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## Water Uptake Patterns of an Invasive Exotic Plant in Coastal Saline Habitats

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### ABSTRACT

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*Schinus terebinthifolius* Raddi (*Schinus*) is one of the most widely found woody exotic species in South Florida. This exotic is distributed across environments with different hydrologic regimes, from upland pine forests to the edges of sawgrass marshes and into saline mangrove forests. To determine if this invasive exotic had different physiological attributes compared to native species in a coastal habitat, we measured predawn xylem water potentials ( $\Psi$ ), oxygen stable isotope signatures ( $\delta^{18}\text{O}$ ), and sodium ( $\text{Na}^+$ ) and potassium ( $\text{K}^+$ ) contents of sap water from plants within: (1) a transition zone (between a mangrove forest and upland pineland) and (2) an upland pineland in Southwest Florida. Under dynamic salinity and hydrologic conditions,  $\Psi$  of *Schinus* appeared less subject to fluctuations caused by seasonality when compared with native species. Although stem water  $\delta^{18}\text{O}$  values could not be used to distinguish the depth of *Schinus* and native species' water uptake in the transition zone,  $\Psi$  and sap  $\text{Na}^+/\text{K}^+$  patterns showed that *Schinus* was less of a salt excluder relative to the native upland species during the dry season. This exotic also exhibited  $\text{Na}^+/\text{K}^+$  ratios similar to the mangrove species, indicating some salinity tolerance. In the upland pineland, *Schinus* water uptake patterns were not significantly different from those of native species. Differences between *Schinus* and native upland species, however, may provide this exotic an advantage over native species within mangrove transition zones.

**ADDITIONAL INDEX WORDS:** water potential,  $\text{Na}^+/\text{K}^+$  ratios, stable isotopes, salinity, Brazilian pepper.

### INTRODUCTION

An invasive exotic is a nonindigenous species that reproduces successfully within its nonnative habitat, independent of human help (RICHARDSON *et al.*, 2000). The ecological impacts of invaders on native communities can be significant both economically and ecologically (PIMENTEL *et al.*, 2000). Although the majority of nonnative plant species do not independently disperse into new habitats, those that do can sometimes pose a significant threat to the integrity of native communities. Invasive exotic species have been shown to alter soil conditions, hydrology, fire regimes, and species diversity (*e.g.*, see reviews in VITOUSEK, 1986; CRONK and FULLER, 1995; GORDON, 1998), significantly altering the structure and function of native communities.

*Schinus terebinthifolius* Raddi (hereafter *Schinus*) is an exotic plant from South America that is 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, this exotic 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 of 13 m in South Florida (BARRETT, 1956). It sprouts easily from the root base and is often multistemmed. *Schinus* has been found from upland pinelands (LOOPE *et al.*, 1979) to coastal mangrove communities (EWEL *et al.*, 1982; MYTINGER, 1985), suggesting that it has physiological tolerance for a broad range of soil and hydrologic conditions.

However, the underlying physiological mechanisms that allow *Schinus* persistence and tolerance of a variety of conditions have never been examined. Previous workers have examined *Schinus* distribution (BARKLEY, 1944; LEMKE, 1992), phenology (MORTON, 1978; TOMLINSON, 1980; EWEL *et al.*, 1982), seedling germination and growth (NILSEN and MULLER, 1980a, 1980b; MYTINGER, 1985), reproductive biology (EWEL *et al.*, 1982), plant-animal interactions (CURNUTT, 1989), and a few studies have briefly described the physiology (PATTISON *et al.*, 1998) and ecology of *Schinus* (FERRITER, 1997; HORVITZ *et al.*, 1998) in its exotic habitat and none in its native habitat. In its native habitat, *Schinus* is often found in the landward fringes of coastal berms (FABRIS *et al.*, 1990), leading to the hypothesis that this exotic may be tolerant of some salinity.

We compared the water uptake patterns of *Schinus* with mangrove and native upland species in coastal areas in two

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## Water Uptake of Brazilian Pepper

