 81°43.1'W) that is only exposed to brackish groundwater during the dry season. Groundwater at this site reaches 9 p.p.t. in the dry season. Soil water availability varies seasonally in both sites (Chapter 2); there is more water in the soil during the wet season than the dry. There is also more water within soils in the transition zone than the pineland each season (Chapter 3). Soil salinity in the transition zone is consistently higher than in the pineland. The dominant canopy species within the pineland is slash pine, *Pinus elliottii* var. densa Little and Dorman. The subcanopy consists of *Schinus* and native species such as *Rapanea punctata*, *Randia aculeata* and *Sabal palmetto.*

Species sampled

In addition to the exotic, four other native woody species were sampled (Table 4.1). All species were major components of the community. Only three species (*Schinus*, *R. punctata, R. aculeata*) were sampled in the upland pineland in the absence of the mangrove species. At both sites, *Schinus* forms a multi-stemmed, spreading small tree. *Rhizophora mangle* and *L. racemosa*, the two mangrove species, attain tree-form. The two freshwater species, *R. punctata* and *R. aculeata* are commonly found in pinelands

Table 4.1. Species sampled at the two different study sites.

Species sampled	Transition zone	Upland pineland
Schinus terebinthifolius	X	X
Rhizophora mangle	X	
Laguncularia racemosa	X	
Rapanea punctata	X	X
Randia aculeata	X	X

(Tomlinson 1980). *Rapanea punctata* is also a common species in closed canopy hammock communities. These latter two species form small trees but some individuals only attained shrub stature at both study sites. Leaf production of all study species was observed to be seasonal; leaves were produced continuously during the wet season but reduced during the dry season. Leaf expansion was continuous much of the year; young leaves produced at the end of wet season continued to mature despite the dry season.

Gas exchange measurements

Gas exchange measurements were made using a portable gas exchange system (LI-6200, LiCor, Lincoln, Nebraska). Measurements were carried out over a two-day period at the end of the dry (April 19 and 20 1999) and wet (28 Nov and 6 Dec 1999) seasons. One site was measured each day. Five individuals per species were sampled at each site and the same plant was measured every season. Measurements were made between 930 – 1600 hrs, after the dew had evaporated from leaf surfaces, and ended when light levels at the sample leaves were less than 1000 μmols m^{-2} s^{-1}. Plants were sampled continuously on a rotation basis. For each plant, the second fully expanded leaves from the tips of lateral branches exposed to full sunlight were sampled.

After equilibrating the 1000 ml^3 gas exchange chamber to a leaf's external environment, the chamber was clamped onto the leaf for 60 seconds to measure instantaneous gas exchange. In cases where leaves were damaged or became detached during sampling, other leaves of similar branch locations at the same or adjacent shoots were selected. At the end of each sampling day, all leaves were harvested, individually bagged and returned to the Stable Isotope Laboratory at the Biology Department,

University of Miami. Individual leaf area was measured on a leaf area meter (LI-3000, LiCor, Lincoln, Nebraska). Leaves were dried in a benchtop freeze-dry system (Labconco, Kansas City, Kansas) at -95°C and 10 μm Hg for one week and leaf dry weight measured. Specific leaf area (SLA, $m^2\ g^{-1}$) was determined by dividing leaf area by weight. Measurements from each individual plant were averaged to provide one value for each parameter. Leaf mesophyll conductance (g_m, $m\ s^{-1}$) was determined by dividing assimilation (A, μmol $CO_2\ m^{-2}\ s^{-1}$) by internal leaf CO_2 concentration (c_i, μmol $CO_2\ m^{-3}$). Intrinsic water-use efficiency (WUE, μmol CO_2 mol H_2O^{-1}) was calculated by dividing A by stomatal conductance (g_s, mol $H_2O\ m^{-2}\ s^{-1}$). Leaves were then individually frozen in liquid nitrogen and ground with a mortar and pestle for use in carbon isotopic and nitrogen analyses.

Stable isotope analyses

Subsamples (approximately 5 mg) of ground leaves were prepared based on the method described by Buchanan and Corcoran (1959) and analyzed using an isotope-ratio gas mass spectrometer (VG Isogas, Middlebury, England). Isotopic abundance (parts per mil (‰)) was expressed as:

$$\delta^{13}C = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000$$

where R_{sample} is the $^{13}C/^{12}C$ ratio of the sample and $R_{standard}$ is the $^{13}C/^{12}C$ ratio of a laboratory standard as referenced to Pee-Dee Belemnite. For multiple leaves taken from a tree, subsamples were combined to provide a single sample prior to sample preparation.

Nitrogen analyses

For the 1999 dry season, nitrogen content was analyzed using the Kjedahl method; leaf nitrogen content for the 1999 wet season was determined using an elemental analyzer (Carlo-Erba NC2100, ThermoFinnigan Italia S.p.A., Milan, Italy). As the Kjedahl technique volatilizes ammonia (< 1% total N) in the sample (Binkley and Vitousek 1989), Kjedahl readings were subsequently standardized to the elemental analyzer values by re-analyzing some dry season leaf subsamples on the elemental analyzer. Leaf nitrogen concentration expressed on a leaf area basis ([N], g N m^{-2} leaf), was then used to determine photosynthetic-nitrogen-use-efficiency (PNUE, μmol CO_2 g^{-1} s^{-1}) by dividing *A* by [N].

Statistical analyses

Seven variables (*A*, [N], g_s, g_m, A/g_s, $\delta^{13}C$, PNUE) were analyzed. For each site, differences across seasons and among species were analyzed with a two-factor Model I analysis-of variance (ANOVA). For *Schinus*, *R. punctata*, and *R. aculeata*, species, season and site differences were analyzed using a three-factor fixed-effects (Model I) ANOVA. For all analyses and post-hoc tests, probability of Type I error was Bonferroni corrected for the number of variables (i.e. $\alpha = 0.05/7$, $P < 0.0071$). All data were analyzed using SPSS-X Version 8.0 (SPSS Inc., Chicago, IL). Factors that were significant were tested using post-hoc Tukey HSD pair-wise comparisons of means using either SPSS-X V8.0 or Statistix 7.0 (Analytical Software, Tallahassee, FL).

RESULTS

Gas exchange and leaf characteristics

There were significant seasonal and species differences in *A* at both study sites (Table 4.2). Assimilation rates increased from the dry to the wet season (Table 4.3), the magnitude of increase being greatest in *Schinus* and *R. punctata* in the transition zone sites.

In the dry season *Schinus* had the lowest *A* recorded (0.74 ± 0.16 μmol CO_2 m^{-2} s^{-1}), similar to native freshwater species in the transition zone and lower than the mangrove species. During the wet season however, *Schinus A* was similar to *R. mangle, R. aculeata* and *R. punctata*, although lower than *L. racemosa* (Table 4.3). In the upland pineland, species differences were from higher *A* in *R. aculeata*. For the three species sampled across sites, each independent factor and a species x site interaction was significant (Table 4.4). Overall, *Schinus A* was lower than native species. Plants within the transition zone also had lower *A* than the upland pineland, and *A* was lower during the dry than wet season regardless of site (Table 4.3).

Nitrogen concentration on a leaf area basis ([N]) was significantly different among species at both sites; there was also a species x season interaction in the transition zone (Table 4.2). Within the transition zone, [N] either remained constant or increased from dry to wet season in all native species (Table 4.3). *Schinus* [N] however, decreased (although not significantly) during that period. Nitrogen concentration of *Schinus* in the upland pineland was similar to that of *R. punctata*; both species had lower [N] than *R. aculeata.* Comparison of [N] across sites showed significant species x site and species x season interactions (Table 4.4). For both seasons combined, transition zone *Schinus* and

Table 4.2. Two-factor (between species and season) Model I ANOVA of: 1. Assimilation, *A* (μmol CO_2 $m^{-2}s^{-1}$); 2. Nitrogen concentration on a leaf area basis, [N] (g N m^{-2} leaf); 3. Stomatal conductance, g_s (mol H_2O $m^{-2}s^{-1}$); 4. Mesophyll conductance, g_m (m s^{-1} x 10^{-5}); 5. Intrinsic water-use efficiency, A/g_s (μmol CO_2 mol H_2O^{-1}); 6. Carbon stable isotope signatures, $\delta^{13}C$ (‰) and 7. Photosynthetic nitrogen-use efficiency, PNUE (μmol CO_2 g N^{-1} s^{-1}) in both study sites. Numbers in bold are significant at the $P < 0.0071$ ($\alpha = 0.05/7$) level.

	Season				Species				Species x Season				Error	
	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*	df	MS
1.*A*														
Transition zone	1	134.	21.7	**<.001**	4	62.2	21.4	**<.001**	4	9.9	1.6	.217	20	6.222
Pineland	1	96.6	38.8	**<.001**	2	18.0	9.3	**.004**	2	0.78	0.31	.737	12	2.488
2. [N]														
Transition zone	1	.013	4.6	.046	4	.001	10.1	**<.001**	4	.017	6.4	**.002**	18	0.003
Pineland	1	.005	.054	.821	2	.015	10.1	**.004**	2	.001[4]	.50	.626	10	0.001
3. g_s														
Transition zone	1	.086	30.1	**<.001**	4	.025	11.8	**<.001**	4	.005	1.8	.176	20	0.003
Pineland	1	.26	68.9	**<.001**	2	.023	9.5	**.003**	2	.007	1.96	.183	12	0.004
4. A/c_i														
Transition zone	1	4.2	15.9	**.001**	4	3.9	34.0	**<.001**	4	.59	2.2	.103	20	0.267
Pineland	1	1.3	16.3	**.002**	2	.386	4.9	.028	2	.06	.81	.468	12	0.078
5. A/g_s														
Transition zone	1	10.5	.059	.811	4	589.	3.7	.021	4	815.	4.6	**.003**	20	178.278
Pineland	1	5866	72.1	**<.001**	2	496.	9.5	**.003**	2	1163	14.3	**.001**	12	81.346
6. $\delta^{13}C$														
Transition zone	1	3.8	3.5	.080	4	5.4	5.0	.008	4	.088	.082	.987	16	1.083
Pineland	1	3.9	2.4	.146	2	2.4	6.6	.012	2	.402	.250	.783	12	1.610
7. PNUE														
Transition zone	1	16.6	9.6	**.006**	4	7.2	7.1	**.001**	4	2.2	1.3	.313	18	1.732
Pineland	1	36.7	25.2	**.001**	2	.16	.13	.879	2	1.3	.89	.440	10	1.456

Table 4.3. Species average (± SEM) for each season. The parameters measured are: 1. Assimilation, A (μmol CO_2 $m^{-2}s^{-1}$); 2. Nitrogen concentration on a leaf area basis, [N] (g N m^{-2} leaf); 3. Stomatal conductance, g_s (mol H_2O $m^{-2}s^{-1}$); 4. Mesophyll conductance, g_m (m s^{-1} x 10^{-5}); 5. Intrinsic water-use efficiency, A/g_s (μmol CO_2 mol H_2O^{-1}); 6. Carbon stable isotope signatures, $\delta^{13}C$ (‰) and 7. Photosynthetic nitrogen-use efficiency, PNUE (μmol CO_2 g N^{-1} s^{-1}) in both study sites. Values followed by the same letter do not differ significantly, within site, at the $\alpha = 0.05/7$ (i.e. $P < 0.0071$) level.

Transition zone:	A	[N]	g_s	g_m	A/g_s	$\delta^{13}C$	PNUE
S. terebinthifolius							
Dry	0.74 ± 0.17 [a]	1.98 ± 0.25 [abcd]	0.02 ± 0.00 [a]	0.14 ± 0.03 [a]	36.9 ± 9.8 [b]	-28.5 ± 0.4	0.37 ± 0.08 [a]
Wet	3.76 ± 0.76 [a]	1.31 ± 0.09 [cd]	0.06 ± 0.01 [a]	0.72 ± 0.18 [a]	61.3 ± 7.0 [ab]	-29.0 ± 0.5	2.79 ± 0.47 [a]
R. mangle							
Dry	4.76 ± 1.27 [b]	2.20 ± 0.15 [abc]	0.07 ± 0.02 [b]	1.08 ± 0.31 [b]	65.0 ± 1.4 [a]	-27.8 ± 0.8	2.24 ± 0.67 [ab]
Wet	6.89 ± 1.75 [b]	2.78 ± 0.14 [a]	0.14 ± 0.03 [b]	1.28 ± 0.32 [b]	53.6 ± 2.2 [ab]	-28.7 ± 0.3	2.47 ± 0.59 [ab]
L. racemosa							
Dry	6.73 ± 0.34 [c]	2.35 ± 0.12 [ab]	0.10 ± 0.01 [c]	1.58 ± 0.09 [c]	67.5 ± 2.1 [a]	-28.0 ± 0.4	2.93 ± 0.33 [b]
Wet	11.21 ± 1.37 [c]	2.47 ± 0.24 [ab]	0.25 ± 0.05 [c]	2.53 ± 0.28 [c]	53.8 ± 9.1 [ab]	-28.3 ± 0.6	4.79 ± 0.87 [b]
R. punctata							
Dry	1.37 ± 0.42 [ab]	1.21 ± 0.11 [d]	0.03 ± 0.01 [ab]	0.28 ± 0.10 [ab]	48.4 ± 7.6 [ab]	-28.7 ± 0.4	1.25 ± 0.44 [a]
Wet	7.30 ± 0.86 [ab]	2.88 ± 0.55 [a]	0.13 ± 0.02 [ab]	1.44 ± 0.17 [ab]	60.4 ± 3.5 [ab]	-29.7 ± 0.2	2.72 ± 0.69 [a]
R. aculeata							
Dry	3.83 ± 0.41 [ab]	1.53 ± 0.11 [bcd]	0.08 ± 0.01 [bc]	0.74 ± 0.09 [ab]	50.0 ± 4.5 [ab]	-29.8 ± 0.4	2.47 ± 0.18 [ab]
Wet	4.68 ± 0.88 [ab]	1.49 ± 0.16 [bcd]	0.15 ± 0.03 [bc]	0.75 ± 0.14 [ab]	34.1 ± 2.8 [b]	-30.0 ± 0.7	2.87 ± 0.45 [ab]
Upland pineland:							
S. terebinthifolius							
\	3.82 ± 0.50 [a]	1.64 ± 0.06 [a]	0.06 ± 0.01 [a]	0.84 ± 0.12	65.0 ± 4.7 [a]	-30.0 ± 0.4	2.33 ± 0.30
Wet	8.04 ± 0.69 [a]	1.51 ± 0.07 [a]	0.20 ± 0.03 [a]	1.40 ± 0.10	42.3 ± 4.8 [b]	-30.6 ± 0.3	5.33 ± 0.41
R. punctata							
Dry	3.40 ± 0.25 [a]	1.17 ± 0.06 [a]	0.05 ± 0.00 [ab]	0.83 ± 0.08	75.7 ± 2.9 [a]	-28.8 ± 0.4	2.75 ± 0.19
Wet	6.75 ± 0.35 [a]	1.20 ± 0.05 [a]	0.29 ± 0.02 [ab]	1.10 ± 0.08	24.0 ± 2.4 [c]	-30.0 ± 0.6	5.62 ± 0.24
R. aculeata							
Dry	6.12 ± 0.22 [b]	2.01 ± 0.08 [b]	0.14 ± 0.01 [b]	1.14 ± 0.03	44.7 ± 2.9 [b]	-30.0 ± 0.4	3.06 ± 0.16
Wet	9.31 ± 1.29 [b]	2.16 ± 0.33 [b]	0.31 ± 0.05 [b]	1.55 ± 0.24	35.3 ± 3.5 [bc]	-30.5 ± 0.4	4.68 ± 1.01

Table 4.4. Three-factor ANOVA of the 7 parameters measured in the 3 species (*Schinus, R. punctata* and *R. aculeata*) sampled over the wet and dry seasons at the two different study sites. The level of significance was Bonferroni corrected to $P < 0.007$ ($\alpha = 0.05/7$).

	A (μmol CO_2 $m^{-2}s^{-1}$)				[N] (g N m^{-2} leaf)				g_s (mol H_2O $m^{-2}s^{-1}$)			
	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*
Species	2	18.6	10.2	**.001**	2	.002	1.15	.337	2	.037	19.9	**<.001**
Site	1	103.5	57.0	**<.001**	1	.002	0.90	.355	1	.141	76.0	**<.001**
Season	1	176.3	72.4	**<.001**	1	.004	1.63	.216	1	.242	96.8	**<.001**
Species x Site	2	13.3	4.3	**.003**	2	.018	10.15	**.001**	2	.001	0.3	.714
Species x Season	2	8.8	3.6	.043	2	.017	7.40	**.004**	2	.010	3.9	.034
Site x Season	1	0.4	0.2	.695	1	.003	1.10	.306	1	.052	20.9	**<.001**
Species x Site x Season	2	8.2	3.4	.051	2	.013	5.53	.012	2	.000	0.2	.806
Error	24	1.8			20	.002			24	.002		

	g_m (m s^{-1} x 10^{-5})				A/g_s (μmol CO_2 mol H_2O^{-1})				$\delta^{13}C$ (‰)				PNUE (μmol CO_2 g N^{-1} s^{-1})			
	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*
Species	2	0.37	5.2	.013	2	770.5	5.83	.009	2	3.23	5.24	.014	2	1.8	1.8	.203
Site	1	3.24	45.1	**<.001**	1	7.2	0.05	.818	1	5.47	8.87	.007	1	40.6	40.1	**<.001**
Season	1	3.73	42.2	**<.001**	1	1673.	12.17	**.002**	1	6.75	5.31	.031	1	44.4	39.8	**<.001**
Species x Site	2	0.50	7.0	**.004**	2	110.2	0.83	.447	2	2.97	4.82	.018	2	1.6	1.6	.237
Species x Season	2	0.32	3.6	.044	2	551.1	4.01	.032	2	0.35	.28	.761	2	3.7	3.4	.056
Site x Season	1	0.12	1.3	.265	1	4543.	33.02	**<.001**	1	.006	.01	.945	1	4.0	3.6	.072
Species x Site x Season	2	0.57	6.5	**.006**	2	1675.	12.18	**<.001**	2	.067	.05	.949	2	0.3	0.2	.795
Error	24	0.72			24	132.1			22	0.62			20	1.0		

R. punctata [N] was higher than in the pineland while the opposite trend was observed for *R. aculeata*. The species x season interaction was because of a decrease in [N] of *Schinus* and an increase for *R. punctata* from the dry to the wet season (Table 4.3).

Stomatal conductance (g_s) increased from dry to wet season at both sites (Table 4.3). Among species, *Schinus* and *R. punctata* had the lowest g_s in the two study sites. However, from dry to wet season in both areas, g_s of *Schinus* and *R. punctata* each increased over 300% while *R. mangle, L. racemosa* and *R. aculeata* increased approximately 200%. The three-factor Model I ANOVA of *Schinus, R. punctata* and *R. aculeata* showed significance for species, site, season, and site x season (Table 4.4). *Schinus* had the lowest g_s while *R. aculeata* had the highest values. Stomatal conductance was lowest in the transition zone during the dry season and highest in the upland pineland during the wet season (Table 4.3).