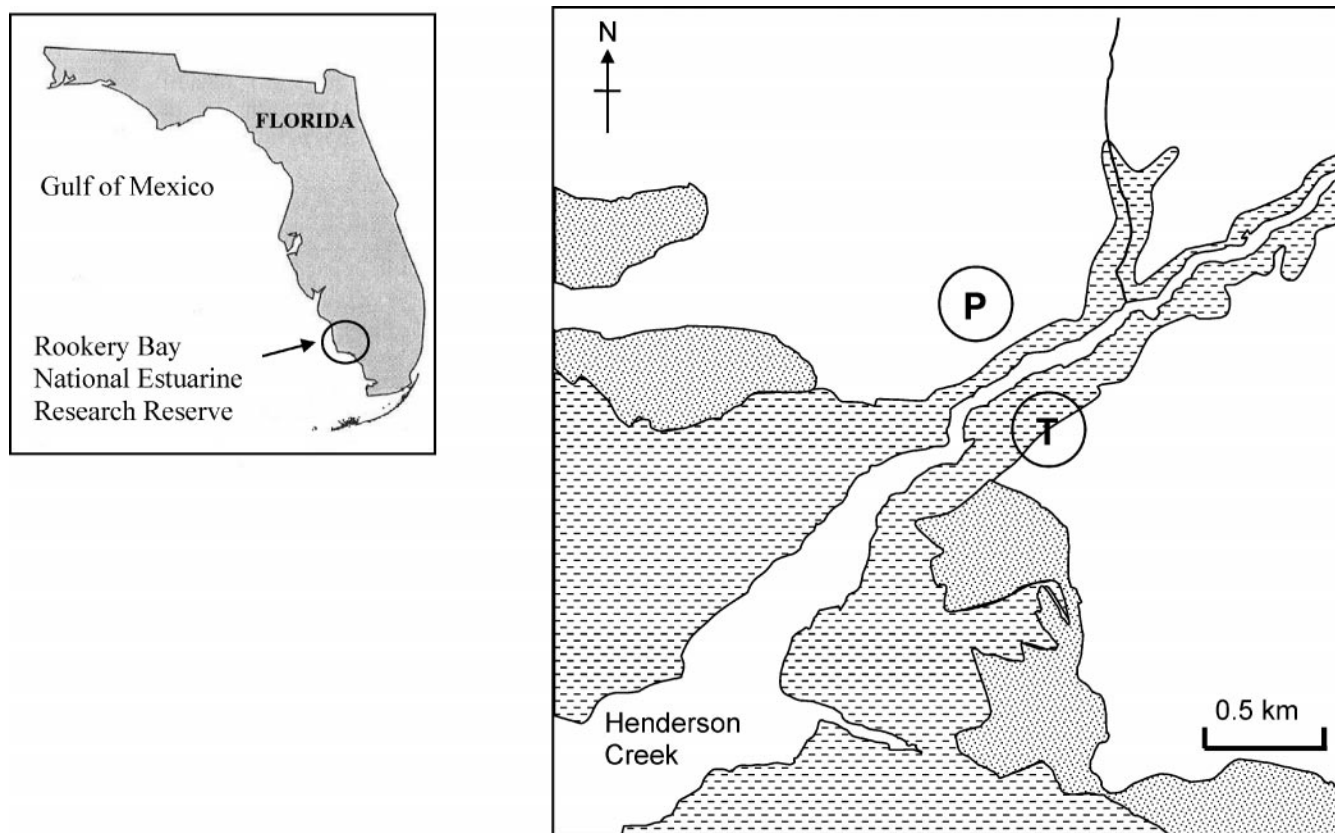


Figure 1. Map of Florida (inset) indicating the location of Rookery Bay National Estuarine Research Reserve. The relative locations of the upland pineland (P) and transition zone (T) sites are shown relative to Henderson Creek. The clear areas are upland areas, usually sandy pinelands. The stippled areas are salt marshes, and the dashed horizontal areas are mangrove forests.

coastal communities: a saline transition zone and an upland pineland. We measured predawn xylem water potentials ( $\Psi$ ), stem and soilwater sodium ( $\text{Na}^+$ ) and potassium ( $\text{K}^+$ ) concentrations, and oxygen stable isotopic ratios ( $\delta^{18}\text{O}$ ) of plant and soilwater to determine if *Schinus* had the same water uptake patterns as native species.

Predawn water potentials are a proxy of plant water status at night, when in the absence of a transpirational force inducing water movement from the root to the shoot, water within the plant has the capacity to equilibrate with that of its surrounding soil (LARCHER, 1995). Water potentials decrease with lower soilwater content and increasing soil salinity. Measured with soil water content and salinity,  $\Psi$  are a useful tool in determining plant water status. We hypothesized that *Schinus*, being tolerant of some salinity, would have lower  $\Psi$  than freshwater natives.

Sap  $\text{Na}^+/\text{K}^+$  ratios are indicative of salt tolerance in woody plants. Sap  $\text{Na}^+/\text{K}^+ > 1$  has been found in plants tolerant of salinity (e.g., FLOWERS *et al.*, 1986; NAIDOO, 1987; FUNG *et al.*, 1998), whereas  $\text{Na}^+/\text{K}^+ < 1$  is needed for normal function in most non-salinity-tolerant plants (i.e., glycophytes) (WYN JONES *et al.*, 1979). We hypothesized that during the dry season, when soil porewater salinity is at its highest, *Schinus* would have sap  $\text{Na}^+$  and  $\text{K}^+$  values similar to the mangroves.

Oxygen stable isotopes have been used in many studies to determine the source and depth of plant water uptake (e.g., STERNBERG and SWART, 1987; EWE and STERNBERG, 2002). In areas of different sources of water available for plant uptake (e.g., soil and groundwater), the fraction of water uptake from each source can be calculated based on a single-isotope dual-source linear mixing model (e.g., WHITE *et al.*, 1985; EWE *et al.*, 1999). We hypothesized that during the dry season,  $\delta^{18}\text{O}$  of sap water of *Schinus* would be more enriched and approach values of the more saline groundwater relative to the upland native species.

## MATERIALS AND METHODS

### Study Site

The two study sites were located in coastal Southwest Florida (Figure 1), within Rookery Bay National Estuarine Research Reserve. This 6000-ha reserve is predominantly comprised of mangrove and shallow marine communities with upland communities occupying only 5% of the reserve. The substrate in this area is a mix of shell and calcium carbonate sand (JOHNSON and BARBOUR, 1990).

Sites were chosen where *Schinus* was one of the major components of the plant community. The first site is a transition

zone (26°02'N, 81°42'W) located between an upland pineland and mangrove community. The second study site (Figure 1) was an upland pineland (26°02'N, 81°43'W) with seasonally brackish groundwater. In addition to *Schinus*, vegetation in the transition zone was a mix of both upland and salt-tolerant species. Plants typical of upland communities such as *Randia aculeata* L., *Rapanea punctata* (Lam.) Lundell (= *Myrsine floridana*), and *Sabal palmetto* (Walt.) Lodd. ex Schult. occur alongside salt-tolerant species such as *Rhizophora mangle* L., *Avicennia germinans* L., *Laguncularia racemosa* (L.) Gaertn. f., and *Conocarpus erecta* L.

The transition zone was located close to the estuary of Henderson Creek and exposed to belowground tidal effects (Figure 1). Annually, groundwater depths ranged from 1.5 cm to over 50 cm deep. During the wet season, groundwater was predominantly freshwater runoff from upland areas. In the dry season, freshwater input was reduced, allowing greater seawater intrusion; hence, the groundwater was a mix of both water sources (ROOKERY BAY NATIONAL ESTUARINE RESEARCH RESERVE, unpublished data). This mix of water sources resulted in a patchy hypersaline soil surface because of evaporation.

The upland pineland was farther inland (Figure 1) and less exposed to salinity fluxes than the transition zone. Groundwater in this site was consistently deeper year-round than in the transition zone, and annual salinity ranged from 0 to 9 parts per thousand (ppt). This site had an open canopy of *Pinus elliottii* var. *densa* (Little & Dorman) with an understory shrub layer of *Sabal palmetto*, *Randia aculeata*, *Rapanea punctata* as well as *Schinus* and *Melaleuca quinquenervia* (Cav.) S.T. Blake seedlings.

Southwest Florida receives an average of 1500 mm of rainfall annually (SNYDER *et al.*, 1990). Rainfall is seasonal, and approximately 75% of annual precipitation occurs during the warm wet season (May–November). Cool drier days characterize the dry season (November–May). Hurricanes occur during the wet season, with a hurricane 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

Water uptake by *Schinus* was compared to native codominant species within each community. In the transition zone, *Schinus* was compared to two native salt-tolerant mangrove species and two native upland species. The mangrove species were *Rhizophora mangle* (Rhizophoraceae) and *Laguncularia racemosa* (Combretaceae). *Rhizophora mangle* (red mangrove) is the most widely occurring mangrove species in South Florida (TOMLINSON, 1986); this species reaches its northernmost extent in north-central Florida (ODUM *et al.*, 1985). *Laguncularia racemosa* (white mangrove) has an overlapping geographic distribution with *R. mangle* but is generally found toward the landward fringe of a mangrove community, in disturbed or irregularly flooded areas (BALL, 1980). The native upland species sampled were *Rapanea*

*punctata* (Myrsinaceae) and *Randia aculeata* (Rubiaceae). *Rapanea punctata* is a tropical species commonly found in pineland and hammock communities. *Randia aculeata* is a subtropical plant found growing in pinelands. Both species attain the stature of either small trees or shrubs (TOMLINSON, 1980).

In the absence of mangrove species from the pineland, *Schinus* was only compared to the upland species at this site. Five individuals per species within each site were tagged and sampled 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 was sampled to determine belowground spatial and temporal heterogeneity. To characterize spatial salinity heterogeneity within the transition zone, a 10 m × 10 m grid was constructed within the area. Fifty centimeter deep PVC wells (2.5 cm inner diameter) were established at 1.0-m intervals (total = 121 wells). Wells were capped between sampling periods to prevent evaporative loss of groundwater. From September 1997 to February 1998, groundwater was extracted from each well at monthly intervals, and salinity measured using a refractometer. Sampling was terminated in mid-February when groundwater levels decreased to below 50 cm.

To characterize the vertical patterns of soilwater salinity and isotopic composition, three soil cores were randomly taken from each site every sampling period (18 April and 30 October 1998, 27 April 1999). Cores (12 cm diameter) were collected from the soil surface and at 15-cm intervals until groundwater was reached. Samples were individually stored in 50-mL borosilicate tubes, sealed with Parafilm, and 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 weighed before and after cryogenic extraction to determine water content. Percentage water content was expressed as a function of soil water fraction divided by its dry weight. Subsamples of the dried soils were rehydrated with known amounts of water for Na<sup>+</sup> and K<sup>+</sup> analyses (described below).

### Na<sup>+</sup> and K<sup>+</sup> 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 distilled water was used to determine soilwater Na<sup>+</sup> and K<sup>+</sup> concentrations using a flame photometer (IL 943, Instruments Laboratory, Lexington, Massachusetts). Salinity (in ppt) was extrapolated from the Na<sup>+</sup> ionic content based on full-strength seawater Na<sup>+</sup> concentrations (*i.e.*, Na<sup>+</sup> = 10.5 ppt).

Stem samples were collected from plants in the transition

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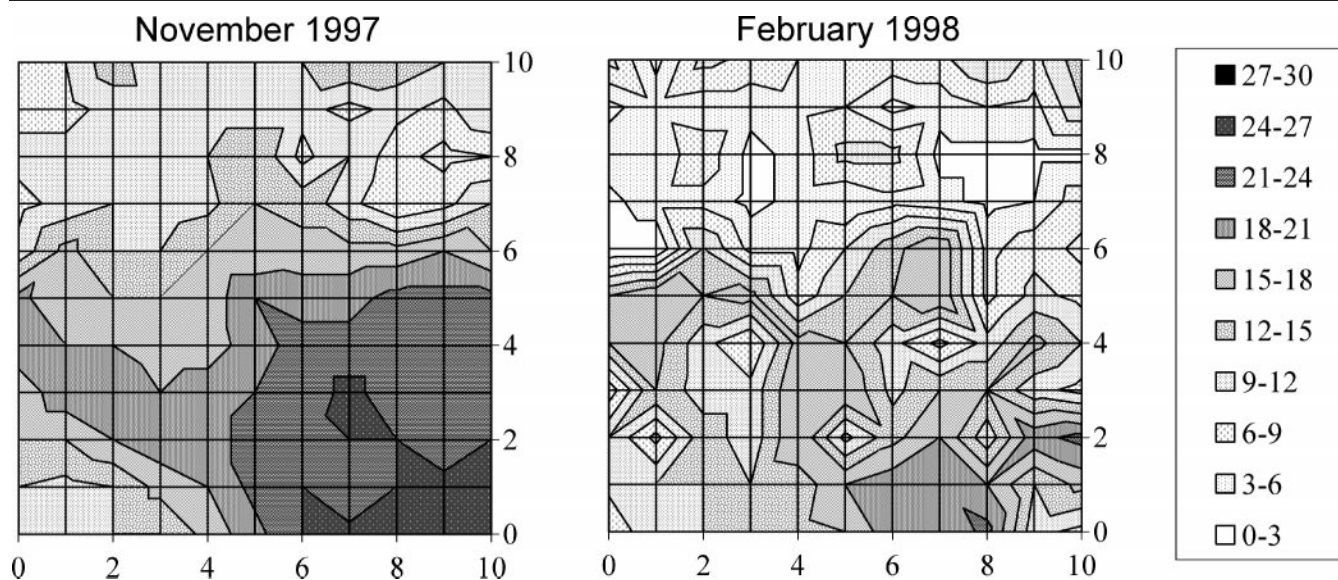


Figure 2. Spatial heterogeneity of salinity (in ppt) at 50 cm depth within a 10 m  $\times$  10 m grid at the end of the wet season (November 1997) and at the middle of the dry season (February 1998). Porewater was sampled at 1-m intervals within this grid. These data are a subset from Ewe (2001).

zone during the wet season (15 June 1997) and again during the 1999 dry season (27 April 1999). Sap expressed from plant samples using the Scholander pressure chamber were collected in 100- $\mu$ L glass micropipets. Exposed ends of the micropipets were immediately sealed with Cryto-Seal<sup>®</sup>. All samples were taken back to the laboratory and diluted with known amounts of distilled water for Na<sup>+</sup> and K<sup>+</sup> analysis using the flame photometer.