Mesophyll conductance (g_m) was seasonally different at both study sites but only among species in the transition zone (Table 4.2). Mesophyll conductance was significantly lower in the dry than the wet season (Table 4.3). *Schinus* had the lowest g_m in the transition zone. Mesophyll conductance of the exotic was similar to that of native freshwater species but lower than for the mangrove species. Comparison of *Schinus* and native freshwater species across sites showed differences in site, season, species x site and an interaction of all three factors (Table 4.4).

Water-use efficiency (WUE)

Season and species differences were observed in intrinsic WUE (A/g_s) only in the pineland, but season x species interactions were found in both study sites (Table 4.2). The

two mangrove species had the highest dry season A/g_s in the transition zone. *Schinus* from the transition zone had the lowest A/g_s in the dry season but the highest values in the wet season, representing a 250% increase from dry to wet season (Table 4.3). The only other species at this site which showed a similar dry to wet season trend in A/g_s was *R. punctata* that increased approximately 130% during this period. All other native species showed a decrease from dry to wet season. *Schinus* and *R. punctata* A/g_s decreased from dry to wet season in the upland pineland but *R. aculeata* remained constant over season (Table 4.3).

Intrinsic WUE differed between seasons, site x season, and all three factors for the species common to both sites (Table 4.4). *Schinus* A/g_s in the transition zone was lower than in the pineland during the dry season. However, this trend was reversed in the wet season with the transition zone plants having higher A/g_s than in the pineland. The same pattern was observed in *R. punctata*, but there were no differences in *R. aculeata* (Table 4.3).

There were no season or species differences in $\delta^{13}C$ signatures in either study site (Table 4.2). There were also no site differences for any of the species sampled (Table 4.4).

Photosynthetic nitrogen-use efficiency (PNUE)

Seasonal differences in PNUE were found in each study site. Species differences were found only in the transition zone (Table 4.2). Dry season PNUE was significantly lower than that of the wet season for both sites. The largest seasonal difference was found for *Schinus* in the transition zone where wet season *Schinus* PNUE was approximately 8-

times greater than in the dry season (Table 4.3). Within the pineland, a seasonal increase in PNUE from dry to wet seasons was observed for both *Schinus* and *R. punctata* but not *R. aculeata* (Table 4.3). In the transition zone, species differences were a consequence of lower PNUE of *Schinus* and *R. punctata* compared to the other species. Site comparisons of *Schinus, R. punctata* and *R. aculeata* revealed significant site and season differences (Table 4.4); PNUE was lower in plants from the transition zone than those from the upland pineland (Table 4.3).

DISCUSSION

The findings do not support either a-priori hypothesis tested. Evidence for this is seen in gas exchange where *Schinus A*, g_s and g_m were the lowest of all transition zone species. In both sites *Schinus* gas exchange patterns were similar to native freshwater species. Seasonality also affected all species (Table 4.2); dry season *A*, g_s and g_m were lower than wet season values for most species in either study site, indicating that all species were affected by seasonality. However**,** *Schinus* dry season *A* in the transition zone was lower than the wet season values by approximately 5-fold (Table 4.3) indicating that the exotic is not assimilating CO_2 as rapidly as the other native species, and appears to be most affected by seasonality. Field *A* rates of the mangrove species from the transition zone in the wet season are similar to those of previous studies. Gas exchange properties of the two mangrove species are comparable with that from other studies--mangrove species growing under saline field conditions have been shown to have *A* exceeding 25 μmols CO_2 $m^{-2}s^{-1}$ in the field (Clough and Sim 1989) although most species

have averages of between 10-15 μmols CO_2 $m^{-2}s^{-1}$ (e.g. Andrews and Muller 1985, Ball and Farquhar 1984, Sobrado 1999) under favorable conditions.

In seasonal subtropical environments such as Florida, two environmental parameters that are thought to have the greatest effect on plant physiological function in this coastal saline environment are: 1) seasonal wet-dry cycles and 2) seasonal fluctuations in salinity. Examination of the soil profile (Chapter 2) in the two study sites showed fluxes in both soil water content and pore water salinity during the dry season.

In the pineland, low gas exchange by the plants during the dry season is most likely because of drier environmental conditions. In the saline transition zone however, the decreases, significant in *Schinus* and *R. punctata*, are most likely because of a combination of soil moisture and salinity conditions. Depression of A, g_s, and g_m have been shown to be common plant responses to salinity (Ball and Farquhar 1984, Huang et al. 1996). Salts within the plant can change cell turgor, alter organelle function, and eventually disrupt photosynthesis (Greenway and Munns 1980, Munns and Termaat 1986, Flowers and Yeo 1986). In comparing site effects, the magnitude of *Schinus* difference across sites was either similar to or greater than for *R. punctata* and *R. aculeata*. Seasonal effects on native species seem to affect *Schinus* similarly. Increase of wet season A, g_s and g_m in both study sites is most likely because of a physiologically less stressful abiotic environment during this season.

Species differences in [N] could reflect plant physiological function because there is a significant positive correlation between A and leaf [N]. Previous studies have shown that assimilation rates are often related to nitrogen concentration (Wan and Sosebee 1990, van den Boogaard 1995). Under saline conditions, A appears to be related to leaf [N] in

native species but not in *Schinus*. However, under high salt contents NO_3^- uptake is often depressed in plants, most likely because of salt-induced disruption of the root system (Pessarakli 1991, Botella et al. 1997, Kurban et al. 1999). Although there was a trend for lower [N] in the dry season than in the wet, the only species to show a significant seasonal increase in [N] was *R. punctata* in the transition zone. In *Schinus*, the opposite trend (although not significant) was observed—leaf [N] was lower in the wet season than in the dry. Higher leaf [N] coupled with low gas exchange levels during the dry season could be indicative of accumulation of secondary plant substances in the leaf. Biosynthesis of nitrogenous compounds such as polyamines, stress metabolites (e.g. mannitol, pinitol), osmolytes (e.g., proline, alanine, glutamine) and stress hormones are commonly observed responses in plants (Larcher 1995).

Intrinsic WUE decreased from dry to wet season in most species at both sites. In many studies (e.g. Martin and Ruiz-Torres 1992, Raeini-Sarjaz 1998) this pattern is attributed to greater water availability, hence the reduced need to conserve water. Low intrinsic WUE can be the result of high A and g_s indicating that water is readily available to the plant. Low WUE has been associated with high productivity in some agricultural crops (e.g. Acevedo 1993, Li 1999). Most species at both sites in this study had lower wet season intrinsic WUE compared to the dry season. The only exceptions were *Schinus* and *R. punctata* in the transition zone site. For these two species in the transition zone, intrinsic WUE increased from the dry to the wet season due to greater increases in A relative to g_s (Table 5.2).

Schinus had the lowest intrinsic WUE of all species during the dry season because of low A and g_s. *Schinus* appears to derive no advantage from growing in the transition

zone and in the long run, seems to be the most affected compared to other species. The presence and prevalence of *Schinus* in this coastal transition zone is most likely because of another mechanism, not a dirct contribution of its gas exchange patterns.

Despite small numerical differences in $\delta^{13}C$ signatures from dry to wet season in all the species, none of these differences were significant either over species or season (Tables 4.2 and 4.4). The impact of salinity or drier soils during the dry season does not appear to considerably affect leaf carbon stable isotope signatures or functionally distinguish *Schinus* from native species. Lack of significant $\delta^{13}C$ response may be caused by the integrative effect of this parameter. Carbon isotopic signatures represent assimilative patterns over the growing season. A significant proportion of carbon within the leaves could have been formed prior to the end of the season when conditions became more extreme.

Also, in this study $\delta^{13}C$ signatures do not seem to be closely linked to short-term intrinsic WUE (Table 4.3) although the relationship has been shown in many studies (e.g. Farquhar et al. 1982b). Several explanations may underlie this discrepancy between daily and long-term measures. First, the leaves sampled at the end of each season are most likely to have been completely developed and hence not actively expanding anymore. Therefore carbon gain of leaves sampled would not reflect the daily patterns as most of the photosynthates is likely being translocated from those leaves. *A* second explanation could be that the single-day measurement does not completely capture the overall variation in the plants over seasons. The measures from individual sample days reflect the conditions at the end of the dry season and may not be fully representative of average conditions encountered throughout the dry season. Third, the leaves sampled from one

season to the next could also have been of different ages. It has been shown (e.g. Kitajima et al. 1997) that photosynthetic rates of older leaves tend to be lower than younger, fully mature leaves. Although the leaves sampled were definitely leaves produced during that season, some leaves could have developed and matured sooner than others, leading to greater variability in daily measurements than seasonal integrated values.

Lastly, the resultant low PNUE from the low assimilation rate in *Schinus* in the transition zone during the dry season indicates (Table 4.3) that *Schinus* photosynthetic capacities are significantly inhibited by salinity, much more so than either native freshwater or mangrove species in this site. Although *Schinus* gas exchange closely resembles that of native freshwater species, these natives in the transition zone appear to be less vulnerable to salinity than *Schinus*. During the wet season and in the absence of salinity (i.e. pineland for both seasons), *Schinus* behaves like the native species with regard to PNUE and does not seem to be physiologically different from any of the other study species.

CONCLUSION

Contrary to expectations, *Schinus* is the species most affected by the changing environmental conditions found in this coastal study area. *Schinus* assimilation, stomatal conductance, water-use efficiency and PNUE are depressed significantly by salinity during the dry season, more so than those of native species. This indicates that *Schinus* photosynthesis and gas exchange is not very robust to dry soil coupled with saline conditions. The wet season, with lowered salinity and greater water availability,

represents a physiologically more favorable season for all plants with regard to gas exchange. *Schinus* gas uptake patterns are most likely not contributing to its success in this saline habitat. In fact, *Schinus* is the species most adversely affected by salinity in this study. Although *Schinus* is widely found in coastal areas throughout Florida, it is likely that some other component of its biology contributes to its success in these habitats.

Chapter 5

Seasonal gas exchange characteristics of *Schinus terebinthifolius* in a native and disturbed upland community.

INTRODUCTION

Since historical times, humans have transported both plants and animals for their own purposes (Gordon and Thomas 1997). Non-native species have been deliberately imported into the United States for agricultural, commercial and ornamental purposes. South Florida is a hub for the importation of both plants and animals into the United States (U.S. Congress 1993); it is believed that this ready supply of plants has contributed to the high numbers of exotic plant species found in Florida (Simberloff 1997). The high proportion of invasive exotics in peninsular Florida has also been attributed to this region's subtropical weather and unique island-like biogeography (Elton 1958). Florida, together with Hawaii, is one of the two regions of North America most threatened by invasive exotics (Simberloff 1997).

The most widespread invasive exotic in Florida is *Schinus terebinthifolius* Raddi (*Schinus*), a species that is found in over 280 000 ha of South Florida (1993 South Florida Water Management Survey as cited in Schmitz et al. 1997). Imported from South America over a hundred years ago, this exotic is now widely found in a variety of Florida habitats. *Schinus* can grow in high densities that can lower species diversity (Olmsted and Loope 1981) and reduce faunal use of the area (Curnutt 1989).

The purpose of this study was to determine if gas exchange responses of *Schinus* were significantly different from those of native species in two inland communities, a native rock pineland community and a disturbed area. I measured plant gas exchange, intrinsic water use efficiency (WUE) and photosynthetic nitrogen-use efficiency (PNUE) over a wet and dry season. Integrated plant WUE was also determined via carbon stable isotopes. Under water stress, integrated WUE often increases as plants discriminate less against ^{13}C during CO_2 uptake. Farquhar et al. (1982a, 1982b) have shown a relationship between integrated WUE and carbon stable isotopes both theoretically and empirically. Therefore I used carbon isotopic ratio as a proxy measure of a plant's seasonal WUE.

As the efficiency of a plant's resource utilization has implications for survival, growth and reproductive capacity (Lambers and Poorter 1992), higher resource use efficiency in a plant is advantageous in spatially and temporally variable environments. Many studies (e.g. Field et al. 1983, Lambers and Poorter 1992, Schieving and Poorter 1999) have shown that plants with high PNUE have high growth rates. Under conditions of limited water availability, however, WUE often becomes a more important indicator of a plant's physiological performance than PNUE because intrinsic WUE (assimilation/stomatal conductance) provides an estimate of a plant's efficiency in taking up CO_2 versus water loss under conditions of limited water availability (Larcher 1995).

METHODS AND MATERIALS

Study sites

Both study sites are located in Everglades National Park, on the Miami Rock Ridge limestone outcrop (Fig. 3.1, inset). The ridge, a Pleistocene era limestone

formation (Hoffmeister 1974), extends from the east coast of South Florida at an elevation of approximately 7.0 m and slopes westward into the Florida Everglades. Both sites (Fig. 3.1) are on part of the Rock Ridge known as Long Pine Key, about 1.0 m above sea level.

Historically, both sites were agricultural areas. During the 1950's, the rock-plow was introduced into South Florida to break the limestone substrate into a rock-soil surface. After agriculture ceased in the late 1970's, areas not rock-plowed reverted to native vegetation while the 2000 ha of rock-plowed areas succeeded into a non-native vegetational complex. There is no soil profile development in either study site (Snyder et al. 1990).

The first site (LPK), a non-rock plowed area, is now a native pineland community. At this site, soil is only found in limestone pockets within the bare rock substrate. The community is composed of an open canopy of *Pinus elliottii* var. densa Little and Dorman, with a subcanopy of native species such as *Myrica cerifera* L. (Myricaceae), *Baccharis halimifolia* L. (Asteraceae), *Tetrazygia bicolor* (Mill.) Cogn. (Melastomataceae) and *Metopium toxiferum* (L.) Krug and Urban (Anacardiaceae). The invasive *Schinus* is also a co-dominant species in this site. The main seed source of *Schinus* in the LPK is from the rock-plowed area that is known as the Hole-in-the-Donut. The second site (HID) is located within this disturbed, previously farmed area. The substrate is a mix of soil and crushed limestone rock that varies in depth from a few centimeters to about 30 cm (Snyder et al. 1990). The canopy dominant in HID is the exotic *Schinus*. A few native species such as *M. cerifera*, *B. halimifolia* and *M. toxiferum*

also can be found in this site. The canopy in the HID is approximately 5 m tall, and is relatively dense compared to the adjacent LPK.

Rainfall in South Florida is strongly seasonal (Chen and Gerber 1990). South Florida receives about 75% of its annual rainfall during the wet season. At both study sites, average annual rainfall from 1940-1998 was 1450 mm. The rainy season starts in May and ends in November. The wet season is followed by a slow dry-down during the winter months and by the end of April, conditions are often extremely dry. Wildfires are prevalent towards the end of the dry season and at the start of the rainy season because of high incidence of lightning (Taylor 1980). The pineland site is fire-managed by the Park Service. Upland areas in Long Pine Key are burned approximately every two years. Because of the seasonal availability of rainfall in South Florida, groundwater depths range from more than 1.5 m during the dry season to approximately 12 cm belowground during the wet season (Ewe, unpublished data). Although both sites are not flooded during the wet season, soil within the two sites is saturated when water levels are at their highest near the end of the wet season in late October. Despite no standing water in the LPK site, shallow pools were observed in the HID within depressions of exposed limestone.

Species studied

Schinus is a dioecious, shrubby evergreen perennial that averages about 5 m in South Florida. In a closed stand, the plant forms a multi-stemmed tangle of non-abscising branches beneath a dense canopy that precludes understory plant growth (Ewel et al. 1982). *Schinus* litter decomposes quickly so there is very little ground fuel within a

mature *Schinus* stand, resulting in poor burning conditions (Ewel 1986). Unlike some native South Florida communities, a community dominated by mature *Schinus* is not easily controlled by fire (Clark 1997, Doren and Whiteaker 1990). *Schinus* resprouts vigorously and once juvenile *Schinus* plants are over one meter high, mortality from fire significantly decreases (Doren and Whiteaker 1990).

Gas exchange of the exotic *Schinus* was compared to that of native species widely found within the community. In the LPK, *Schinus* was compared to four native species, *Myrica cerifera*, *Baccharis halimifolia*, *Rapanea punctata* (Lam) Lundell (Myrsinaceae) and *Randia aculeata* L. (Rubiaceae). Study species within LPK were mostly small and shrubby because of park fire management practices. Only two other native species (*M. cerifera* and *B. halimifolia*) were compared to *Schinus* in the HID because *R. punctata* and *R. aculeata* were not prevalent within this community. Five individuals of each species were sampled every season at each site. Measurements were made at the end of the wet and dry seasons of 1999. Different individuals were measured during the dry season than the wet season because the National Park Service burned the initial LPK study plot. Plants in an adjacent pineland and HID section (< 800 m distant) were sampled during the wet season.

Gas exchange measurements

Gas exchange was measured on a portable gas exchange system with a 390 mL chamber attachment (LI-6200, LiCor, Logan, Utah). Measurements were made between 930 – 1600 hrs, starting after dew had evaporated from leaf surfaces and ending when light levels at sample leaves were less than 1000 μmols m^{-2} s^{-1}. Each site was sampled on

two consecutive days at the end of a dry (12 and 14 April 1999) and wet (16 and 17 November 1999) season; only one site was measured per day. Plants were sampled continuously on a rotation basis throughout the day. For each plant, the second fully expanded leaf from the tip of an east-facing lateral branch exposed to full sunlight was sampled. Attempts were made to measure the same leaf throughout the day. In the case where leaves were damaged or became detached during sampling, other leaves of similar locations at the same or adjacent branches were selected.

After equilibrating the chamber to the environment surrounding a leaf, the chamber was clamped onto the leaf for approximately 60 seconds to measure instantaneous gas exchange. Measurements made from each individual plant for that day were then averaged. Intrinsic water-use efficiency (WUE, μmol CO_2 mol H_2O^{-1}) was calculated by dividing assimilation (A, μmol CO_2 m^{-2} s^{-1}) by stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}). Mesophyll conductance (g_m, m s^{-1}) was determined by dividing A by internal CO_2 concentration (c_i, μmol CO_2 m^{-3}).

Leaf measures

Gas exchange has been shown to decrease with increasing leaf age (Kitajima et al. 1997). Therefore, general patterns of leaf development in the focal species were noted throughout the study period. Leaf production of all study species was observed to be seasonal; leaves were produced towards the end of the dry season and production continued throughout the wet season. Young leaves produced at the onset of the dry season continued to mature despite the dry season. An attempt was made to measure leaves of similar age.

All leaves used for gas exchange were harvested at the end of the day, bagged and returned to the Stable Isotope Laboratory at the Biology Department of the University of Miami. Individual leaf area was determined on a leaf area meter (LI-3000, LiCor, Logan, Utah) before leaves were dried in a benchtop freeze-dry system (Labconco, Kansas City, Kansas) at -95°C and 10 μm Hg for one week. Leaf dry weight was then measured. Plant specific leaf area (SLA, $m^2\ g^{-1}$) was determined by dividing leaf area by its weight.