### Stable Isotope Analysis

Fully suberized (*i.e.*, having fully developed cork tissue) plant stem sections (< 1 cm diameter) were collected from both sites between 0900 and 1100 h on 18 April and 30 October 1998. Live stem sections without leaves were selected to minimize isotopic fractionation. The stem samples were stored in a similar manner as the soil cores. Water cryogenically extracted from the soil and stem samples were prepared for oxygen isotopic analysis according to EPSTEIN and MAYEDA (1953). The samples were analyzed on an isotope ratio gas mass spectrometer (VG Isogas, Middlebury, England). We did not determine the hydrogen isotopic ratios 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 is expressed using the following equation:

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

where  $R_{\text{sample}}$  is the O<sup>18</sup>/O<sup>16</sup> ratio of the sample and  $R_{\text{standard}}$  is the O<sup>18</sup>/O<sup>16</sup> ratio of standard mean ocean water (SMOW).

### Predawn Xylem Water Potentials ( $\Psi$ )

Plant  $\Psi$  were measured between 0200 and 0530 h 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 and three seasons (minus 2 November 1997 sampling) in the upland pineland. Stems 5–20 cm in length ( $\leq$  0.8 cm diameter) were collected, and  $\Psi$  measured immediately using a Scholander pressure chamber (PMS 600, PMS Instruments, Corvallis, Oregon).

## RESULTS

### Soil and Water Measurements

Groundwater salinity from the 10 m  $\times$  10 m grid of wells showed significant spatial and temporal heterogeneity (EWE, 2001). Groundwater salinity ranged from 2 to 25 ppt over the period sampled. Small pools (1–5 m<sup>2</sup>) of fresher water ( $5 \pm 3$  ppt) were always found within the more saline matrix (median = 16 ppt), but these pools did not remain spatially constant (Figure 2). The vertical salinity profile from soil cores (in the unsaturated layer) was analyzed with a two-factor analysis of variance (ANOVA). Significant difference was found between sites ( $F_{1,46} = 128.33$ ,  $p < 0.01$ ) and among seasons ( $F_{2,46} = 12.50$ ,  $p < 0.01$ ) (Figure 3). The transition zone had higher-salinity soilwater than the pineland, and at both sites, dry season salinity was greater than that in the wet season. Although soil salinity was not statistically different across depths ( $F_{3,46} = 1.29$ ,  $p > 0.10$ ), salinity was higher at the soil surface in the transition zone during the dry season (Figure 3).

### Na<sup>+</sup> and K<sup>+</sup> Analysis

Native species were pooled into their functional groupings as either mangrove or upland species for statistical analyses comparing seasonal differences. For Na<sup>+</sup>/K<sup>+</sup> ratios, a two-fac-

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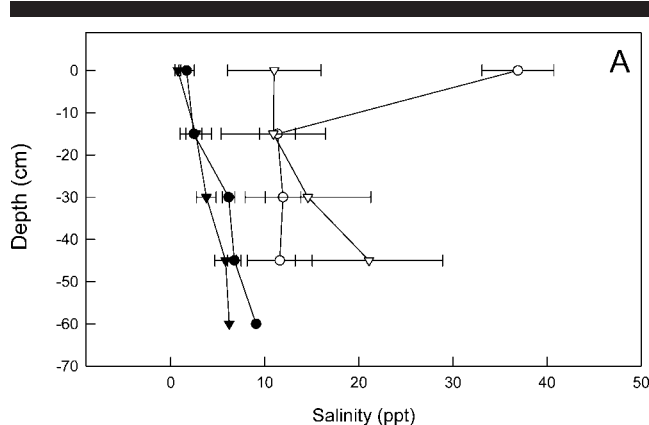


Figure 3. Vertical profiles of soil salinity (ppt). Circles indicate means ( $\pm$  SEM) from the transition zone (dry season 1998,  $\square$ ; wet season 1998,  $\blacksquare$ ), and the freshwater pineland site is shown in triangles (dry season,  $\nabla$ ; wet season,  $\blacktriangledown$ ). For clarity, only two seasons are shown in each of the graphs. Salinity and water content from the third season (dry season 1999) are not significantly different from those of the previous dry season.

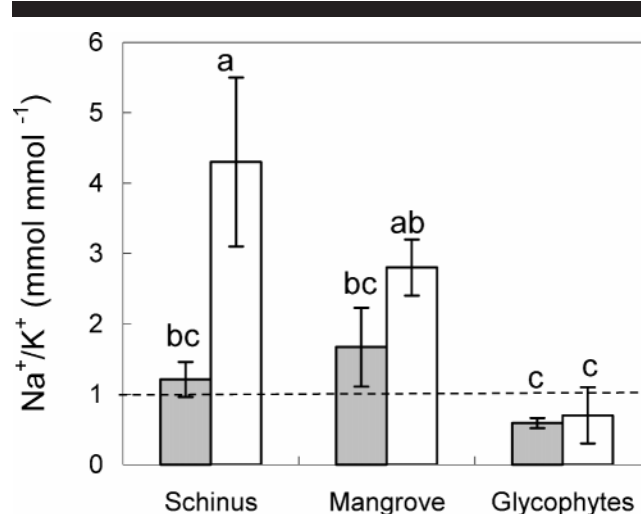


Figure 4. The  $\text{Na}^+/\text{K}^+$  ratios ( $\pm$  SEM) of extruded sap water from *Schinus* compared to the mangrove and upland species for a wet (dark bars) and dry (clear bars) season within the transition zone. Above each bar, the same letters indicate that these values do not differ significantly at the  $p = 0.05$  level using a *post-hoc* Bonferroni comparison of means.

tor ANOVA of the pooled samples showed significant differences between *Schinus* and the other two functional groups ( $F_{2,30} = 14.28, p < 0.01$ ), site ( $F_{1,30} = 18.91, p < 0.01$ ) as well as a group  $\times$  season interaction ( $F_{2,30} = 6.73, p < 0.01$ ). *Post-hoc* Bonferroni comparisons of means for the interaction effect showed that *Schinus*  $\text{Na}^+/\text{K}^+$  ratios were higher in the dry than in the wet season, but seasonal shifts were not observed in either the mangrove or upland species (Figure 4). *Schinus* and the mangrove species had significantly higher  $\text{Na}^+/\text{K}^+$  ratios than upland species only during the dry season (Figure 4).

Total  $\text{Na}^+ + \text{K}^+$  contents of all groups, analyzed using a two-factor ANOVA, was significant for groups ( $F_{2,30} = 4.58, p < 0.05$ ) and season ( $F_{1,30} = 148.24, p < 0.01$ ). The  $\text{Na}^+$  and  $\text{K}^+$  contents of *Schinus* and native upland species were consistently lower than those of the mangroves (Table 1). In all groups, average total ionic content increased approximately 14–45 times from the wet to dry season (Table 1).

**Stable Isotope Analysis**

A three-factor ANOVA of soil  $\delta^{18}\text{O}$  showed significant differences among depths ( $F_{3,30} = 17.53, p < 0.01$ ) and sites ( $F_{1,30} = 8.35, p < 0.01$ ) but not between seasons ( $F_{1,30} = 0.69, p > 0.10$ ). Soil surface water was isotopically enriched relative to the deeper samples (Figure 5). Oxygen isotopic sig-

natures at 15, 30, and 45 cm depth, however, were not significantly different seasonally or vertically (*post-hoc* Tukey HSD,  $p > 0.05$ ). Because of this overlap, specific depth of water uptake by plants could not be determined at either site (Figure 5). Visual inference from stable isotope (Figure 5) and soil salinity data (Figure 3), however, indicate that *Schinus*, like most native species in the transition zone, was most likely utilizing water from at least 10 cm depth and encountering salinity levels averaging 12 ppt (range 5–20 ppt). The only exception was *L. racemosa*, which is extracting water either from shallower or deeper layers than most species. In the pineland, *R. aculeata* was consistently the deepest rooting species both seasons sampled, followed by *R. punctata* and *Schinus*.

The two-factor ANOVA revealed seasonal ( $F_{1,40} = 9.510, p < 0.01$ ) and species ( $F_{4,40} = 4.493, p < 0.01$ ) differences in the  $\delta^{18}\text{O}$  values of stemwater in the transition zone. All species had enriched  $\delta^{18}\text{O}$  values during the dry season. *Schinus*  $\delta^{18}\text{O}$  was similar to that of most species within the transition zone; *L. racemosa*, however, had the most enriched  $\delta^{18}\text{O}$  signatures of all species for both seasons (Figure 5). In the pineland, *Schinus* was not significantly different from both native species, although greater variance in isotopic signatures

Table 1. Sodium ( $\text{Na}^+$ ) and potassium ( $\text{K}^+$ ) contents (in  $\text{mmol/L}$ ) ( $\pm$ SEM) of plant sap in the transition zone during the wet and dry seasons.

Plants	Wet Season			Dry Season		
	Na	K <sup>+</sup>	Na <sup>+</sup> + K <sup>+</sup>	Na <sup>+</sup>	K <sup>+</sup>	Na <sup>+</sup> + K <sup>+</sup>
<i>Schinus terebinthifolius</i>	3.6 $\pm$ 0.5	3.2 $\pm$ 0.3	6.7 $\pm$ 0.3 <sup>a</sup>	163.6 $\pm$ 24.3	48.8 $\pm$ 9.8	211.93 $\pm$ 15.3 <sup>c</sup>
Mangroves	16.9 $\pm$ 9.0	21.3 $\pm$ 17.1	38.2 $\pm$ 25.9 <sup>b</sup>	249.2 $\pm$ 25.3	96.9 $\pm$ 10.9	346.1 $\pm$ 30.6 <sup>d</sup>
Upland species	4.3 $\pm$ 2.1	7.8 $\pm$ 3.4	12.1 $\pm$ 5.5 <sup>a</sup>	76.9 $\pm$ 32.0	203.3 $\pm$ 38.2	280.5 $\pm$ 119.8 <sup>c</sup>

\* The  $\text{Na}^+ + \text{K}^+$  values followed by the same superscript letters do not differ significantly ( $\alpha = 0.05$  level) using a *post-hoc* Bonferroni comparison of means after analysis with a two-factor ANOVA (factors: functional groups, season).

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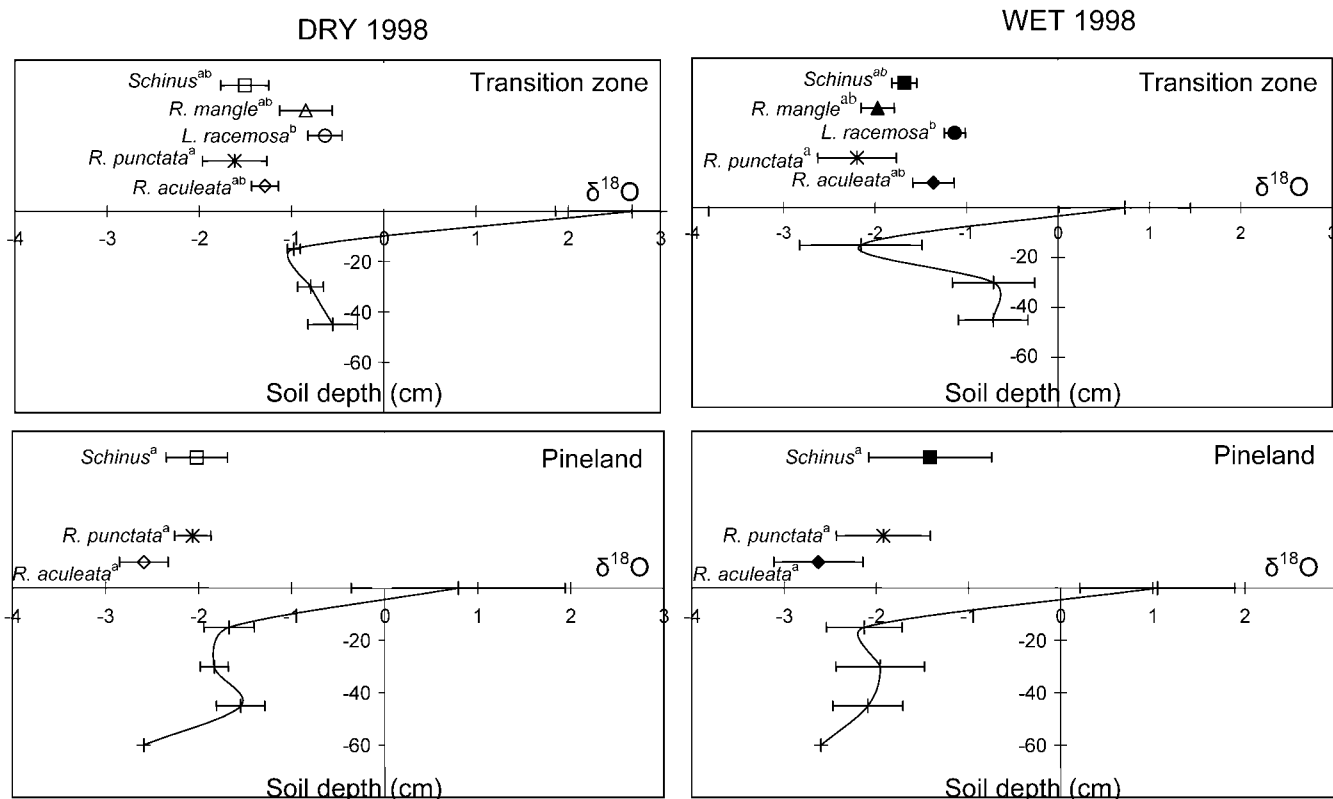