Stable isotope analyses

Dried and weighed leaves (described above) were frozen in liquid nitrogen and ground using a mortar and pestle. Subsamples (approximately 5 mg) were prepared for stable isotope analysis using the method described by Buchanan and Corcoran (1959). In the case of multiple leaves taken from a tree, subsamples were combined to provide a single sample for stable isotope analysis. Purified samples of leaf CO_2 were analyzed on an isotope-ratio gas mass spectrometer (VG Prism, Micromass, Middlebury, England). Isotopic abundance, in per mil units (‰) was determined by the following equation:

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1]\ 1000,$$

where R_{sample} was the $^{13}C/^{12}C$ ratio of the sample and $R_{standard}$ was the $^{13}C/^{12}C$ ratio of the Pee-Dee Belemnite standard.

Nitrogen analyses

A second set of subsamples of the collected and processed leaves was used for nitrogen analyses. In the dry season, nitrogen concentration (g N g^{-1} leaf) of leaves was analyzed using the Kjedahl method; wet season leaves were analyzed using an elemental

analyzer (Carlo Erba NC2100, ThermoFinnigan Italia S.p.A., Milan, Italy). As the Kjedahl technique volatilizes ammonia in the sample, values obtained from this technique were subsequently standardized to elemental analyzer values by re-analyzing some dry season leaf samples on the elemental analyzer. Nitrogen contents ([N]) were reported on a leaf area basis (g N m^{-2} leaf) by dividing nitrogen concentration by SLA. Photosynthetic nitrogen-use-efficiency (PNUE) was determined by dividing *A* by [N].

Statistical analyses

All data were tested for normality using a Shapiro-Wilkes normality test of Statistix 7.0 (Analytical Software, Tallahassee, FL). Seven parameters (*A*, [N], g_s, g_m, A/g_s, $\delta^{13}C$, PNUE) were analyzed independently using two-factor Model I analysis-of-variance (ANOVA) with probability of significance adjusted with a Bonferroni correction at $P = 0.007$ (i.e. $\alpha = 0.05/7$). Factors that were significant were further analyzed by Tukey honestly-significant difference (HSD) test. A three-factor Model I ANOVA was used to compare gas exchange of species common to both sites. All data analyses were carried out using either Statistix 7.0 (Analytical Software, Tallahassee, FL) or SPSS 8.0 (SPSS Inc., Chicago, IL).

RESULTS

All data were normally distributed. Assimilation rates were not significantly different between seasons or among species at either site (Table 5.1). *Schinus A* was similar to native species at both sites within each season (Table 5.2). Nitrogen concentration on a leaf area basis ([N]) varied with season and species at both sites

Table 5.1. Two-factor (species and season) ANOVA of: 1. Assimilation, A (μmol CO_2 $m^{-2}s^{-1}$); 2. Nitrogen concentration on a leaf area basis, [N] (g N m^{-2} leaf); 3. Stomatal conductance, g_s (mol H_2O $m^{-2}s^{-1}$); 4. Mesophyll conductance, g_m (m s^{-1} x 10^{-5}); 5. Intrinsic water-use efficiency, A/g_s (μmol CO_2 mol H_2O^{-1}); 6. Carbon stable isotope signatures, $\delta^{13}C$ (‰) and 7. Photosynthetic nitrogen-use efficiency, PNUE (μmol CO_2 g N^{-1} s^{-1}) in both sites. Values in bold are significant at $P < 0.0071$.

	Seashon				Species				Species x Season				Error	
	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS
1. *A*														
Pineland	1	34.53	5.90	0.020	4	22.7	3.88	0.009	4	16.14	2.76	0.041	40	5.86
HID	1	5.52	1.10	0.305	2	3.77	0.75	0.483	2	11.13	2.21	0.130	24	5.03
2. [N]														
Pineland	1	0.001	18.71	**<0.001**	4	0.01	6.88	**<0.001**	4	0.003	3.50	0.016	38	0.001
HID	1	2.324	15.20	**0.001**	2	1.20	7.85	**0.002**	2	0.002	0.16	0.849	24	0.153
3. g_s														
Pineland	1	0.012	0.562	0.458	4	0.04	2.32	0.073	4	0.057	2.71	0.043	40	0.021
HID	1	0.286	11.30	**0.003**	2	0.03	1.55	0.233	2	0.023	0.89	0.423	24	0.025
4. g_m														
Pineland	1	0.455	2.17	0.148	4	0.77	3.71	0.012	4	0.560	2.67	0.046	40	0.209
HID	1	0.186	1.11	0.302	2	0.50	3.04	0.067	2	0.215	1.30	0.294	24	0.167
5. A/g_s														
Pineland	1	601.9	10.26	**0.003**	4	128.	2.19	0.087	4	64.94	1.11	0.366	34	58.63
HID	1	4119	58.74	**<0.001**	2	149.	2.12	0.141	2	288.1	4.11	0.029	24	70.13
6. $\delta^{13}C$														
Pineland	1	9.60	11.13	**0.002**	4	2.52	2.92	0.035	4	0.977	1.13	0.357	35	0.862
HID	1	5.25	3.66	0.069	2	0.48	0.334	0.720	2	0.157	0.11	0.897	22	1.434
7. PNUE														
Pineland	1	0.537	0.274	0.604	4	12.3	6.32	**0.001**	4	1.46	0.744	0.568	38	1.960
HID	1	0.184	0.038	0.847	2	18.9	3.93	0.033	2	6.25	1.30	0.292	24	4.824

Table 5.2. Species average (± SEM) for each season. The parameters measured are: 1. Assimilation, *A* (μmol CO_2 $m^{-2}s^{-1}$); 2. Nitrogen concentration on a leaf area basis, [N] (g N m^{-2} leaf); 3. Stomatal conductance, g_s (mol H_2O $m^{-2}s^{-1}$); 4. Mesophyll conductance, g_m (m s^{-1} x 10^{-5}); 5. Intrinsic water-use efficiency, A/g_s (μmol CO_2 mol H_2O^{-1}); 6. Carbon stable isotope signatures, $\delta^{13}C$ (‰) and 7. Photosynthetic nitrogen-use efficiency, PNUE (μmol CO_2 g N^{-1} s^{-1}) in both sites. Values followed by the same letter do not differ significantly between species within a site at $\alpha = 0.05/7$ ($P < 0.0071$) by post-hoc Tukey HSD.

	A	[N]	g_s	g_m	A/g_s	$\delta^{13}C$	PNUE
Long Pine Key							
S. terebinthifolius							
Dry	9.0 ± 1.4	1.50 ± 0.10 ^{ab}	0.46 ± 0.09	1.56 ± 0.25	23.0 ± 3.3	-30.1 ± 0.6	5.9 ± 0.8 ^{a}
Wet	10.9 ± 0.6	1.93 ± 0.12 ^{ab}	0.32 ± 0.03	1.95 ± 0.10	38.1 ± 1.3	-28.7 ± 0.4	5.8 ± 0.4 ^{a}
M. cerifera							
Dry	6.9 ± 1.9	1.70 ± 0.14 ^{c}	0.26 ± 0.04	1.22 ± 0.22	27.6 ± 3.0	-30.0 ± 0.8	4.4 ± 1.1 ^{ab}
Wet	11.8 ± 1.2	2.68 ± 0.10 ^{c}	0.40 ± 0.04	1.92 ± 0.24	32.2 ± 2.5	-29.1 ± 0.3	4.4 ± 0.3 ^{ab}
B. halimifolia							
Dry	9.1 ± 0.9	1.49 ± 0.22 ^{ab}	0.53 ± 0.08	1.52 ± 0.16	19.1 ± 2.5	-29.6 ± 0.3	6.3 ± 0.3 ^{a}
Wet	9.0 ± 0.9	1.77 ± 0.12 ^{ab}	0.36 ± 0.02	1.39 ± 0.16	27.0 ± 1.6	-29.2 ± 0.2	5.1 ± 0.5 ^{a}
R. punctata							
Dry	8.3 ± 0.9	1.61 ± 0.17 ^{a}	0.33 ± 0.03	1.59 ± 0.27	31.3 ± 7.9	-30.2 ± 0.5	5.2 ± 0.7 ^{ab}
Wet	6.8 ± 0.9	1.51 ± 0.12 ^{a}	0.22 ± 0.04	1.14 ± 0.16	32.9 ± 1.5	-30.0 ± 0.4	4.6 ± 0.8 ^{ab}
R. aculeata							
Dry	4.7 ± 1.0	1.79 ± 0.13 ^{bc}	0.23 ± 0.06	0.78 ± 0.16	23.9 ± 3.3	-31.5 ± 0.5	2.6 ± 0.5 ^{b}
Wet	7.8 ± 1.6	2.19 ± 0.12 ^{bc}	0.36 ± 0.14	1.23 ± 0.27	29.4 ± 2.2	-29.7 ± 0.4	3.6 ± 0.8 ^{b}
Hole-in-the-Donut							
S. terebinthifolius							
Dry	11.3 ± 1.2	1.37 ± 0.21 ^{ab}	0.49 ± 0.13	2.05 ± 0.20	21.6 ± 1.6	-29.8 ± 0.4	6.6 ± 2.1
Wet	9.9 ± 1.5	2.04 ± 0.17 ^{ab}	0.20 ± 0.05	1.92 ± 0.29	57.3 ± 6.1	-28.9 ± 0.5	4.9 ± 0.8
M. cerifera							
Dry	8.7 ± 1.0	1.98 ± 0.28 ^{b}	0.35 ± 0.08	1.51 ± 0.15	23.9 ± 2.0	-29.5 ± 0.4	2.6 ± 0.8
Wet	10.1 ± 0.8	2.47 ± 0.12 ^{b}	0.25 ± 0.02	1.66 ± 0.15	43.3 ± 2.0	-28.9 ± 1.0	4.1 ± 0.3
B. halimifolia							
Dry	8.4 ± 0.5	1.32 ± 0.11 ^{a}	0.52 ± 0.06	1.38 ± 0.10	24.5 ± 2.7	-30.2 ± 0.3	5.4 ± 0.4
Wet	11.1 ± 0.6	1.82 ± 0.09 ^{a}	0.33 ± 0.02	1.84 ± 0.13	39.8 ± 5.4	-29.1 ± 0.3	6.1 ± 0.1

(Table 5.1). Leaf [N] in both the LPK and HID were significantly higher in the wet season than in the dry (Tables 5.2 and 5.3). *Myrica cerifera* at both sites consistently had the highest wet season [N] of all species compared in either site (Table 5.2); *Schinus* [N] at both sites was similar to all native species except *M. cerifera* in the pineland (Table 5.2). Nitrogen concentration was significantly different among species and across seasons for the three species common to both sites (Table 5.3). It was highest in *M. cerifera*, followed by *Schinus* and *B. halimifolia*.

Stomatal conductance (g_s) was seasonally different in the HID but not significantly different among species at both sites (Table 5.1). All HID species had lowered average g_s from dry to wet seasons (Table 5.2). No site difference was found among the three species sampled at both sites (Table 5.3) but dry season g_s were higher than wet season values. Mesophyll conductance (g_m) was not significantly different among species or between seasons at either site (Table 5.2). There were also no g_m differences among *Schinus*, *M. cerifera* or *B. halimifolia* at either site both seasons sampled (Table 5.3). Although there were no significant seasonal effects on g_m, many species had higher g_m during the wet season. Mesophyll conductance was positively correlated with [N] in the LPK (n = 25, Pearson correlation = 0.450, $P = 0.024$) during the wet season.

Intrinsic WUE (A/g_s) was seasonally different at both sites (Table 5.1); wet season intrinsic WUE was higher than the dry season. Within each site, no differences were observed among species (Table 5.1). Across sites comparisons of *Schinus, M. cerifera* and *B. halimifolia* showed significance for season, site, season x site, and season x species (Table 5.3). Site differences resulted from lower LPK values than those for HID.

Table 5.3. Independent three-factor Model I ANOVAs for each of the 7 parameters measured for the three species (*Schinus, R. punctata* and *R. aculeata*) sampled over the wet and dry seasons at both study sites. The level of significance has been adjusted using a Bonferroni correction procedure to compensate for testing seven variables. Values in bold are significant at $P < 0.0071$ ($\alpha = 0.05/7$).

	A (μmol CO_2 $m^{-2}s^{-1}$)				[N] (g N m^{-2} leaf)				g_s (mol H_2O $m^{-2}s^{-1}$)			
	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*
Species	2	5.154	0.982	.382	2	1.896	14.973	**<.001**	2	.072	3.558	.036
Site	1	3.243	0.618	.436	1	0.002	0.014	.905	1	.016	0.795	.377
Season	1	36.301	6.919	.011	1	4.435	35.016	**<.001**	1	.241	11.956	**.001**
Species x Site	2	0.670	0.128	.880	2	0.010	0.082	.921	2	.000	0.033	.967
Species x Season	2	10.528	2.007	.146	2	0.134	1.059	.355	2	.081	4.013	.024
Site x Season	1	7.301	1.392	.244	1	0.000	<0.001	.983	1	.071	3.513	.067
Species x Site x Season	2	16.889	3.219	.049	2	0.198	1.561	.221	2	.015	0.718	.493
Error	48	5.247			46	0.127			48	.020		

	g_m (m s^{-1} x 10^{-5})				A/g_s (μmol CO_2 mol H_2O^{-1})				$\delta^{13}C$ (‰)				PNUE (μmol CO_2 g $N^{-1}s^{-1}$)			
	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*
Species	2	.672	3.776	.030	2	271.2	5.385	.008	2	0.097	0.086	.918	2	21.34	6.303	**.004**
Site	1	.252	1.417	.240	1	783.8	15.56	**<.001**	1	0.000	0.000	.987	1	1.898	0.560	.458
Season	1	.852	4.787	.034	1	3988.	79.18	**<.001**	1	10.26	9.013	**.004**	1	0.295	0.087	.769
Species x Site	2	.060	0.334	.718	2	46.70	0.927	.403	2	0.407	0.358	.701	2	1.531	0.452	.639
Species x Season	2	.129	0.725	.490	2	307.9	6.113	**.004**	2	0.219	0.192	.826	2	3.092	0.913	.408
Site x Season	1	.098	0.553	.461	1	762.4	15.13	**<.001**	1	0.000	0.000	.984	1	1.286	0.380	.541
Species x Site x Season	2	.530	2.980	.060	2	53.26	1.057	.355	2	0.416	0.366	.696	2	3.698	1.092	.344
Error	48	.178			48	50.37			42	1.139			46	3.386		

There were significant seasonal differences in $\delta^{13}C$ values from the LPK but not the HID (Table 5.1). At LPK, carbon isotope signatures were more enriched during the wet than the dry season for *Schinus*, *M. cerifera* and *B. halimifolia* (Table 5.2). The same trend was also found in the three-factor ANOVA (Table 5.3). No significant among-species differences were observed (Table 5.3) although *Schinus* had the highest wet season $\delta^{13}C$ values in the LPK (Table 5.2).

Photosynthetic nitrogen-use efficiency was not seasonally different at either site (Table 5.1). There was a significant species difference in PNUE only for the LPK (Table 5.1). *Schinus* and *B. halimifolia* had the highest values while *R. aculeata* had the lowest PNUE in LPK. For plants sampled at both sites (Table 5.3), species differences were a consequence of *M. cerifera* PNUE being lower than that of *Schinus* and *B. halimifolia*.

DISCUSSION

Overall, *Schinus* seasonal gas exchange patterns were not significantly different from those of most native species (Table 5.2). Some invasive exotics co-occurring with native species have higher *A*, WUE and PNUE than native species (Busch and Smith 1995, Pattison et al. 1998, Horton et al. 2001, Durand and Goldstein 2001), but *Schinus* in this study did not. It is however worth noting that *Schinus* had the highest wet season g_m, intrinsic WUE, $\delta^{13}C$, and PNUE in the LPK of all species (Table 5.2). A similar pattern was shown by Schierenbeck and Marshall (1993) for *Lonicera* where gas exchange trends were not significantly different but maximum g_s and WUE of the exotic were consistently higher than its native congener.

Studies have shown (Mooney et al. 1978, Field et al. 1983, Lambers and Poorter 1992) plant PNUE to be positively correlated with growth. *Schinus* PNUE was similar to that of all native species except *R. aculeata* in the LPK. Thus, when compared on a leaf area basis, *Schinus* and the native species with the exception of *R. aculeata*, would be expected to have the same growth potential. *Myrica cerifera* had the highest [N] at both sites (Table 5.2), most likely because of its nitrogen-fixing ability (Tomlinson 1980).

Both sites showed increased [N] and intrinsic WUE from dry to wet season (Table 5.2). One possible explanation for higher [N] is greater nitrogen availability in the soils. Koch and Snedaker (1997) have shown high ammonium concentrations in Everglades marsh porewater. A second explanation could involve phosphorus availability. The Everglades is a phosphorus-limited system and phosphorus concentrations are higher in the ENP during the wet season because of increased atmospheric inputs (via rainfall) or hydrologic mobilization of phosphorus (see Davis 1994). According to Liebig's Law (Salisbury and Ross 1995), growth is limited by the least available element relative to the amount needed. Increased availability of phosphorus either from localized pools or atmospheric inputs could allow for increased plant [N]. High [N] could potentially contribute to high g_m in many species, indicating more efficient biochemical assimilation.

For some species at both sites, there was a trend toward higher A and lower g_s in the wet season than the dry which contributed to an increase in intrinsic WUE (Table 5.2). Greater water availability often results in the increase of intrinsic WUE because of increase in A that is accompanied by decrease in g_s (Cheng and Luo 1997). For some species, higher intrinsic WUE could also be due to lower g_s, possibly induced as a reponse to flooding. In this study, the increase in wet season intrinsic WUE because of

low g_s may be an indirect result of saturated soils. Low g_s is a commonly observed plant response to flooding (e.g. Naidoo 1983, Kozlowski and Pallardy 1984, Davies and Flore 1987). Although the precise mechanisms of physiological interference have not been elucidated, it is believed that lowered g_s can be caused by hormonal imbalance (Reid and Bradford 1984). Prolonged flooding often leads to soil anoxia that can alter plant physiological behavior through physical (Hook 1984) and chemical changes (Jackson and Drew 1984, Kozlowski and Pallardy 1984). In this study, g_s of *Schinus* and *B. halimifolia* at both sites, as well as *R. punctata* in LPK, were lower in the wet season than in the dry, supporting this explanation of low g_s as a response to flooding. Unfortunately, the degree of substrate anoxia (common characteristic of flooded soils) around the study plants could not be determined because of the continuous limestone bedrock.