Figure 5. Vertical profile of soil  $\delta^{18}\text{O}$  values (average  $\pm$  SEM) for both the wet and dry seasons at the two study sites. Average plant  $\delta^{18}\text{O}$  ( $\pm$  SEM) are shown along the positive range of the y-axis. Species names followed by the same letters indicate that these values are not significantly different at the  $p = 0.05$  level using a *post-hoc* Bonferroni comparison of means.

within species was observed during the wet season. The exotic, however, showed a shift to isotopically more enriched  $\delta^{18}\text{O}$  values from the wet to dry season (Figure 5), corresponding to shallower soilwater uptake. On average, *R. aculeata* had the most negative  $\delta^{18}\text{O}$  values among the three species both seasons sampled (Figure 5).

### Predawn Xylem Water Potentials ( $\Psi$ )

Predawn xylem water potentials from each site were analyzed separately with a two-factor ANOVA (Table 2, Figure 6). At both sites, lower  $\Psi$  was observed in the dry season. In the transition zone, when averaged over all seasons, both mangrove species had the lowest  $\Psi$ , followed by *Schinus* and the upland species. The species  $\times$  season interaction in the transition zone (Table 2) was the result of lower  $\Psi$  in the 1999 dry season observed in all species except *Schinus*. In the pineland, however, the exotic was not distinct from both native species.

For the three seasons in which both sites were sampled, a three-factor ANOVA (Table 3) was used to compare *Schinus*, *R. punctata*, and *R. aculeata* in both communities. There were significant differences in  $\Psi$  between sites, species, and seasons (Table 3). There were also interactions between site  $\times$  season and species  $\times$  season (Table 3). *Post-hoc* Bonferroni pairwise comparisons of means showed that  $\Psi$  were generally

lower in the transition zone compared to the upland pineland during the dry season. Both native species also had lower  $\Psi$  compared to *Schinus* during the 1999 dry season in the transition zone but not in the pineland (Figure 6).

### DISCUSSION

Although *Schinus* is found in mangrove forests, it has not been quantitatively determined that this species is utilizing full-strength seawater ( $\approx 35$  ppt). In this study, although *Schinus* occurred within the mangroves and salinity at the surface reached a maximum of 40 ppt, the exotic was not extracting water from the more saline, top 5 cm of soil. We determined that *Schinus* was most likely utilizing water between 5 and 20 ppt salinity, corresponding to 15–45 cm depth, during the driest time of the year in the transition zone (Figures 2 and 4). This finding indicates that in this transition zone, vegetation patterns are not reflective of soil surface salinity levels during the dry season.

The large range in salinities of soilwater available for *Schinus* water uptake can be attributed to the horizontal and vertical heterogeneity in salinity found within the sandy transition zone soils (EWE, 2001). Pools (= lenses) of fresher water most likely form when water from Henderson Creek seeps into the surrounding mangrove areas via belowground flow (Figure 2). Because of low mixing between freshwater

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Table 2. Two-factor ANOVAs of plant  $\Psi$  examining the effects of species and season in the transition zone and the upland pineland.

	Transition Zone				Upland Pineland			
	DF	Mean Square	F	Probability	DF	Mean Square	F	Probability
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 $\times$ season	12	17.590	2.491	0.008	4	9.023	3.890	0.010
Error	80	7.061			36	2.319		

and seawater in this transition zone, lower-density freshwater flows over the more dense seawater, contributing to the formation of the freshwater lenses observed (Figure 2). The presence of freshwater lenses in soils have been shown in many studies from coastal and arid areas (e.g., LANGEVIN *et al.*, 1998; KWARTENG *et al.*, 2000). In our study, fluctuating freshwater inputs as well as groundwater levels, magnified by the dry season result in (1) distinct pools of fresher water overlying the saline groundwater (Figure 2) and (2) higher salinity at the soil surface where evaporation is occurring (Figure 3). Overall, salinity at 50 cm belowground was lower during the end of the wet season (November 1998) compared to the dry season (Figure 2). Lower salinity values recorded

during the end of the wet season are most likely caused by sampling of a deeper layer of groundwater relative to the middle of the wet season. In the dry season, as freshwater input from the creek declined, pools of fresher water remained on the more saline seawater. In February, decreased freshwater inputs resulted in lower groundwater levels and hence the sampling of a shallower strata of the groundwater at 50 cm (Figure 2). Nonetheless, these lenses of water are still potentially accessible to plants during the dry season.

Xylem sap content is a function of soil water availability coupled with root uptake properties. Despite  $\text{Na}^+$  being one of the most common ionic elements in seawater, high cellular  $\text{Na}^+$  concentrations can disrupt cell function. Plants regulate

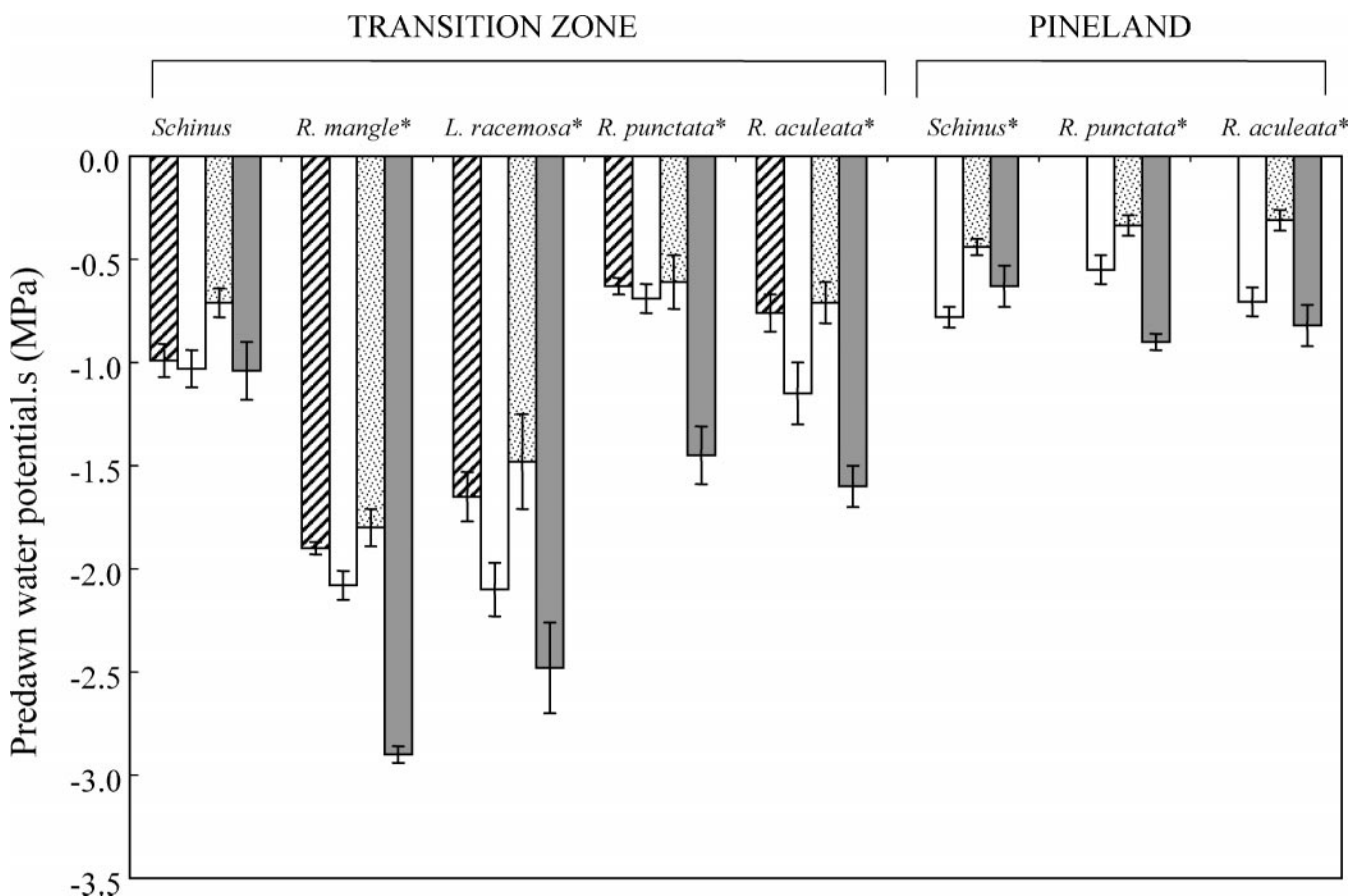


Figure 6. Predawn xylem water potentials ( $\pm$  SEM) of two dry and wet seasons in both the transition zone and upland pinelands. Striped bars represent the 1997 wet season; clear bars represent the 1998 dry season; stippled bars represent the 1998 wet season; and the gray bars represent the 1999 dry season. Asterisks (\*) indicate significant seasonal differences within species when analyzed with a *post-hoc* Bonferroni test for season  $\times$  species interaction.

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Table 3. A three-factor ANOVA of *Schinus*, *Rapanea punctata*, and *Randia aculeata* predawn water potentials for the two sites and three seasons sampled.

Source	DF	Mean Squares	F-ratio	Probability
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 × species	2	12.4	2.765	0.070
Site × season	2	21.33	4.730	0.012
Species × season	4	29.6	6.582	0.000
Site × species × season	4	1.745	0.388	0.817
Error	72	4.5		

Na<sup>+</sup> uptake via mechanisms such as restricting salt intake, secreting and excluding salts, or storing excess Na<sup>+</sup> in specific organs (SALISBURY and ROSS, 1992; LARCHER, 1995). In the transition zone, although all plants were exposed to higher salinity levels in the dry season (as evidenced by higher stem Na<sup>+</sup> + K<sup>+</sup> values [Table 1]), responses differed significantly among *Schinus* and the native species. In the upland species, Na<sup>+</sup>/K<sup>+</sup> ratios remained constant over season (Figure 4), but sap Na<sup>+</sup> + K<sup>+</sup> increased during the dry season, caused by an approximately 18-fold increase in Na<sup>+</sup> and a 26-fold increase in K<sup>+</sup> (Table 1). Some freshwater species selectively exclude Na<sup>+</sup> while preferentially taking up K<sup>+</sup> against a large external gradient, resulting in lower Na<sup>+</sup>/K<sup>+</sup> ratios than halotolerant species (GREENWAY and MUNNS, 1980; LAMBERS *et al.*, 1998). It is probable that during the dry season, native upland species from the transition zone are taking up K<sup>+</sup> but excluding Na<sup>+</sup> to a greater extent, as the Na<sup>+</sup>/K<sup>+</sup> ratios in these plants are lower than the mangroves or *Schinus* (Table 1, Figure 4). Both mangrove species showed significant increase in Na<sup>+</sup>/K<sup>+</sup> ratios and Na<sup>+</sup> + K<sup>+</sup> contents during the dry season, indicating greater salinity exposure and uptake during the dry season. There was also a disproportionate increase in Na<sup>+</sup> content relative to K<sup>+</sup> in the mangrove sap during the dry season, indicating less discrimination in Na<sup>+</sup> relative to K<sup>+</sup> uptake. Although mangroves are capable of restricting uptake of salts during water uptake, the sap of these plants, like that of most vascular plant species, will nonetheless reflect the ionic concentrations in the soil to some degree (NAIDOO, 1987; TEAS *et al.*, 1995).