There was also a trend for higher wet season $\delta^{13}C$, indicating higher integrated WUE (Table 5.2). The relation ship between $\delta^{13}C$ and a plant's c_i has been shown by Van Caemmerer and Farquhar (1981). Greater $\delta^{13}C$ is caused by low c_i, which is often caused by low g_s. Despite differences in substrate structure, there were no site differences in most gas exchange responses of the three species (Table 5.3). It is possible that the degree of soil saturation affected all three species equally during the wet season regardless of substrate type. Studies have shown that plants are most affected by flooding during their growing season (Kozlowski 1984). The wet season is the primary growing season for almost all plant species in this seasonal environment. In this study, however, there were no signs of outward damage to the plant such as wilting or chlorosis (pers. obs.). After an initial reduction, gas exchange capacities of flood-tolerant plants have been shown to increase to nearly pre-flooded levels after prolonged exposure to flooded

conditions (Hook 1984). It is possible that when sampling was conducted towards the end of the wet season, all plants at both sites could have been equally affected and eventually become adapted to the saturated soil conditions after prolonged root inundation.

The only species that responded differently from the others was *M. cerifera* within the LPK. *Myrica cerifera* at this site seemed to be responding more positively to saturated ground conditions than the other species because it showed increases in wet season A, [N], g_s and g_m. This species has been reported to be flood-tolerant (Gunderson 1994) and produces pneumatophores under controlled glasshouse flooding (Ewe, pers. obs.).

Compared to other species in the LPK, *Schinus* gas exchange, WUE and PNUE does not appear to significantly differ from those of native species. In HID, *Schinus* responds similarly to both native species sampled. Thus *Schinus* gas exchange characteristics per se do not appear to confer the exotic any physiological advantages over native species.

CONCLUSION

I conclude that *Schinus* gas exchange patterns were not significantly different from those of native species, and that *Schinus* is similarly affected by seasonality when compared to the native species sampled. *Schinus* does not seem to have any physiological advantage over native species with regard to gas exchange. *Schinus* dominance in the disturbed HID and its spread into the LPK is probably attributable to other aspects of its physiology and biology, than those studied here.

Chapter 6

Growth and gas exchange of Brazilian pepper (*Schinus terebinthifolius*) and native South Florida species in response to salinity treatments

INTRODUCTION

An invasive exotic is defined as a non-native species that has escaped cultivation, is reproducing freely in the environment and is capable of sustaining viable populations in the wild (Baker 1986). Pimentel et al. (2000) estimate that about 50,000 exotic plant and animal species have been introduced into the United States, either on purpose or by accident. Since the earliest days of human history, we have always transported plants for food, medicinal and ornamental value (diCastri 1989). The rate of transport, however, has significantly increased because of greater human mobility in the modern age of easily accessible transport (Bright 1998, Simberloff 1997). The last two centuries have seen greater rates of plant mobility than the prior thousand. Examples of exotics able to outcompete native species in their introduced habitats include *Tamarix ramosissima* (Busch and Smith 1995, Cleverly et al. 1997), *Lonicera japonica* (Schierenbeck and Marshall 1993), *Aegeratum conyzoides* (Baker 1965) and *Sphaeropteris cooperi* (Durand and Goldstein 2000).

One of the most widely found invasive exotic species in Florida is *Schinus terebinthifolius* Raddi (*Schinus*). This invasive exotic is found in disturbed and native habitats, ranging from upland rock pinelands into coastal mangrove forests. Also known as the Brazilian pepper, Christmas berry and Florida holly, this plant was first imported

into Florida about 150 years ago as an ornamental (Austin 1978). Its current widespread distribution in Florida is in part contributed by Dr. George Stone who in the late 1890's, strongly advocated its ornamental value by distributing seedlings to anyone interested (Nehrling 1933). Dispersal by birds, raccoons and deer attracted to the red berries during winter months of food scarcity (Ewel 1986) is also believed to contribute to *Schinus*' success. Although studies have been carried out on *Schinus* germination (Mytinger 1985, Nilsen and Muller 1980a,b), this species survival post-germination has not been fully explored. Moreover, once *Schinus* reaches 1 m in height, individuals are not easily killed by fire as they resprout (Doren et al. 1991).

Previous field measurements have suggested that *Schinus* may be more tolerant of salinity than glycophytic native species (Chapter 2). Here, I compared the response of *Schinus* and native Florida species to different salinity treatments under controlled glasshouse conditions. I hypothesized that:

1. *Schinus* would grow faster than native species at all salinities, and
2. *Schinus* gas exchange would be less affected by salinity than that of native species.

METHODS AND MATERIALS

Species studied

I compared *Schinus* to native mangrove (*Rhizophora mangle* L. and *Laguncularia racemosa* L.) and upland species (*Rapanea punctata* (Lam.) Lundell and *Randia aculeata* L.) often found growing with the exotic in brackish saline areas. During fruiting, seeds of *Schinus* and native freshwater species were collected from plants in a brackish transition

zone (between mangroves and pineland) of coastal southwest Florida where all study species co-occurred. *Schinus* seeds were collected in March 1999, and *R. punctata* and *R. aculeata* seeds were collected in September - October 1999. Two hundred fifty seeds of each species were washed in 1.0% sodium hypochlorite and germinated on wet paper towels in individual dishes. The papery exocarp of *Schinus* seeds was removed prior to bleaching.

Seeds were germinated under 40W fluorescent Gro-Lights at 12-hour photoperiods. After complete emergence of the first two cotyledons, seedlings were transplanted into starter trays with individual 2.5 cm x 1.25 cm containers. Fifty four days after first observing germination, five seedlings from each of the five parent plants were selected for the experiment. Seedlings were transplanted into 3.8 L and subsequently 7.6 L pots. Only *Schinus* seedlings were successfully grown with this treatment. Seedlings of the other two native freshwater species were purchased from a local nursery where *R. punctata* had been germinated from wild-collected seeds and *R. aculeata* grown from cuttings.

Propagules of *R. mangle* and *L. racemosa* were collected from the same area as *Schinus* in October 1999 and returned to the Biology Department shadehouse at the University of Miami. All propagules were cleaned in freshwater and planted in 3.8 L pots. Seedlings of all species were transplanted (December 1999) into 7.6 L pots containing mixed, equal volumes of washed sand, sterilized potting soil, and coarse-grained vermiculite. Seedlings were kept on 1 m tall wire-frame benches in the shadehouse (approximately 70% ambient light) and watered twice daily with fresh water until January 2000 when they were moved into an adjacent glasshouse. The experiment

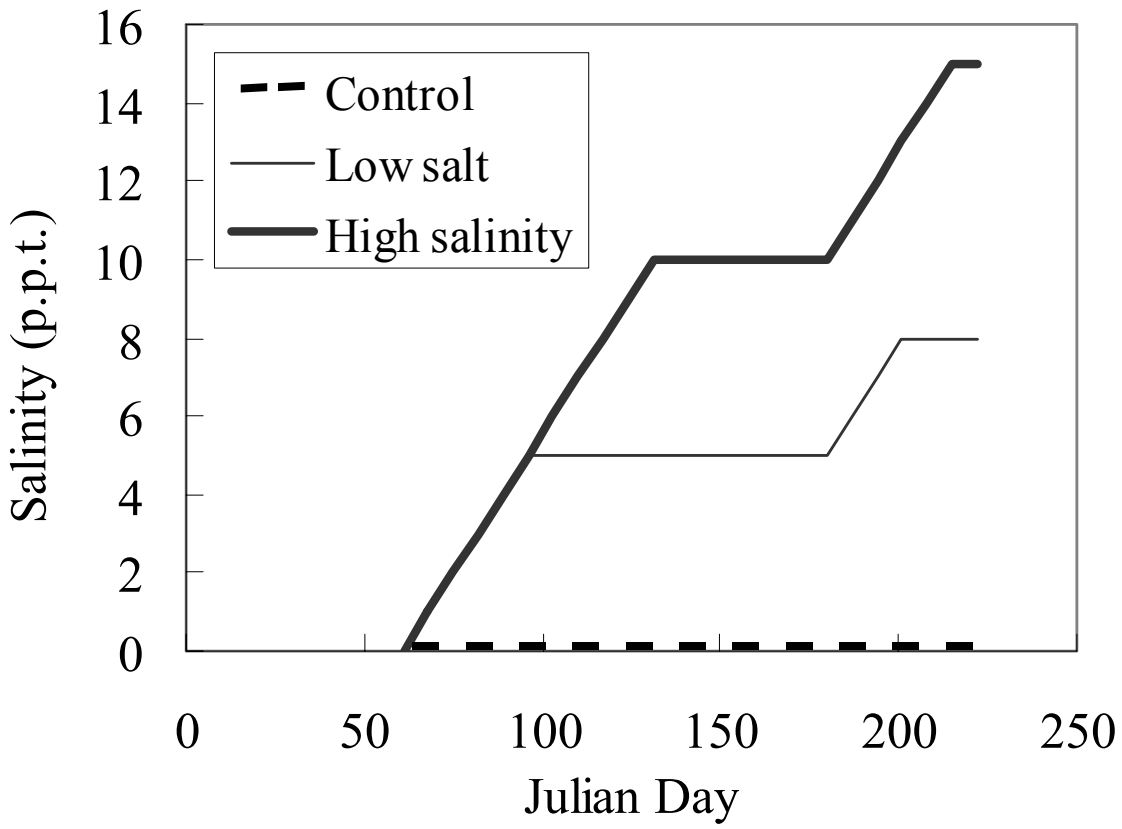
was carried out on 1 m high metal tables that supported 25 rows of three plants each, spaced at approximately 20 cm intervals between and within rows. The setup was divided into five blocks of one individual per species for each treatment (five rows x three deep = 15 plants each). Five individual per species were randomly placed in each row, one per block. All plants were individually labeled. Plants also were moved within and between adjacent blocks throughout the experiment to reduce position effects.

Each pot was individually watered using an automated drip irrigation system. Watering was initiated with timers at 0830 hrs each day, for 0.25 hours. Approximately 1.6 L of water was delivered to each plant during watering, completely saturating the soil. Excess water was allowed to freely drain from the pots. Control plants were irrigated with tap water while the two treatments were irrigated with different salinity seawater from two 100-gallon tanks. Throughout the experiment, the plants were fertilized on average once every three weeks using Peters Professional 20-20-20 (N-P-K) Plant Food with micronutrients. Plants were hand-watered with approximately 0.34 g of the fertilizer, dissolved in 1L of either the appropriate tap water or seawater solution. Plants were irrigated once a day from March through June but during the warmer months of July and August (35°C average), supplemental afternoon irrigation was periodically applied.

Salinity treatments

The experiment started on March 8th 2000 (Julian Day 68), timed to coincide with the earliest possible initiation of seasonal growth. The three treatments were control (0 parts per thousand (p.p.t.)), low (8 p.p.t.) and high (15 p.p.t.) salinity, with 25 plants (five of each species) per treatment. Seawater solutions were prepared using untreated

Figure 6.1. Salinity levels in parts per thousand (p.p.t.) imposed on plants under the three treatment conditions.



Sea-Salts and tap water. Salinity treatments started at 1g L^{-1} (1 p.p.t.) and raised 1 p.p.t. each week until 0, 5 and 10 p.p.t. were reached (Fig. 6.1). Plants were maintained at those values for approximately a month before salinity was increased weekly until final values were achieved. The experiment was terminated after 181 days (5th September 2000), approximately 1 month after high salinity levels were reached.

Measurements

Two individuals of each species grown with the experimental plants were harvested at the start of the experiment for determination of relative growth rates. Plant height, leaf area, number of leaves and branches, and stem circumference were measured. All plants were oven-dried at 65°C for two weeks and individual organs weighed.

Plant morphometric (plant height, stem circumference, leaf number, largest leaf width and length) measures were taken after the start of the experiment, when both salinity treatments were at 5 p.p.t., at high salinity treatment of 10 p.p.t., and just prior to harvest (0, 8 and 15 p.p.t.). Because of multiple stems in *R. punctata* and *R. aculeata*, longest stem length was measured in place of plant height. Basal stem circumference was measured on the largest diameter stem in cases of multi-stemmed individuals; stem circumference was found to be a more precise measure of plant girth than plant diameter as *R. aculeata* stems were often asymmetrical. At the start of the experiment, one stem per plant was tagged midway along its length, and the number of leaves and branches distal to the marked point counted.

At harvest (September 5th 2000), all plants were defoliated and growth media washed off the roots. Fresh leaf weight of all plants was measured (Sartorius 4000,

Sartorius Corp., Goettingen, Germany). Whole plant leaf area was measured (LI-3000, LiCor, Lincoln, Nebraska) for three individuals per species within each treatment. For all plants, the second fully mature leaf from the longest shoot (that had been used for gas-exchange) was bagged separately for use in isotope and nitrogen analyses. All leaves were dried in a freeze-dryer (Labconco, Kansas City, KA) for one week. After drying, leaf weight of each plant was obtained. For individuals for which leaf area had been measured previously, specific leaf area (SLA, $m^2\ g^{-1}$) was obtained by dividing leaf area by total dry leaf weight. Stem and roots were air-dried for two months before weighing. Relative growth rate (RGR) was expressed by the equation:

$$RGR = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_2 = plant biomass at harvest (g), W_1 = initial plant biomass (g), t_2 = harvest date (month) and t_1 = start date of experiment (month). Additionally, proportions of leaves, stems and roots to total plant biomass were calculated. Root:shoot (R:S) ratio was also determined for all plants.

Dried leaves selected for isotopic analyses were frozen in liquid nitrogen before being ground using a mortar and pestle. Pure CO_2 was extracted from approximately 5 mg of leaf tissue based on the methods of Buchanan and Corcoran (1959), and analyzed on a mass spectrometer (VG Prism, Micromass, Middlebury, England). Leaf carbon isotopic signatures, in per mil units (‰), were determined using the following equation:

$$\delta^{13}C = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000 ,$$

where R_{sample} is the $^{13}C/^{12}C$ ratio of the sample, and $R_{standard}$ is the $^{13}C/^{12}C$ ratio of a standard referred to Pee-Dee Belemnite.

Total leaf nitrogen content ([N], g N g leaf^{-1}) was analyzed using an autoanalyzer (Carlo Erba NC2100, ThermoFinnigan Italia S.p.A., Milan, Italy) and expressed on a leaf weight basis (g N g leaf^{-1}). Nitrogen concentration was also expressed on a leaf area basis ([N], g N m^{-2} leaf).

Throughout the experiment, instantaneous gas exchange was measured with a LI-6200 (LiCor, Lincoln, Nebraska) on sunny days with light levels over 1000 μmol m^{-2}s^{-1} within the glasshouse. Three blocks of plants (total = 45 individuals) were selected, and gas exchange of all plants within the blocks measured between 0900 and 1500 hours. The second fully mature leaf on the longest stem of was measured using a 390 ml chamber attachment for 60 seconds. Different blocks were sampled each time. Gas exchange data from the last two sample days (Julian Day 197 and 217) were compared among species to determine plant salinity responses. Intrinsic water-use efficiency (WUE, μmol CO_2 mol^{-1} H_2O) was calculated by dividing net assimilation (A, μmol CO_2 m^{-2}s^{-1}) by stomatal conductance (g_s, mol H_2O m^{-2}s^{-1}), while mesophyll conductance (g_m, m s^{-1}) was determined by dividing A by internal CO_2 concentration (c_i, μmol CO_2 m^{-3}). Photosynthetic nitrogen-use efficiency (PNUE, μmol CO_2 g^{-1} N s^{-1}) was determined by dividing A over [N]. As the variance between days was smaller than that among species, data from both days were pooled to increase sample size; values from individuals sampled on both days were averaged before analysis.

Data analysis

To measure plant morphometric response to salinity, the first set of growth measures (Julian Day 77) made shortly after the start of the experiment were excluded

because the measures were not significantly different among treatments when analyzed with a one-factor analysis-of-variance (ANOVA) for each species. Instead, analyses were carried out only on subsequent sets of morphometric measures (Julian Days 111, 210, and 253). Change in growth (%) was measured using the second date (Julian Day 111) of sampling (when salinity for both treatments was 5 p.p.t.) as the initial start point (normalized to 100%). For stem length, leaf number and stem circumference, differences over time and treatment in each species were analyzed using a repeated-measures ANOVA. Largest leaf length and width were analyzed with a multivariate analysis-of-variance (MANOVA), once at the start and again at the end of the experiment. This method of analysis was used because different leaves were measured in the experiment. Percentage leaf, stem and root biomass was also analyzed with a MANOVA. For all analyses described above, the probability of Type I error was set at 0.05 (i.e. $\alpha = 0.05$).

Parameters related to plant biomass (RGR, leaf area ratio (LAR, $m^2\ kg^{-1}$), SLA, and R:S), gas exchange(A, g_s, g_m, A/g_s, $\delta^{13}C$, and PNUE), and [N] were first analyzed independently using a two-factor fixed-effects (Model I) ANOVA to determine overall differences among species and treatments. Level of significance was then Bonferroni-corrected for the number of parameters tested within each group (biomass: $\alpha = 0.05/4$, $P < 0.0125$; gas exchange: $\alpha = 0.05/6$, $P < 0.0083$, [N]: $\alpha = 0.05$, $P < 0.05$). If there was a difference among species, this difference was further tested using the Tukey HSD. If treatment effects were significant, each species was then analyzed, using single-factor ANOVAs, to determine which species showed significant treatment effects. These single-

Figure 6.2. Changes in longest stem length (%) for each species from the start of data analysis (growth at start normalized to 100%). Averages of the control (◆), low salinity (■), and high salinity (▲) treatments are shown with their standard errors. Asterisks (*) indicate significant differences among treatments. For each sample period, symbols with the same letters do not differ significantly at $P > 0.05$ by post-hoc Tukey HSD.