Although *Schinus* Na<sup>+</sup>/K<sup>+</sup> ratios were similar to the mangroves during the dry season (Figure 4), the Na<sup>+</sup> and K<sup>+</sup> values of the exotic were more similar to those of the upland species both seasons (Table 1). These findings did not support the hypothesis that *Schinus* would have sap Na<sup>+</sup> and K<sup>+</sup> contents similar to mangrove species. *Schinus* Na<sup>+</sup> concentration during the dry season in the transition zone indicates that this exotic is most likely being exposed to water that is less saline than the mangroves, and this exotic most likely does not discriminate against Na<sup>+</sup> uptake to a similar degree as the upland species (Table 1). This finding is similar to that of BUSCH and SMITH (1995), who found the invasive exotic *Tamarix ramossissima* had higher Na<sup>+</sup>/K<sup>+</sup> contents relative to native glycophytes in the riparian habitats of western United States.

The absence of a strong salinity-δ<sup>18</sup>O relationship in both sites did not allow us to identify the precise depth of water uptake for each species. Unlike previous studies from coastal

areas (*e.g.*, ISH-SHALOM *et al.*, 1992; LIN and STERNBERG, 1994), there was not a significant linear relationship between soilwater δ<sup>18</sup>O values and depth in this study. Although there was a significant relationship between soilwater salinity and δ<sup>18</sup>O values, the inflection at 15 cm precludes the exact estimation of water uptake depth by the plants. We estimated that all species were utilizing water from between 15 and 45 cm depth and encountering water of 5–20 ppt. Therefore, the hypothesis that *Schinus* utilizes more saline groundwater relative to native upland species could not be proved. The shift to shallower water uptake from the dry to wet season by *Schinus* in the pineland has also been observed in other South Florida communities. A similar seasonal shift has been shown in *Schinus* and native species within the Hole-in-Donut area in the Everglades (EWE and STERNBERG, 2002) as well as in native rock pineland species such as *Lysiloma latiliqua*, *Baccharis halimifolia*, and *Myrica cerifera* (EWE *et al.*, 1999; EWE and STERNBERG, 2002).

The hypothesis that *Schinus* would have lower Ψ relative to freshwater native species was not supported by our findings. For all seasons sampled, *Schinus* Ψ were similar to the upland species, although the exotic was least affected by seasonality relative to native species at both study sites. High Na<sup>+</sup>/K<sup>+</sup> in the exotic during the dry season, similar to mangrove species, coupled with seasonally high Ψ can be explained by the selectivity in ion uptake by *Schinus*. Less selectivity or discrimination in ion uptake by the exotic would cause lower osmotic potential differences between stem water and the soil. This would then result in higher dry season Ψ in the exotic relative to the salt-excluding mangroves (Figure 6).

In the transition zone, *Schinus* Ψ seemed buffered from seasonal changes in soil matric or osmotic potential (Figure 6). Soil matric potential is a function of its water retention capabilities (via capillary action) while osmotic potential is affected by the ionic content of the soil. Drier soils coupled with higher ionic contents during the dry season at the transition zone will reduce both soil matric and osmotic potentials. These soil conditions can cause “physiological drought” in plants unable to take up sufficient water or utilize the brackish soilwater. Significant decline in dry season Ψ of all native species at the transition zone indicated that the plants were water and/or salinity stressed. Compared to native species, lack of consistent seasonal variability in *Schinus* Ψ indicates that the exotic is continually accessing water and not discriminating against brackish water uptake during the dry season. Lack of differences in Ψ between *Schinus* and the

native species in the pineland across all seasons indicate that at this site, the exotic is functionally similar to natives in terms of its water uptake.

Both sap water  $\text{Na}^+$  and  $\text{K}^+$  values and  $\Psi$  of the species compared support the hypothesis that *Schinus* exhibits some salinity tolerance. This is not surprising because many invasive exotics originating from coastal or arid areas such as *Casuarina equisetifolia* (see references in LANGELAND and CRADDOCK-BURKS, 1998), *Tamarix ramosissima* (BUSCH and SMITH, 1995), *Mesembryanthemum crystallinum* (VIVRETTE and MULLER, 1977), and *Cupaniopsis anacardioides* (OLIVER, 1992) have also been shown to tolerate salinity. The extent to which physiological salinity tolerance of these non-native species can potentially facilitate biological invasions into native coastal and arid plant communities, particularly where access to seasonal pools of fresher soilwater is available, needs to be further examined.

EWE and STERNBERG (in press) have shown that *Schinus* gas exchange is severely curtailed at the end of the dry season in the brackish transition zone, when soil salinity levels are high. Yet this exotic is widely found in coastal transition zones throughout much of Florida. We believe that in the wet season, when freshwater is readily available, *Schinus* probably has no competitive advantage over native species in the transition zone. However, when freshwater availability is patchy and limited during the dry season, *Schinus* salinity tolerance in this environment potentially allows this exotic to outcompete native plants. Tolerance of salinity within the sap and lowered stomatal conductance (hence reducing water loss) allows this exotic to persist in a state of "physiological dormancy" during stressful conditions within brackish environments. Native freshwater species unable to physiologically tolerate increasing soil salinity toward the end of the dry season would have reduced growth rates and suffer leaf dieback or even plant death. Indeed, some individuals of *R. aculeata* in the transition zone failed to grow sufficiently for continual sampling. Native plants unable to regulate their physiological function are thus less able to outcompete the exotic for resources such as light and nutrients when the wet season starts again.

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 pine forests and increase in mangrove forest acreage. Sea level rise would provide the exotic a competitive edge over native species as belowground intrusion of seawater into previously freshwater areas would curtail the growth of native species to the benefit of *Schinus*. Therefore, the conversion from one native community to another will not be continuous if *Schinus* is present and able to outcompete native species in the transition zone.

## CONCLUSIONS

Although oxygen stable isotope ratios of the exotic were unable to qualitatively determine the depth of *Schinus* water uptake within both study communities, the  $\Psi$  and  $\text{Na}^+/\text{K}^+$  ratios of the exotic indicate that this species is tolerant of some salinity, allowing it to persist together with mangrove

and freshwater species in a seasonally saline environment. *Schinus* shows evidence of salt tolerance, but its degree of tolerance, compared to native species, needs to be further explored.

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