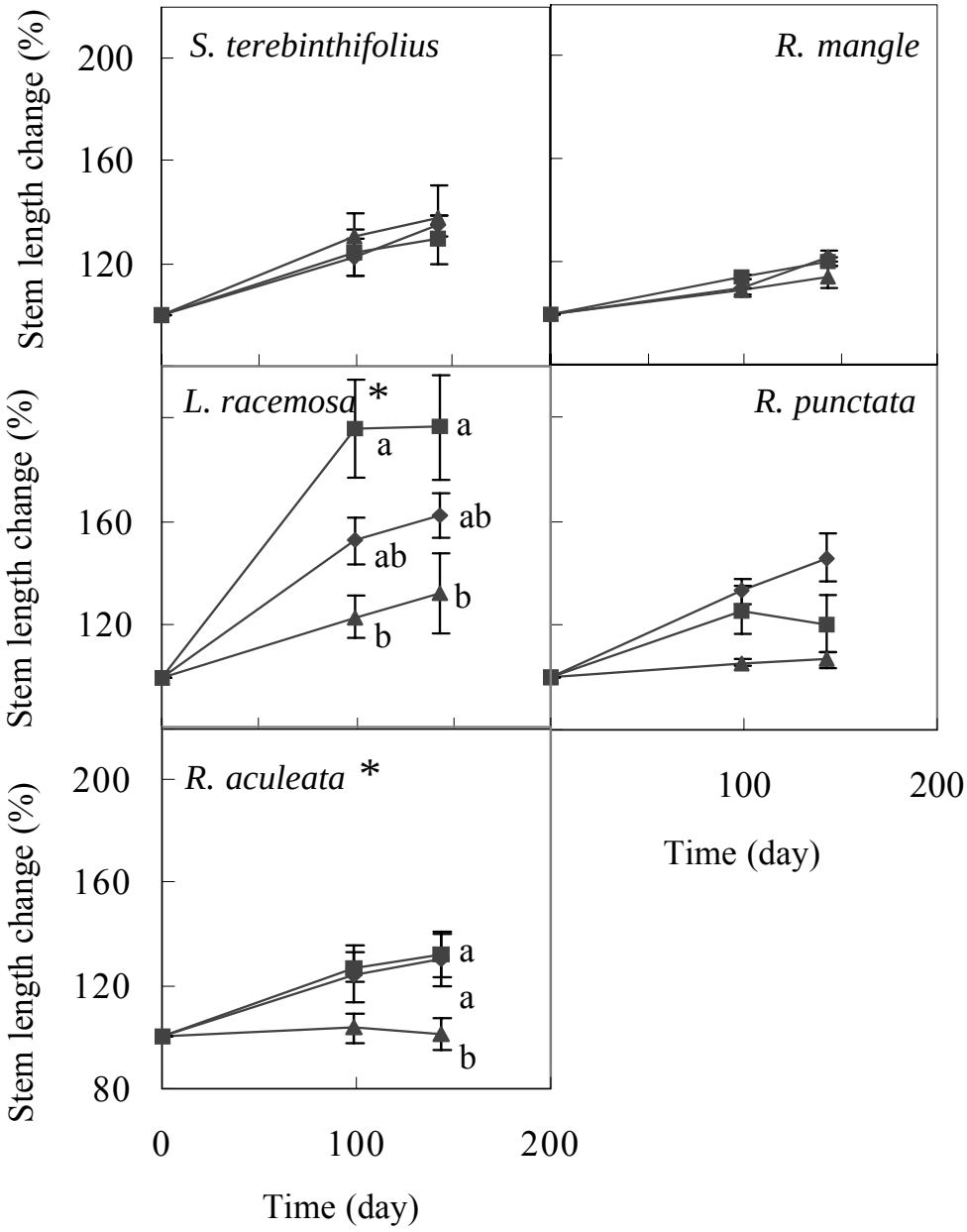

S. terebinthifolius
R. mangle
L. racemosa *
R. punctata
R. aculeata *
Stem length change (%)
Time (day)
200
160
120
80
0
100
200
a
ab
b

Table 6.1. Repeated measures two-factor ANOVA among treatments and across times for the exotic *S. terebinthifolius* and four native species grown in 7.6 L pots under different salinity treatments. Asterisks by species' names indicate that Mauchly's Sphericity assumptions were not met in that repeated-measures ANOVA; hence, lower-bound degrees of freedom were used in reporting *P*-values. Numbers in bold are significant at the $\alpha = 0.05$ level ($P < 0.05$).

Change in growth	df, error df	$P_{(Treatment)}$	df, error df	$P_{(Time)}$	df, error df	$P_{(Treatment \times Time)}$
Stem length						
S. terebinthifolius	2, 11	0.881	2, 22	**<0.001**	4, 22	0.770
R. mangle	2, 12	0.542	2, 24	**<0.001**	4, 24	0.224
*L. racemosa**	2, 12	**0.032**	1, 24	**<0.001**	2, 24	**0.024**
*R. punctata**	2, 12	0.102	1, 24	**<0.001**	2, 24	**0.025**
*R. aculeata**	2, 12	**0.028**	1, 24	**0.002**	2, 24	0.075
Stem circumference						
S. terebinthifolius	2, 10	0.480	2, 20	**0.003**	4, 20	0.054
*R. mangle**	2, 12	0.473	1, 24	0.221	2, 24	0.260
L. racemosa	2, 10	0.418	2, 20	**<0.001**	4, 20	0.237
R. punctata	2, 11	**0.044**	2, 22	0.866	4, 22	0.820
R. aculeata	2, 11	**0.044**	2, 22	0.182	4, 22	0.242
Leaf number						
S. terebinthifolius	2, 10	0.408	1, 10	0.920	2, 10	0.374
R. mangle	2, 12	0.146	1, 12	**0.014**	2, 12	**0.030**
L. racemosa	2, 11	**<0.001**	1, 11	0.933	2, 11	0.055
R. punctata	2, 12	**0.007**	1, 12	0.062	2, 12	**0.004**
R. aculeata	2, 10	**0.048**	1, 10	**0.015**	2, 10	0.268

factor ANOVA levels of significance were Bonferroni corrected (five species sampled: $\alpha = 0.05/5$, $P < 0.01$). A species that showed significant treatment effects was further tested with the Tukey HSD.

RESULTS

Growth rates and biomass changes

All species had high survivorship with treatment. With the exception of one *L. racemosa* that died and another that suffered leaf loss under high salinity, all individuals survived the experiment. All plants grew in hight over time, but only *L. racemosa* and *R. aculeata* (Table 6.1, Fig. 6.2) were significantly affected by treatment. Although stem length in *Schinus* and *R. mangle* did not vary significantly among salinity treatments (Table 6.1, Fig. 6.2), *L. racemosa* grown under intermediate salinity grew more than in the other two treatments while for *R. aculeata*, plants under high salinity conditions actually became smaller because of terminal tip death and abscission (Fig. 6.2).

Changes in stem circumference across treatments were only significant for *R. punctata* and *R. aculeata* for which salinity conditions resulted in plant stems decreasing in size (Fig. 6.3). Both *Schinus* and *L. racemosa* showed an increase in stem circumference over time but *R. mangle* did not increase significantly in girth throughout the sample period (Table 6.1).

Leaf numbers were significantly different among treatments for *L. racemosa*, *R. punctata* and *R. aculeata* (Table 6.1 and Fig. 6.4). Low salinity treatment plants of *L. racemosa* had the highest number of leaves, followed by the control and the high salinity treatment (Fig. 6.4). In *R. punctata* and *R. aculeata*, however, both salinity treatments

Figure 6.3. Changes in basal stem circumference (%) for each species from the start of data analysis (growth at start normalized to 100%). Averages of the control (◆), low salinity (■), and high salinity (▲) treatments are shown with their standard errors. Asterisks (*) indicate significant differences among treatments. For each sample period, symbols with the same letters do not differ significantly at $P > 0.05$ by post-hoc Tukey HSD.

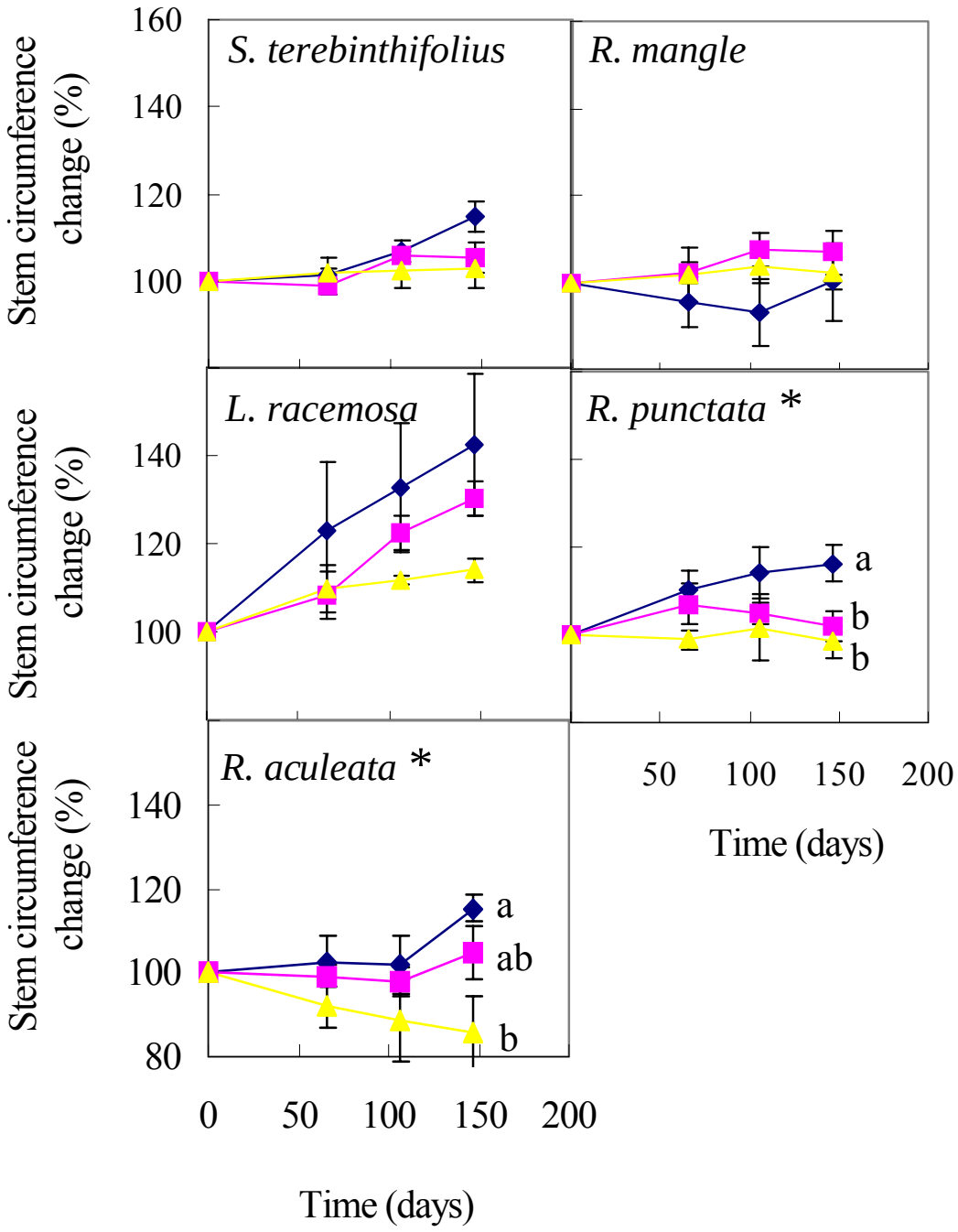
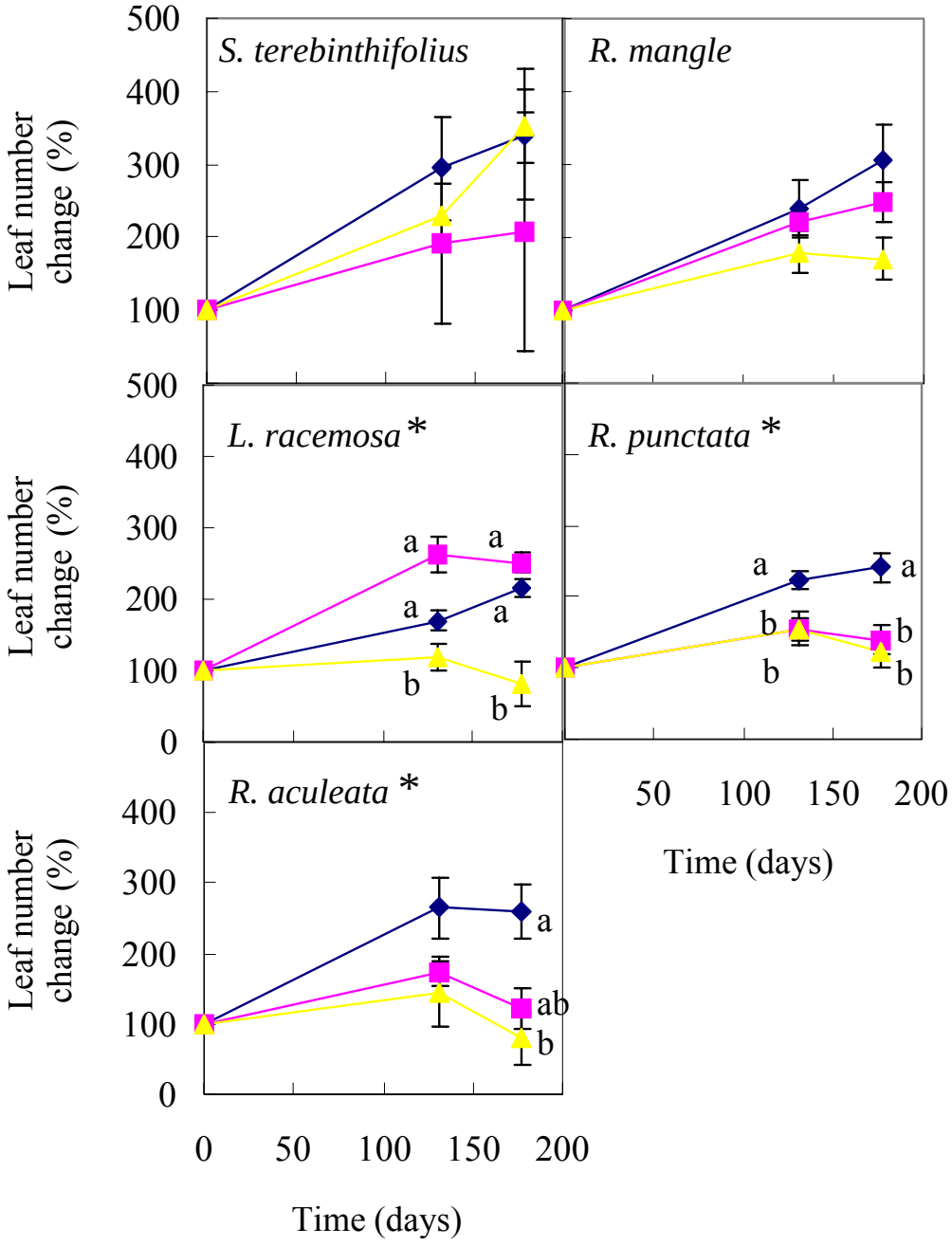

S. terebinthifolius
R. mangle
L. racemosa
R. punctata *
R. aculeata *
Stem circumference change (%)
Time (days)
160
140
120
100
80
0
50
100
150
200
a
b
b
a
ab
b

Figure 6.4. Changes in leaf number (%) for each species from the start of data analysis (growth at start normalized to 100%). Averages of the control (◆), low salinity (■), and high salinity (▲) treatments are shown with their standard errors. Asterisks (*) indicate significant differences among treatments. For each sample period, symbols with the same letters do not differ significantly at $P > 0.05$ by post-hoc Tukey HSD.


S. terebinthifolius
R. mangle
L. racemosa *
R. punctata *
R. aculeata *
Leaf number change (%)
Time (days)
0
100
200
300
400
500
50
150
a
b
ab

resulted in plants with fewer leaves than the controls (Fig. 6.4). The number of leaves did not change in either *R. mangle* or *Schinus*. Leaf lengths and widths, analyzed with MANOVAs, were not significantly different either across treatments or among species both at the start and at the end of the experiment.

Relative growth rates varied among species but not across treatments. Among species, RGR was highest in *L. racemosa* and *R. punctata* (Fig. 6.5A). *Laguncularia racemosa* growth rates, unlike all other species, was actually stimulated by the low salinity treatment (single-factor ANOVA: $F_{2,9} = 4.79$, $P = 0.038$) (Fig. 6.5A). Leaf area ratios (Fig. 6.5B) varied across treatments ($F_{2,28} = 6.21$, $P < 0.012$). Despite an overall decrease in LAR (Fig. 6.5B) with increasing salinity, the only species to significantly show a treatment effect was *R. aculeata* (single-factor ANOVA: $F_{2,5} = 8.42$, $P = 0.025$).

Biomass allocation was not significantly different across treatments (Table 6.2A) but was significantly different among the species compared (Table 6.2B). *Schinus* allocated more of its biomass to stem compared to native species, and the smallest proportion to leaves. *Schinus* only allocated an average 15.4% of its total biomass towards leaves whereas most species leaves were over 20% of their total biomass.

There was a difference in SLA across treatments ($F_{2,28} = 6.21$, $P < 0.012$) but not among species ($F_{4,28} = 2.32$, $P > 0.012$). Increasing salinity decreased the SLA of *R. aculeata*. For the low salinity treatment, *Schinus* SLA was marginally significantly higher than native species (one-factor ANOVA, $F_{4,14} = 2.74$, $P = 0.067$) indicating thinner leaves than those of native species. Root:shoot ratios showed no differences among treatments ($F_{2,53} = 1.12$, $P > 0.012$) for the species sampled (Fig.s 6.5C and D). There were species differences in R:S ratios ($F_{4,53} = 3.22$, $P = 0.019$), but no interaction between treatment

Figure 6.5. Averages (± standard errors) of *Schinus* (□), *R. mangle* (▨)), *L. racemosa* (■), *R. punctata* (▧), and *R. aculeata* (▨) under control, low, and high salinity treatments. Graphs show: A. Relative growth rates (RGR), B. Leaf area ratio (LAR), C. Specific leaf area (SLA), and D. root:shoot ratios (R:S). Treatments followed by the same letters do not differ significantly at the $P > 0.012$ by post-hoc Tukey HSD after analysis with a two-factor ANOVA. Letters atop bars show differences among treatments within species at $P < 0.012$ by post-hoc Tukey HSD.

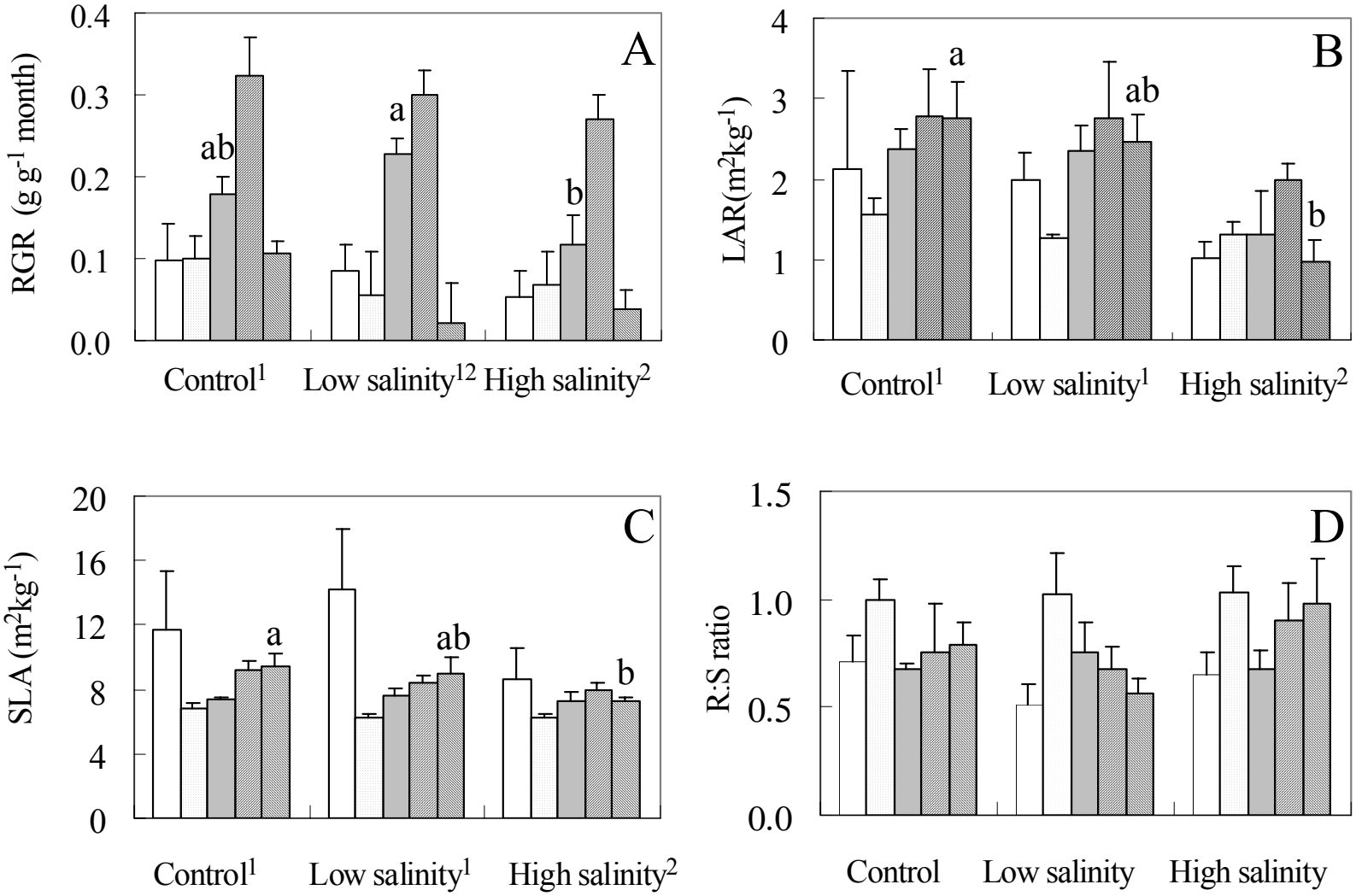

A
RGR (g g-1 month)
0.4
0.3
0.2
0.1
0.0
ab
a
b
Control1
Low salinity12
High salinity2
B
LAR(m2kg-1)
4
3
2
1
0
a
ab
b
Control1
Low salinity1
High salinity2
C
SLA (m2kg-1)
20
16
12
8
4
0
a
ab
b
Control1
Low salinity1
High salinity2
D
R:S ratio
1.5
1.0
0.5
0.0
Control
Low salinity
High salinity

Table 6.2. (A) Percentage leaf, stem, and root from total plant biomass *P*-values from a two-factor (for the five species across three salinity treatments) multivariate analysis-of-variance (MANOVA). (B). Percentage biomass fraction (± SEM) of each plant organ. Because of non-significance across treatments (shown in Table 6.2A), fractions for each species regardless of treatment were pooled. Values followed by the same letter do not differ significantly at $\alpha = 0.05$ by Tukey HSD following the MANOVA.

(A)

Factor	df	Leaf	df	Stem	df	Root
Treatment	2	0.059	2	0.197	2	0.648
Species	4	**0.003**	4	**<0.001**	4	**0.023**
Treatment x Species	8	0.179	8	0.407	8	0.388

Error df = 51

(B)

Species	df	Leaf	Stem	Root
S. terebinthifolius	15	15.4 ± 2.5 [a]	46.9 ± 1.7 [b]	37.7 ± 2.3 [a]
R. mangle	15	20.6 ± 0.9 [ab]	30.1 ± 1.9 [a]	49.3 ± 2.1 [b]
L. racemosa	15	21.8 ± 3.7 [ab]	34.5 ± 2.9 [a]	43.7 ± 2.4 [ab]
R. punctata	15	27.9 ± 2.3 [b]	31.7 ± 1.5 [a]	40.3 ± 2.5 [ab]
R. aculeata	15	20.6 ± 2.3 [ab]	37.5 ± 2.9 [a]	41.9 ± 2.6 [ab]

and species ($F_{8,53} = 0.519$, $P > 0.012$). *Schinus* R:S ratios were not different from those of most native species but were lower than those of *R. mangle* (which allocated almost 50% of its total biomass to roots) (Table 6.2B). Leaf [N] (Fig. 6.6) was significantly different among treatments ($F_{2,53} = 3.64$, $P < 0.05$) and among species ($F_{4,53} = 13.28$, $P < 0.05$) but there was no interaction between the two factors ($F_{8,53} = 0.93$, $P > 0.05$); [N] was lower in the controls than in the two salinity treatments. Across-treatment [N] was similar for all species except for *R. mangle*, which had significantly greater [N] contents across all treatments than the other species (Fig. 6.6).

Gas exchange and stable isotopes

Assimilation rates differed significantly among treatments ($F_{2,44} = 11.44$, $P < 0.008$) and species ($F_{4,44} = 4.98$, $P < 0.008$) but there was no significant interaction between the two factors ($F_{8,44} = 1.97$, $P > 0.008$). Assimilation rates were significantly lower in the high salinity treatments than in low salinity and control treatments (Fig. 6.7A). *Schinus* had the lowest *A* of all species, significantly lower than *R. aculeata* and *R. mangle* (which had the highest *A* rate of all species compared) (Fig. 6.7A). Individual species' one-factor ANOVAs showed that differences between treatments within species were only present in *R. mangle* ($F_{2,9} = 21.64$, $P < 0.01$) and *R. punctata* ($F_{2,9} = 17.35$, $P < 0.01$).

Stomatal conductance was significantly different among treatments ($F_{2,44} = 4.93$, $P = 0.012$) but not among species ($F_{4,44} = 2.40$, $P > 0.008$). There was also a significant interaction between both factors ($F_{8,44} = 3.11$, $P < 0.008$). Stomatal conductance was

Figure 6.6. Leaf nitrogen concentration on an area basis ([N]). The bars show averages (± SEM) of *Schinus* (□), *R. mangle* (▭), *L. racemosa* (■), *R. punctata* (▨), and *R. aculeata* (▨) under control, low, and high salinity treatments. Asterisks (*) indicate treatment differences at $P < 0.05$ by Tukey HSD after one-factor analyses-of-variance within each treatment (for species differences).

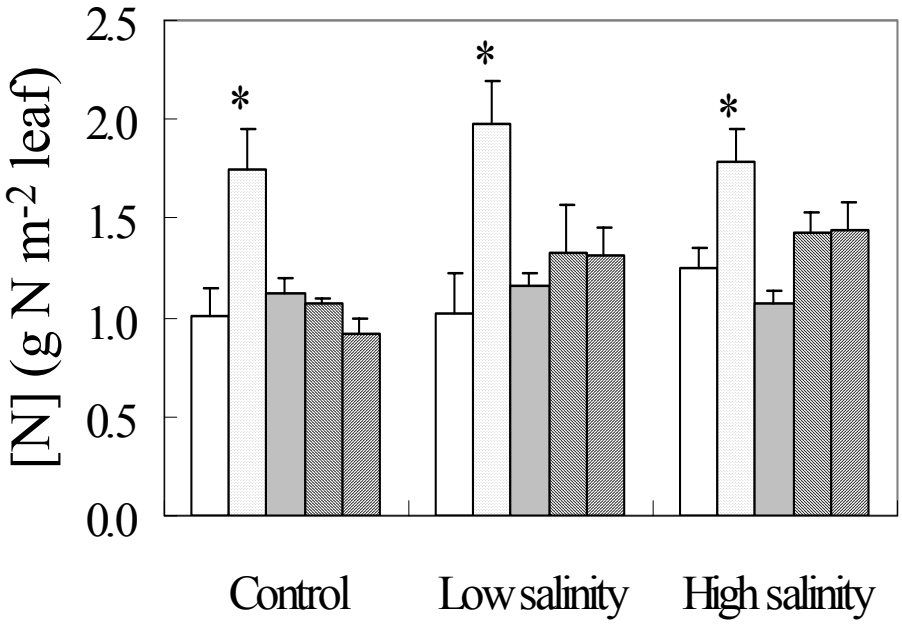
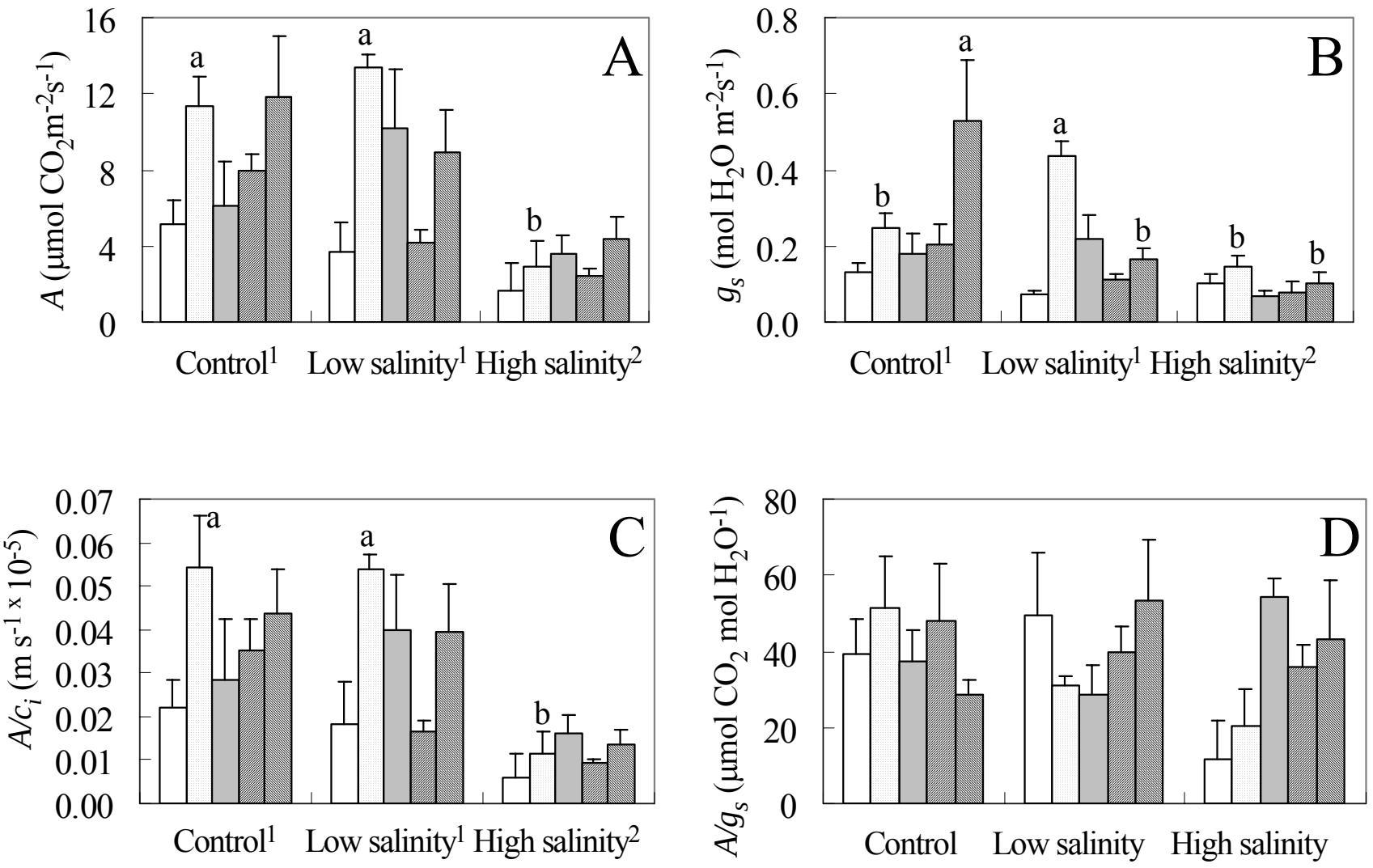


Figure 6.7 Graphs of: A. Assimilation (A), B. Stomatal conductance (g_s), C. Mesophyll conductance (g_m), and D. Intrinsic water-use efficiency (A/g_s) of study plants. Bars show averages (± SEM) of *Schinus* (□), *R. mangle* (▒), *L. racemosa* (■), *R. punctata* (▨), and *R. aculeata* (▨) under control, low, and high salinity treatments. Treatments followed by the same letter do not differ significantly at $P > 0.0083$ by Tukey HSD after analysis with a two-factor ANOVA. Species averages, denoted by the same letter, do not differ at $P > 0.01$ by Tukey HSD after analysis with a single-factor ANOVA.

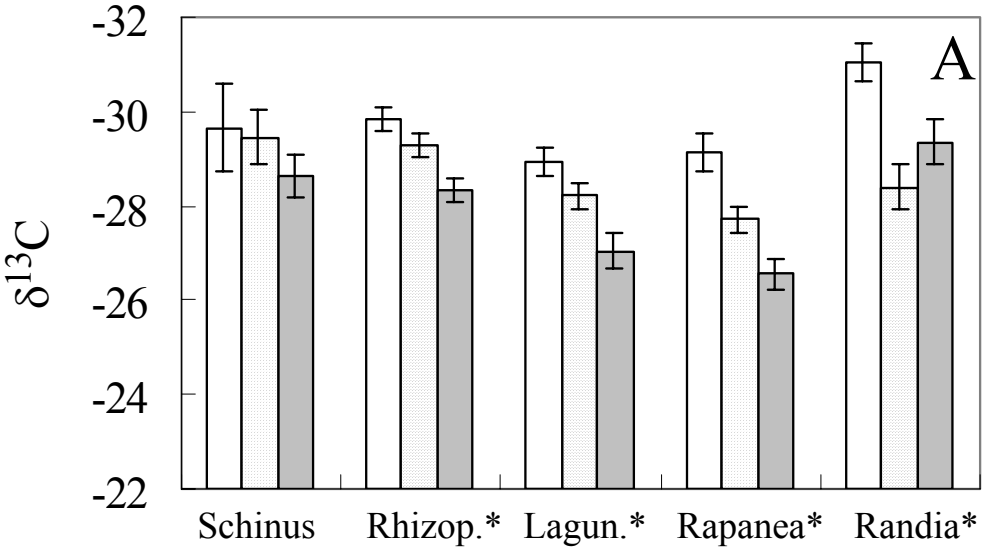

A
B
C
D
A (μmol CO2m-2s-1)
gs (mol H2O m-2s-1)
A/ci (m s-1 x 10-5)
A/gs (μmol CO2 mol H2O-1)
Control1
Low salinity1
High salinity2
Control
Low salinity
High salinity
a
b

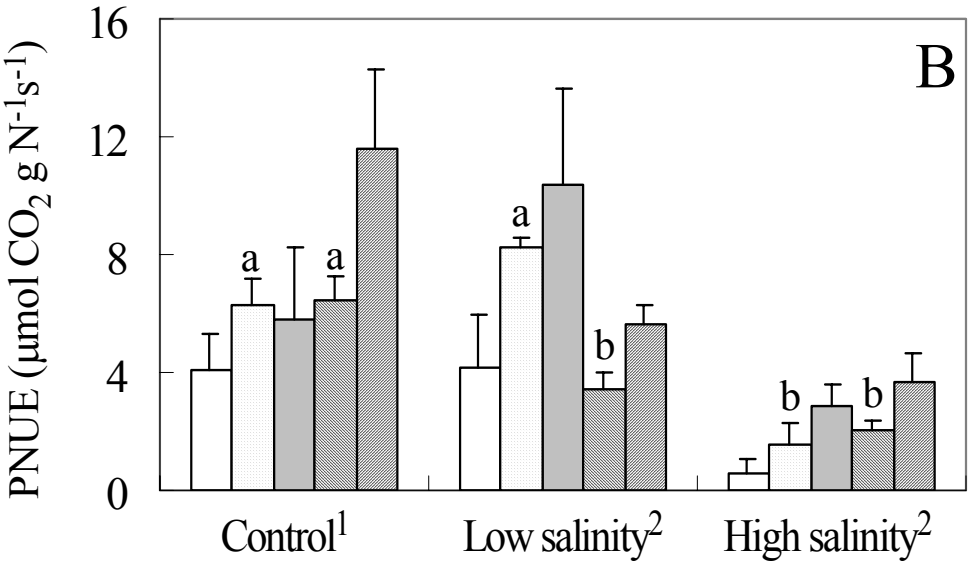
similar between the low salinity treatment and the control but greater than the high salinity treatment (Fig. 6.7B). One-factor ANOVAs for each species showed that *R. mangle* ($F_{2,12} = 15.72$, $P < 0.01$) was affected by salinity. Mesophyll conductance, A/c_i (Fig. 6.7C), was significantly different among treatments ($F_{2,44} = 6.18$, $P < 0.008$) but not among the five species compared ($F_{4,44} = 3.40$, $P > 0.008$). There was also no interaction between factors ($F_{8,44} = 0.80$, $P > 0.008$). Mesophyll conductance was significantly lower in the high salinity treatment than in the other two treatments and was significantly lower in *Schinus* than in *R. mangle*. Within species, there were no differences observed among treatments except in *R. mangle* which showed greater g_m in the low salinity treatments than the control and high salinity treatments. Mesophyll conductance of *Schinus* and the other native species, however, did not significantly differ.

Intrinsic WUE (Fig. 6.7D) showed no significant differences among treatments ($F_{2,44} = 0.58$, $P > 0.008$) or species ($F_{4,44} = 0.82$, $P > 0.008$). Overall, carbon isotopic signatures (Fig. 6.8A) were also not significantly different either among species ($F_{4,60} = 2.27$, $P > 0.008$) or among treatments ($F_{2,60} = 2.65$, $P > 0.008$). However, within each species, differences within treatments were observed in all native species ($P < 0.01$) (Fig. 6.8A) with the exception of *Schinus*.

Photosynthetic nitrogen-use efficiency (Fig 6.8B) was significantly different over treatments ($F_{2,42} = 13.94$, $P < 0.008$) and among species ($F_{4,42} = 3.33$, $P = 0.019$); PNUE was lower in plants from the high salinity treatment than in the controls and low salinity plants. Among species post-hoc comparisons showed that PNUE was significantly different between *Schinus* and *R. aculeata*. *Schinus* had the lowest PNUE of all species while *R. aculeata* had the highest values (Fig. 6.8B). Individual species comparisons

Figure 6.8. Leaf: A. Carbon isotope signatures ($\delta^{13}C$), and B. photosynthetic nitrogen-use efficiency (PNUE). Carbon isotope data (A.) are grouped by species as there were no overall treatment or species differences. Averages (± SEM) are denoted as such: control (□), low (▨), and high salinity (■). Species names marked with asterisks (*) indicate treatment differences at $\alpha = 0.01$ using a post-hoc Tukey HSD after one-factor analyses-of variance within each species (for treatment differences). Average PNUE (B.) (± SEM) of *Schinus* (□), *R. mangle* (▨), *L. racemosa* (■), *R. punctata* (▧), and *R. aculeata* (▨) under control, low and high salinity treatments. Treatments followed by the same letter do not differ significantly at $\alpha = 0.008$ ($P < 0.008$) using a post-hoc Tukey HSD after analysis by two-factor analysis-of-variance. Letters atop bars show within-species treatment differences at $P < 0.01$ by post-hoc Tukey HSD.


A
-32
-30
-28
-26
-24
-22
δ13C
Schinus
Rhizop.*
Lagun.*
Rapanea*
Randia*


B
16
12
8
4
0
PNUE (μmol CO2 g N-1s-1)
a
a
a
b
b
b
Control1
Low salinity2
High salinity2

showed significant differences among treatments in *R. mangle* and *R. punctata*; plants grown under high salinity had the lowest PNUE among the three treatments.

DISCUSSION

Plant responses to salinity have been well documented by various workers (e.g. see reviews by Ball 1988, Greenway and Munns 1980, Flowers and Yeo 1986, Munns 1993). Studies have shown that plant responses are varied and non-uniform, even within functional groups (e.g. Warwick and Bailey 1997). In this study, salinity significantly affected many aspects of growth and morphology of native species but not *Schinus* (Fig.s 2 - 4). With regards to changes in stem length, circumference or leaf length, *Schinus* and *R. mangle* were not significantly affected by salinity while *L. racemosa* was actually stimulated by low salinity with respect to stem length and circumference. This indicates that growth patterns in the exotic are less sensitive to salinity than those of native freshwater species. Both native upland species, *R. punctata* and *R. aculeata*, showed poor morphometric growth under saline conditions. Decrease in stem length growth is a common response to salinity. For example, Agastian and Vivekanandan (1997) showed a reduction in shoot length with increasing salinity with a mulberry (*Morus alba* L.) genotype.

My general findings concur with previous studies on salinity (e.g. Allen et al 1994, Lissner and Schierup 1997, Morris and Ganf 2001), which showed that salinity affected RGR (Fig. 6.5A). Most non-halophytes grow slower under salinity treatments than under control conditions (Munns and Termaat 1986). Halophytes, however, can show greater growth rates under intermediate salinity conditions (e.g. Munns et al. 1983,

Cheeseman et al. 1986). Growth rates (Fig. 6.5A), leaf traits (Fig.s 6.5B and C) and biomass partitioning (Table 6.2A) of all plants showed that *Schinus*' response to salinity was not significantly different from those of native species across treatments. However, among all species compared, *Schinus* invested the most biomass in stems and least of all in its leaves (Table 6.2B). Therefore, even though the exotic allocated very little biomass into leaves, it still had a similar leaf area/dry plant biomass ratio (Fig. 6.5B) and [N] (Fig. 6.6) to native species. *Schinus* leaf area was comparable to other species except that the leaves were thinner and most likely less costly to construct. Baruch and Goldstein (1999) have shown that leaf construction costs of thin leaves are lower than those of thick leaves in some exotic Hawaiian species.

Leaf area is one of the first plant traits to be affected by salinity; plants that are unable to tolerate saline conditions often have smaller leaf areas because of salts affecting leaf expansion (Marcelis and van Hooijdonk 1999). None of the study species showed either reduced leaf areas (Fig. 6.5B) or thicker leaves (Fig. 6.5C) with increasing salinity. High growth rates have been shown in plants with high SLA (Poorter and Lambers 1992). Based on this premise, *Schinus* should potentially have the highest RGR based on leaf thickness (i.e. SLA) but this exotic did not demonstrate greater RGR or morphometric growth than native species (Fig.s 6.2-6.5A).

Plant R:S ratios also have been shown to be affected by salinity whereby salinity-tolerant plants show a reduction in R:S ratios (Cheeseman and Wickens 1986) while salinity intolerant plants have decreased shoot growth which results in greater R:S ratios (Munns and Termaat 1986) than in control plants. Salinity did not affect R:S ratios of any of the study plants (Fig. 6.5D). It is possible that the slow, weekly increase in salinity

allowed the plants time to acclimatize and become hardened to the salts within the substrate, thereby maintaining their R:S ratios. On the other hand, root restriction by pots also could have affected the R:S ratios.

Plant gas exchange of some species was affected by salinity. Gas exchange in *R. mangle* was greater under low salinity conditions than in either fresh water or high salinity conditions (Fig. 6.7A-C). In the glycophytes, *R. punctata* (Fig. 6.7A) and *R. aculeata* (Fig. 6.7B), however, it decreased linearly. These findings are consistent with those of other workers. Decreased gas exchange with increasing salinity has been documented in glycophytic species (e.g. Downton et al. 1985, Perry and Williams 1996, Marcelis and Hooijdorik 1999, Asch et al. 2000). At high salinities, gas exchange is most likely limited because of cells being biochemically disrupted by the presence of salts (Munns 1993). Ma et al. (1997) have shown that under low salinity conditions, decreased *A* in apple trees is caused by inhibition of the light independent reaction and not because of damage to the photosynthetic apparatus. Halophytic species under low salinity conditions (e.g. 200 mmol NaCl) have been shown to have greater *A* than when under either high salinity or control conditions (Cheeseman et al. 1986, Maggio et al. 2000, Lin and Sternberg 1992).

Contrary to patterns found in other woody C_3 invasive exotic species (e.g. Pattison et al. 1998, Baruch and Goldstein 1999), despite having greater SLA, *Schinus* did not have greater *A*, g_s or g_m than native species (Fig.s 6.7A-C). However, *Schinus*' consistently low gas exchange resulted in similar intrinsic WUE (Fig. 6.7D) and PNUE (Fig. 6.8B) between *Schinus* and most of the native species. Further evidence of *Schinus*'

invariant responses to salinity is also seen in its carbon isotope signatures. *Schinus* was the only species to not show a $\delta^{13}C$ response across treatments (Fig. 6.8A).

Physiological differences have been found between native and exotic species. For example, Baruch and Goldstein (1999) found that greater *A* and SLA corresponded to lower construction costs within invasive exotic species. Plants with greater *A* have been shown to have greater nitrogen concentrations (on a mass basis) and SLAs (Reich 1993), which can potentially translate into greater RGR and hence contribute to the invasive capacity of the exotic plant species. Poorter and Evans (1998) found that species with inherently high SLA used more of their nitrogen to produce thylakoid membranes and rubisco bisphosphate carboxylase (rubisco) molecules, which potentially translated into an increase in leaf PNUE. Unlike the study (Baruch and Goldstein 1998) showing a greater daily *A* capacity in invasive species than native plant species, *Schinus A* in this study was not significantly different from that of native species.

CONCLUSION

Plants that express high phenotypic plasticity are believed to have the capability of being successful invaders (Kutch and Kappen 1991, Vicker 1974). The interpretation of phenotypic plasticity is complicated, however, because high phenotypic plasticity in one set of characters often is at the "cost" of phenotypic plasticity in another character (Lambers et al. 1998). Further, phenotypic plasticity of morphological characters is not always associated with increased tolerance to environmental variation. As a successful invader of south Florida ecosystems, *Schinus* does not appear to be very plastic in its

morphometric responses to salinity treatments. Its gas exchange and resource use (as measured by WUE, PNUE and $\delta^{13}C$), is comparable to those of native species.

Schinus may be more tolerant of salinity, however, as many of its morphological/physiological characteristics were not affected by salinity. In contrast, the glycophytic species (*R. punctata* and *R. aculeata*) were inhibited by increasing salinity. This tolerance could confer an advantage to *Schinus* over native glycophytes in transitional zones where salinity can fluctuate. The results reported here are consistent with my field observations of water uptake by *Schinus* which was not influenced by salinity to the same extent as native glycophytic species (Chapter 3).

Chapter 7

Growth and gas exchange responses of flooded *Schinus terebinthifolius* and native South Florida species.

INTRODUCTION

Humans have transported plants for food, medicinal and ornamental values since the earliest days of our history (diCastri 1989). A recent study by Pimentel et al. (2000) estimate that about 50,000 exotic plant and animal species have been introduced into the United States, either on purpose or by accident. This rate of transport has significantly increased because of greater human mobility in the modern age of easily accessible transport (Bright 1998, Simberloff 1997) as the last two centuries have seen higher rates of plant transport than the last thousand.

South Florida has always been a hub for import of non-native species from around the world. Over 456 million plants were imported into the United States via Miami International Airport in 1990 (U.S. Congress 1993). This disproportionately high number of imported exotic plants as well as human disturbance of the South Florida landscape has been conducive for the establishment of invasive exotics.

One of the most problematic invasive exotic species in Florida is *Schinus terebinthifolius* Raddi (*Schinus*). Also known as the Brazilian pepper, Christmas berry and Florida holly, this plant was first imported into Florida about 150 years ago (Schmitz et al. 1997) as an ornamental (Austin 1978). Its current wide distribution in Florida is believed to be in part contributed by Dr. George Stone who in the late 1890's, strongly

advocated its ornamental value by distributing seedlings to anyone interested (Nehrling 1933). Today, *Schinus* is found in about 280,000 ha of both disturbed and native habitats in South Florida (1993 South Florida Water Management District Survey as cited in Schmitz et al. 1997). This exotic can be found growing from upland habitats into lowland mangrove forests but one of the areas most threatened by *Schinus* is the Long Pine Key Pinelands in Everglades National Park. Rock pinelands occupy only about 10% of their original range (Lodge 1994) and are currently being threatened by *Schinus* growing adjacent to the pinelands in a disturbed previously farmed area known as Hole-in-the-Donut. Seasonal conditions in South Florida result in fluctuating annual groundwater levels (Chen and Gerber 1990) but human manipulations of hydrology over the last 40 years are believed to have resulted in larger seasonal differences in hydrology that may contribute to the success of Schinus in native freshwater upland systems (Lodge 1994).

In a previous field study, native species water uptake patterns were more affected by the wet season than were those of the exotic (Chapter 3), probably as a result of root flooding. This may be caused by the tolerance of *Schinus* to root flooding. The purpose of this study was to compare *Schinus* growth rates and gas exchange patterns with those of native species commonly found in pinelands, under controlled flooded conditions. It was hypothesized that *Schinus* gas exchange and growth rates would be less affected by flooding than those of native species. If this hypothesis was true, it is possible that *Schinus* tolerance of flooded conditions may contribute to its success in Florida.

METHODS AND MATERIALS

Species studied

Schinus is a dioecious evergreen perennial widely found in South Florida. This exotic grows to about 5 m in the Everglades, but can reach 13 m in South Florida (Barrett 1956). The three native evergreen species compared with *Schinus* were *Baccharis halimifolia* L. (Asteraceae), *Rapanea punctata* (Lam.) Lundell (Myrsinaceae) and *Randia aculeata* L. (Rubiaceae). All are either small trees or shrubs commonly found in native upland pinelands of Everglades National Park.

Seeds of *Schinus* and *B. halimifolia* were collected from five parent plants of each species from pinelands in Everglades National Park from September to October 1998. Prior to germination, *Schinus* exocarps were removed by vigorously rubbing the seeds on a coarse-grade (2-mm mesh) sieve under running water. The glabrous pappus hairs of *B. halimifolia* seeds were manually removed prior to washing. All seeds were then washed in 1% sodium hypochlorite for approximately 10 minutes before being rinsed in distilled water. Fifty seeds from each parent tree were germinated on paper towels in individual 6-cm diameter aluminum dishes under 40-watt fluorescent Gro-Lights at 12-hour photoperiods in late November 1998. Germination was faster in *Schinus* (initiated after one week) than *B. halimifolia* (initiated after about 3 weeks).

After complete expansion of the two cotyledonary leaves, seedlings were transplanted into starter trays with individual 2.5 cm x 1.25 cm containers. The growth medium used throughout this experiment was a mix of equal volumes of washed sand, twice-autoclaved potting soil and vermiculite. The soil was sterilized to prevent mycorrhizal fungal infections. Twelve seedlings of each species growing in starter trays

were randomly chosen for individual transplant into bleach-washed 3.8 L plastic pots. All pots were placed in approximately 70% ambient light in the shadehouse of the Biology Department at the University of Miami. All seedlings were fertilized with 18-6-12 NPK Osmocote fertilizer and watered twice a day using an automated sprinkler system. Seeds of *R. punctata* and *R. aculeata*, collected from the same areas as the other species, failed to germinate in sufficient numbers. Seedlings in 3.8 L pots were obtained from a commercial grower where *R. punctata* had been grown from wild-collected seeds and *R. aculeata* from cuttings.

Plants of all species were grown in these 3.8 L pots for 4 months prior to transplant into clean 7.6 L pots. The plants were then moved onto 1 m tall wire-frame benches in the glasshouse at the University of Miami. The experiment was carried out with plants arranged in two columns of 25 rows; blocks were defined as five rows each. Ten individuals of each species were randomly selected for use in the experiment; two individuals of each species were randomly placed in each block, one per row. A total of 50 plants were used in the experiment (5 individuals/species/treatment). Each column of plants was subjected to either the flooded or control treatments for 197 days. Pots in the flooded treatment were placed into two-gallon Zip-Loc bags. All plants were spaced at 20 cm intervals. Individual pots were moved between blocks approximately every fortnight to prevent position effects. The two remaining plants of each species not used in the experiment were harvested at the start of the experiment. Plants were dried at 65°C for two weeks and weighed.

Control and treatment plants were watered with tap water for 15 minutes each morning (at 0800 hours). Treatment plants also received two extra 15-minute waterings

(at 1200 and 1600 hours). Approximately 1.6 L was delivered to each plant every watering period. Excess water was allowed to drain from control plants, but treatment plants, in Zip-Loc bags, had standing water at the soil surface. All plants were provided 0.34 g of Peter's Professional Plant Food with micronutrients (20-20-20 NPK), dissolved in 1L of water approximately every 3 weeks. Hydrologic turnover (via overflow spill) in the flooded treatments occurred on average every two days as the bags surrounding the pots held excess irrigated water.

The experiment was initiated on March 16th 2001. Stem circumference and length, leaf number, leaf length and width, were measured throughout the experiment. For some multi-stemmed *R. punctata* and *R. aculeata*, the longest stem was measured. Stem length increase (ΔS_{length}) was determined according the following equation:

$$\Delta S_{length} (\%) = [(Length_{Final} - Length_{Initial})/ Length_{Initial}] \times 100\%,$$

where $Length_{Initial}$ = first measure of stem length, and $Length_{Final}$ = final measure of stem length. Changes in all other morphometric parameters were calculated using similar equations.

Leaf gas exchange was measured on 22nd August and 5th September using a LI-6200 portable gas exchange system (LiCor, Lincoln, Nebraska) with a 390 ml chamber attachment. For each day, three individuals per species within each treatment were measured. The second fully expanded leaf on the longest stem was measured. As variance among species was greater than between days, data from both days were pooled. Data from plants sampled on both days were averaged before being pooled. Assimilation (A, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2}) and intrinsic water-use efficiency (A/g_s, μmol CO_2 mol H_2O^{-1}) were then averaged for each species. Mesophyll

conductance was determined by dividing *A* by internal CO_2 concentration (c_i, μmol CO_2 m^{-3}).

All plants were defoliated on Sept 21st 2001. Leaf area was measured using a LI-3000 (LiCor, Lincoln, Nebraska) before leaves were dried in convection ovens at 65°C for a fortnight. Stems and roots were air-dried separately for two months. Before drying, leaves used for gas exchange were set apart and dried in a freeze-dryer (Labconco, Kansas City, Kansas) for one week. Dried leaves were then weighed (Sartorius 4000, Sartorius Corp., Goettingen, Germany) to determine specific leaf area (SLA = leaf area/leaf mass, m^2 kg^{-1}). Plants harvested at the start of the experiment were not used for RGR calculations because use of these values showed no growth despite physical observations of growth in all plants. Instead, plant height of control plants were regressed against biomass at harvest and the equation used to estimate initial biomass for RGR calculations; all regression equations were significant (Table 7.1). Additionally, root:shoot (R:S) ratios also were calculated.

Leaves used for gas exchange measurements were subsequently frozen in liquid nitrogen and ground using a mortar and pestle. Approximately 5 mg of leaf sample was used for stable isotope analysis and 2 mg for nitrogen analyses. Pure carbon dioxide gas was extracted from the leaf samples based on the method of Buchanan and Corcoran (1959) and isotopic ratios determined on an isotope-ratio gas mass spectrometer (VG Isogas, Middlebury, England). Isotopic signatures (‰) were then expressed according the following equation:

$$\delta^{13}C = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000 \quad ,$$

Table 7.1. Regression of control plants' stem length (Lt.) against plant weight (Wt.) at harvest.

Species	n	Regression equation:	r	F	*P*
S. terebinthifolius	5	Wt. = 1.27 (Lt.)	0.883	10.58	.047
B. halimifolia	4	Wt. = 1.06 (Lt.)	0.916	20.84	.010
R. punctata	5	Wt. = 2.76 (Lt.)	0.916	15.37	.003
R. aculeata	2	Wt. = 2.16 (Lt.)	1.000	-	<.001

where R_{sample} is the $^{13}C/^{12}C$ ratio of the sample and $R_{standard}$ is the $^{13}C/^{12}C$ ratio of a laboratory standard as referenced to Pee-Dee Belemnite. Farquhar et al. (1982b) has shown a significant positive relationship between leaf isotopic signatures and integrated water-use efficiency (WUE) (i.e. the more enriched the isotopic signature, the greater a plant's integrated WUE).

Leaf nitrogen content (%) was analyzed using an elemental autoanalyzer (Carlo Erba NC2100, ThermoFinnigan Italia S.p.A., Milan, Italy). Nitrogen concentration ([N], g N m^{-2} leaf) was obtained by dividing nitrogen content by SLA. Plant photosynthetic nitrogen-use efficiency (PNUE, μmol CO_2 g N s^{-1}) was then determined by dividing *A* by [N].

Variables were separated into either morphological (RGR, R:S ratios, SLA, stem circumference and length, leaf number, length and width,) or gas exchange (A, g_s, A/g_s, [N], $\delta^{13}C$, PNUE) groups. Two-factor (treatment and species) Model I analysis-of-variance (ANOVA) was used to analyze all parameters, which were then Bonferroni corrected separately according to group. Factors that were significant were analyzed by Tukey HSD at the Bonferroni-corrected significance level for that group. Analysis was carried out using SPSS-X Version 8.0 (SPSS Inc., Chicago, IL).

RESULTS

Relative growth rates (Table 7.2) were not significantly different between treatments but were significant among species. *Schinus* and *B. halimifolia* had the highest growth rates while *R. punctata* and *R. aculeata* showed very little growth throughout the season (Table 7.3). Root:shoot ratios were not significantly different either between

Table 7.2. Two-factor (treatment and species) Model I ANOVA of: 1. Relative growth rate, RGR (g g^{-1} $month^{-1}$), 2. root:shoot ratio, R:S (g g^{-1}), 3. specific leaf area, SLA (m^2 g^{-1}), 4. change in stem circumference (ΔS_{circ}, %), 5. stem length change (ΔS_{length} ,%), 6. change in leaf number (Δ Leaf # ,%), 7. change in leaf length (ΔL_{length},%), and 8. change in leaf width (ΔL_{width}, %). Values in bold are significant at the $P < 0.0062$ ($\alpha = 0.05/8$).

	Treatment				Species				Treatment x Species				Error	
	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*	df	MS
1. RGR	1	.009	.635	.432	3	.107	8.124	**.002**	3	.001	.131	.941	29	.013
2. R:S	1	1.326	2.990	.094	3	.413	.933	.437	3	1.265	2.862	.054	9	.442
3. SLA	1	61.612	10.108	**.005**	3	81.543	3.253	.049	3	1.805	.317	.813	16	5.701
4. ΔS_{circ}	1	14.735	.045	.834	3	517.06	1.566	.218	3	426.161	1.29	.096	30	330.241
5. ΔS_{length}	1	10706	4.547	.041	3	6991.9	2.970	.048	3	1311.41	.557	.647	30	2354.43
6. Δ Leaf #	1	158670	3.276	.082	3	3201	24.350	.582	3	59698	1.232	.319	25	48439
7. ΔL_{length}	1	.589	.003	.958	3	384.36	1.811	.166	3	198.662	.936	.435	31	212.181
8. ΔL_{width}	1	89.822	.571	.455	3	1214.115	7.723	**.001**	3	62.981	.401	.754	31	157.210

Table 7.3. Relative growth rate (RGR), root:shoot ratios (R:S) and specific leaf area (SLA) of control and flooded plants. Values followed by the same letter do not differ significantly among species at $P > 0.0062$ ($\alpha = 0.05/8$).

	RGR (g g^{-1} $month^{-1}$)		R:S		SLA (m^2 g^{-1})	
	Control	Flooded	Control	Flooded	Control	Flooded
S. terebinthifolius	0.15 ± 0.04^{a}	0.16 ± 0.03^{a}	10.4 ± 0.5	9.1 ± 1.2	0.8 ± 0.1^{ab}	0.7 ± 0.1^{ab}
B. halimifolia	0.17 ± 0.07^{a}	0.15 ± 0.09^{a}	13.8 ± 1.5	9.8 ± 0.9	1.3 ± 0.4^{a}	0.9 ± 0.1^{a}
R. punctata	0.03 ± 0.03^{ab}	0.01 ± 0.03^{ab}	9.1 ± 0.7	5.4 ± 1.3	1.0 ± 0.2^{b}	0.4 ± 0.1^{b}
R. aculeata	-0.04 ± 0.02^{b}	-0.11 ± 0.05^{b}	12.1 ± 2.9	8.5 ± 0.2	0.6 ± 0.2^{ab}	1.1 ± 0.2^{ab}

treatments or among species (Table 7.2). Leaf thickness (SLA) changed with treatment (Table 7.2); leaves of flooded plants were thicker than those of controls (Table 7.3). There were no differences between changes in leaf number, leaf length, stem length or circumference between treatment and among species (Table 7.2). However, there was a difference in leaf width between species (Table 7.2)--leaf width of *B. halimifolia* increased more than that of the other species, but there were no treatment differences (Table 7.3).

Gas exchange was only significant between treatments for *A* and PNUE (Table 7.4) where controls had higher *A* than the flooded treatment. Significant difference in PNUE was because of higher *A* and not [N] (Table 7.5). Carbon isotopic signatures were not significantly different between treatments or among species (Tables 7.4 and 7.5). No species differences were found in any of the other gas exchange variables (Table 7.4).

DISCUSSION

Studies (see reviews in Hatfield 1984, Kozlowski and Pallardy 1997) have shown that plants exposed to short-term flooding show a decrease in their root oxygen contents (hypoxia) and higher ethylene concentrations (Batzli and Dawson 1997). Oxygen deficiency has been shown to induce anaerobic metabolism that can result in a build-up of compounds toxic to root cells (Reid and Bradford 1984). There is also root death from anoxia, leading to an decrease in R:S ratios. In cases of long term (> 1 month) flooding of the roots (as in this experiment), nutrient deficiency, reduced RGR, wilting, and plant death have been recorded (Hatfield 1984, Kozlowski 1984, Kozlowski and Pallardy 1997). Flood-tolerant plants however have adaptations such as adventitious roots,

Table 7.4. Two-factor (treatment and species) ANOVA of: 1. Assimilation, A (μmol CO_2 $m^{-2}s^{-1}$), 2. Stomatal conductance, g_s (mol H_2O $m^{-2}s^{-1}$), 3. Intrinsic water-use efficiency, A/g_s (μmol CO_2 mol H_2O^{-1}), 4. Mesophyll conductance, A/c_i (m s^{-1} x 10^{-5}), 5. Nitrogen concentration on a leaf area basis, [N] (g N m^{-2} leaf), 6. Carbon stable isotope signatures, $\delta^{13}C$ (‰), and 7. Photosynthetic nitrogen-use efficiency, PNUE (μmol CO_2 g N^{-1} s^{-1}). Values in bold are significant at the $P < 0.0071$ ($\alpha = 0.05/7$) level using a Tukey HSD.

	Treatment				Species				Treatment x Species				Error	
	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*	df	MS
A	1	68.034	9.54	**.006**	3	4.40	.618	.612	3	1.72	.214	.866	19	7.132
g_s	1	.023	.970	.337	3	.032	1.345	.289	3	.006	.248	.862	19	.024
A/g_s	1	2043.9	6.401	.020	3	1053	3.298	.043	3	181.	.568	.643	19	319.297
A/c_i	1	2.520	8.211	.010	3	.120	.391	.761	3	.760	2.476	.093	19	.307
[N]	1	1.844	6.757	.016	3	1.11	4.082	.018	3	.157	.577	.636	24	.273
$\delta^{13}C$	1	4.803	4.057	.053	1	2.83	2.393	.089	3	2.16	1.824	.165	19	1.184
PNU	1	2.15	3.70	**.002**	3	.303	1.930	.161	3	.030	.189	.903	18	.157

Table 7.5. Species average (± SEM) for control and flooded plants. The parameters measured are: 1. Assimilation, *A* (μmol CO_2 $m^{-2}s^{-1}$), 2. Nitrogen concentration on a leaf area basis, [N] (g N m^{-2} leaf), 3. Stomatal conductance, g_s (mol H_2O $m^{-2}s^{-1}$), 4. Mesophyll conductance, A/c_i (m s^{-1} x 10^{-5}), 5. Intrinsic water-use efficiency, A/g_s (μmol CO_2 mol H_2O^{-1}), 6. Carbon stable isotope signatures, $\delta^{13}C$ (‰) and 7. Photosynthetic nitrogen-use efficiency, PNUE (μmol CO_2 g N^{-1} s^{-1}) in both study sites.

	A	g_s	A/g_s	A/c_i	[N]	$\delta^{13}C$	PNUE
S. terebinthifolius							
Control	9.3 ± 1.3	0.24 ± 0.06	63.3 ± 15.1	1.12 ± 0.37	1.01 ± 0.10	-29.4 ± 0.5	10.43 ± 1.43
Flooded	7.3 ± 1.0	0.15 ± 0.03	51.1 ± 7.3	1.41 ± 0.24	1.35 ± 0.22	-29.6 ± 0.4	4.65 ± 0.55
B. halimifolia							
Control	10.0 ± 1.4	0.36 ± 0.16	39.9 ± 8.3	1.80 ± 0.30	0.78 ± 0.03	-30.5 ± 0.5	13.08 ± 2.28
Flooded	7.0 ± 2.9	0.23 ± 0.12	29.2 ± 3.9	1.24 ± 0.51	0.95 ± 0.05	-29.1 ± 0.6	7.35 ± 3.67
R. punctata							
Control	9.5 ± 0.2	0.16 ± 0.02	65.5 ± 5.8	2.07 ± 0.09	1.36 ± 0.04	-28.5 ± 0.3	7.02 ± 0.20
Flooded	5.1 ± 0.9	0.11 ± 0.03	49.8 ± 7.8	0.93 ± 0.15	2.12 ± 0.50	-28.6 ± 0.4	2.50 ± 0.46
R. aculeata							
Control	8.6 ± 1.9	0.24 ± 0.02	52.7 ± 12.0	1.83 ± 0.44	1.00 ± 0.21	-30.4 ± 0.3	10.72 ± 5.19
Flooded	4.90 ± 1.7	0.27 ± 0.08	19.5 ± 5.5	0.73 ± 0.25	1.66 ± 0.21	-28.6 ± 0.9	2.99 ± 1.06

pneumatophores, and roots with large aerenchyma cells (Hook 1984, Lockhart et al. 1999).

Differences in RGR (Table 7.2) among species but not between treatments indicate that *Schinus* and *B. halimifolia* have higher growth rates compared to *R. punctata* and *R. aculeata* (Table 7.3). No R:S response to flooding (Table 7.2) indicates that no species were significantly affected by the presence of water in and around plant roots. It is possible that despite lack of a long-term growth response, flooding could have lowered plant water potentials and gas exchange.

Field studies of the same species (Chapter 3) in Everglades National Park showed native species having lower predawn water potentials compared to *Schinus* during the wet season when the soil was saturated. Lower A and PNUE in the treatment plants are indicative of flood effects on gas exchange. Assimilation rates in flooded plants were between 30-45% lower than controls (Table 7.3). Davies and Flore (1986) have shown that plant gas exchange can be affected by flooding without signs of outward physical damage. In this study, only A but not g_s and A/c_i were significantly affected. Both g_s and A/c_i showed a decreasing trend with flooding; as A is directly related to both these parameters, the cumulative effect of lowered g_s and A/c_i is a decrease in A. Low PNUE has been associated with low growth rates (e.g. Lambers and Poorter 1992, van den Boorgaard et al. 1995). In this study, PNUE was not correlated with RGR, suggesting that PNUE is not completely coupled with RGR under root flooding or that, more likely, sample sizes used in this study were too small to determine the relationship between these two parameters.

Plant SLA was the only morphological response to treatment (Table 7.2); flooded plants in this study had low SLA (Table 7.3), probably from thicker palisade cells compared to controls. Flooded plants have been shown to have low SLA resulting from more palisade mesophyll cells (Lambers et al. 1998) as an adaptation to waterlogged soils. Nitrogen concentration of the leaves (on a leaf area basis) did not differ between treatments despite thicker leaves in the flooded treatment.

Although control plants had higher *A* than treatment plants (Table 7.5), this difference is most likely not ecologically significant in terms of water relations because there were no differences in the intrinsic or integrated WUE patterns between control and treatment individuals. Higher PNUE in the control plants was reflective of greater *A* but not [N] in control plants. Plants with high PNUE have been shown to have higher growth rates (Lambers and Poorter 1992). Despite the lack of significant differences between the treatment and control plants, trends were observed in g_s, A/g_s, A/c_i, and [N]. Control individuals had higher g_s, A/g_s, A/c_i, than the flooded plants but flooded plants had higher [N] than controls. These consistent observations suggest that overall gas exchange of the flooded plants is affected by the treatment, despite the lack of statistical significance.

There are three components to plant flooding (Poonamperuna 1984): 1) the physical presence of water that changes soil structure, 2) electrochemical effects such as reduced redox potentials, changes in pH and electrical conductivity, and 3) changes in soil chemistry such as removal of oxygen, increase in Fe^{+} and SO_4^{-} and denitrification. Plants naturally flooded by seasonal fluctuations in South Florida would encounter all three components of flooding.

Lack of significant growth and gas exchange differences suggest that the experimental setup could have introduced too much water causing only physical changes to the soil without the accompanying electrochemical or chemical effects. Soil conductivity in the pots (about 7 cm below saturated soil) between the noon and 1600 hrs watering, approximately one month prior to harvest, averaged –9 mV (n = 7) despite pots being permanently inundated. Plant response to flooding is in part from the accompanying lower redox conditions. Although the soil was waterlogged, it is possible the treatments did not simulate flooding to a degree that significantly affected plant ecophysiology because of high rates of hydrologic turnover. A second possibility for the lack of significance is that the sample size used was too small. It is possible that if sample size was increased, the patterns observed would have been significant.

CONCLUSION

Overall, *Schinus* growth and gas exchange responses were not significantly different from those of native species under flooded conditions. All plants showed no growth response to flooding but gas exchange was consistently lower (although not always significant) in the flooded compared to the control plants. Lack of significant response could either be from: 1) flooding but not low oxygen conditions or 2) small sample size.

Chapter 8

Ecophysiology of *Schinus terebinthifolius* in South Florida: Concluding remarks

The success of invasive exotics has generated significant research interest in the last 10 - 15 years (e.g. Pysek et al. 1995a, Simberloff et al. 1997) and this dissertation (Chapters 2 - 7) further contributes to the body of knowledge. Although the causes of success of invasive species cannot be generalized, several theories that could potentially contribute to the success of these species in their non-native habitats have been proposed (Chapter 1). The role of physiology has been considered as one of the possible options. Based on this study, I revisit the hypothesis that *Schinus* success is related to physiological attributes of this species not found in the natives. The purpose of this study was to determine if: 1) *Schinus* ecophysiology (in terms of water uptake and gas exchange) was different from that of native species and 2) if ecophysiology of the exotic could help explain its widespread distribution in Florida.

Schinus survival and persistence in a variety of habitats in Florida imply that this species is tolerant of a wide range of environmental conditions and one of the possible mechanisms for *Schinus* success is via its water uptake patterns. Physiological differences between *Schinus* and native species were found in water uptake patterns in both the saline southwest Florida (Chapter 2) and upland Everglades (Chapter 3) communities. In saline Southwest Florida, predawn water potentials indicated that *Schinus* was less affected by seasonality than native species (Fig. 2.5). High dry season Na^+/K^+ ratios and predawn

water potentials indicated that the exotic also was most likely salt-tolerant (Fig. 2.8). However, the salinity of water utilized by plants could not be quantified using oxygen isotopes because all species sampled were utilizing a mix of saline and fresh water (Fig. 2.6).

In the low (< 1 m above sea level) elevation rock pineland of Everglades National Park, *Schinus* water use patterns showed the exotic to be more tolerant of root flooding than native species (Chapter 3). Dry season predawn water potentials were similar in all species but wet season water potentials of *Schinus* were higher than those of native species (Fig. 3.3). In native species, this decrease in water potentials with increased water availability implied that these species were intolerant of root inundation. Oxygen isotopes showed *Schinus* accessing deep groundwater year-round, unlike most native species that shifted to shallow soil water during the wet season (Fig. 3.2). It is possible that *Schinus* may have aerenchyma cells that provide oxygen to its roots while native species roots die back.

Gas exchange of *Schinus* most likely did not contribute to the success of this exotic in either ecosystem studied because gas exchange rates of the exotic were lower than or similar to those of native species. In the saline transition zone, *Schinus* had lower gas exchange rates than native species during the dry season when salinity was high (Chapter 4). In the glasshouse, gas exchange of *Schinus* grown at 15 parts per thousand salinity was similar to native species (Chapter 6). Although some native species gas exchange decreased with increasing salinity under controlled conditions, this pattern was not seen in *Schinus* (Fig. 6.7).

Schinus gas exchange response was similar to that of native species in the upland Everglades both seasons (Chapter 5). Plants flooded in the glasshouse for several months showed a trend for decreased gas exchange but *Schinus* response did not differ from that of most native species (Table 7.4). Integrated water-use efficiency (representing long-term water uptake) of *Schinus* was not different from native species for all components of this work, indicating that the exotic's gas exchange response was not significantly different from native species.

Schinus relative growth rate and morphology (as measured by change in height, stem circumference, leaf number, leaf length and width) was less affected by salinity than those of native species in the glasshouse (Chapter 6). *Schinus* and *Rhizophora mangle* showed least morphometric response to 15 p.p.t. salinity. However, *Schinus* biomass allocation under controlled saline conditions was different from native species. For all treatments, *Schinus* allocated more of its biomass to stems and less to leaves than native species. The exotic most likely invested most of its biomass in height increase and produced large thin leaves to maintain a leaf area/biomass ratio (Fig 6.5B) similar to that of native species. This indicated that *Schinus* had the potential to grow taller faster than some native species, an ecological strategy that would allow it to shade out its competitors. *Schinus* also had slightly thinner leaves (Fig. 6.5C) than natives which would allow this exotic to maintain its leaf area for less biomass investment than native species. When flooded (Chapter 7), *Schinus* morphology and growth was not significantly different from native species. This finding was most likely because of the absence of anoxic conditions created under flooding.

Schinus produces copious seeds during winter and this high reproductive output has been suggested as a possible explanation for the prevalence of this invasive exotic in South Florida ("seed-rain-of-terror" hypothesis according to Horvitz et al. 1998). However, Daehler (1998) has shown that species with high reproductive output do not necessarily become invasive (Chapter 1). Although beyond the scope of this work, other possibilities of *Schinus* success need to be considered. For example, genetic change could have favored *Schinus* invasion into South Florida. Lack of predators or competitors for the ecological niche (e.g. a subcanopy species in the Everglades pineland) that *Schinus* occupies could also potentially contribute to its prevalence in Florida. A more likely scenario is the interaction of several factors i.e. a genetic predisposition for *Schinus* physiological tolerance of South Florida environment and, ecosystems free of predators and competitors (available niche). Widespread dispersal of seeds may also contribute to its distribution, but I believe that physiology contributes to *Schinus* prevalence in South Florida. Specifically, this work shows that *Schinus* prevalence in South Florida, could be in part because of its water uptake strategies.

Based on the findings in this work, I propose that *Schinus* success in South Florida is most likely a consequence of its capacity to tolerate and persist through adverse conditions rather than being an aggressive competitor. I propose that *Schinus* prevalence in South Florida is because the exotic has a vigorous root system that can continually access water (either fresh or brackish) even when water availability is low, and can tolerate root inundation. It is a hardy species that persists through adverse conditions and grows as fast as natives during favorable conditions.

APPENDIX I

Below is a list of terms used in this work. Because of differing terminology (e.g. Webb 1985, Pysek et al. 1995b) and classification schemes (e.g. Kornas 1990) utilized by various authors, I will explicitly define the terms I use.

Alien—A species that has not evolved in that particular community since the last Ice Age and has been brought in from another geographic location by human activities (Webb 1985).

Colonization—The successful establishment and reproduction of an introduced species in a new habitat (Baker 1965).

Disturbed—either single or multiple events that kill or damage existing organisms resulting in an increase in resource availability, and that allow new individuals to establish (Sousa 1984).

Exotic—used synonymously with alien and non-native.

Indigenous—includes a species that: a) was originally found in the habitat when first encountered by humans and b) arrived at a new site, in recent times, independent of human activities (Webb 1985).

Introduction—The cultivation of a species in a habitat where it historically has never been found.

Invasive—Non native species that has been naturalized and has the capacity to interfere with the structure and function of a community.

Native—synonymous with indigenous

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