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

Abstract *Schinus terebinthifolius* Raddi (*Schinus*) is an invasive exotic species widely found in disturbed and native communities of Florida. This species has been shown to displace native species as well as alter community structure and function. The purpose of this study was to determine if the growth and gas exchange patterns of *Schinus*, under differing salinity conditions, were different from native species. Two native upland glycophytic species (*Rapanea punctata* and *Randia aculeata*) and two native mangrove species (*Rhizophora mangle* and *Laguncularia racemosa*) were compared with the exotic. Overall, the exotic's morphologic changes and gas exchange patterns were most similar to *R. mangle*. Across treatments, increasing salinity decreased relative growth rate (RGR), leaf area ratio (LAR) and specific leaf area (SLA) but did not affect root/shoot ratios (*R:S*). Allocation patterns were however significantly different among species. The largest proportion of *Schinus* biomass was allocated to stems (47%), resulting in plants that were generally taller than the other species. *Schinus* also had the highest SLA and largest total leaf area of all species. This meant that the exotic, which was taller and had thinner leaves, was potentially able to maintain photosynthetic area comparable to native species. *Schinus*' response patterns show that this exotic exhibits some physiological tolerance for saline conditions. Coupled with its biomass allocation patterns (more stem biomass and large area of thin leaves), the growth traits of this exotic potentially provide this species an advantage over native plants in terms of light acquisition in a brackish forested ecosystem.

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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 transported plants for food, medicinal and ornamental value (di Castri 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 years. Examples of exotics potentially 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 pine rocklands 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 attributed to Dr George Stone who, in the late 1890s, 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) 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 post-germination survival has not been fully explored. Moreover, once *Schinus* reaches 1.0 m in height, individuals are not easily killed by fire as they resprout (Doren et al. 1991).

Previous field measurements have shown that *Schinus* water uptake and gas exchange patterns under saline conditions, are different from native species (Ewe 2001). Growth patterns of these species in the field however, were not recorded. This paper addresses the lack of field data by comparing the growth and gas exchange response of *Schinus* with native species under controlled glasshouse conditions. Therefore, it was hypothesized that: (1) *Schinus* would grow faster than native species under different salinity conditions and (2) gas exchange patterns of the exotic would be less affected by salinity than native species.

Materials and methods

Species studied

We compared *Schinus* to native mangrove [*Rhizophora mangle* L. (red mangrove) and *Laguncularia racemosa* L. (white mangrove)] and upland glycophytic species [*Rapanea punctata* (Lam.) Lundell (Florida myrsine) and *Randia aculeata* L. (indigoberry)] often found growing with the exotic in brackish saline areas. *Schinus* seeds and mangrove seedlings were collected from coastal southwest Florida while *R. punctata* and *R. aculeata* seedlings were purchased from a local nursery. Details of seedlings growth and germination are described in Ewe (2001). Seedlings of all species were transplanted into 7.6 l pots (1 plant/pot) 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 set-up was divided into five blocks of one individual per species for each treatment (five rows × three deep =15 plants each). Five individuals per species were randomly placed in each row, one per block. All plants were individually labeled. Plants were moved within and between blocks throughout the experiment to reduce location effects.

All plants were maintained in a glasshouse where daytime maximum light levels ranged from 1,200 μmol m^{-2} s^{-1} to 1,500 μmol m^{-2} s^{-1}. Plants were irrigated once a day to saturation with the appropriate treatment solutions from March through June but during the warmer months of July and August (diurnal average = 32°C; maximum air temperature = 40°C), supplemental afternoon irrigation was periodically applied. Every 3 weeks, 0.34 g of fertilizer (Peters Professional 20–20–20 (N–P–K) Plant Food with micronutrients) dissolved in 1 l of either the appropriate tap water or seawater solution, was added to each plant.

Salinity treatments

The experiment started on 8 March 2000 (Julian day 68), timed to coincide with the earliest possible initiation of seasonal growth. The three treatments were control [0 parts per thousand (ppt)], low (8 ppt) and high (15 ppt) salinity, with five replicates for each species. Seawater solutions were prepared using untreated sea-salts (Cargill Salt, Minneapolis, Minn.) and tap water. Salinity treatments started at 1 g l^{-1} (1 ppt) and were raised 1 ppt each week until 0, 5, and 10 ppt were reached. 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 (5 September 2000), approximately 1 month after high salinity levels were reached.

Measurements

Two individuals of each species grown in addition to experimental plants were harvested at the start of the experiment to be able to determine relative growth rate (RGR) at the end of the experiment. The number of leaves ($L_\#$), longest stem length (S_{length}), basal circumference (S_{circ}) and leaf area (LA) were measured. All plants were oven-dried at 65°C for 2 weeks and individual organs weighed.

All morphometric parameters ($L_\#$, S_{length}, S_{circ}, largest leaf width and length) were measured: (1) shortly after start of experiment (Julian day 77), (2) when the high salinity treatment reached 10 ppt (Julian day 210), and (3) just prior to harvest (Julian day 253). For *R. punctata* and *R. aculeata*, longest S_{length} was measured instead of height due to multiple stems. Basal stem circumference was measured on the largest diameter stem 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 (5 September 2000), all plants were defoliated and growth media washed off the roots. Fresh leaf weight of all plants was measured (Sartorius 4000, Sartorius, Goettingen, Germany). Whole plant LA was measured (LI-3000, LiCor, Lincoln, Nebr.) for three individuals per species within each treatment. For all plants, leaves used in gas exchange were bagged separately for determination of carbon isotope (δ^{13}C) and nitrogen content. All leaves were dried in a freeze–dryer (Labconco, Kansas City, Kan.) for one week. After drying, leaf weight of each plant was obtained. For individuals where LA had been measured previously, specific leaf area

(SLA, m^2 g^{-1}) was obtained by dividing total LA by leaf dry weight. Leaf area ration (LAR) was determined by dividing LA over total plant weight. Stem and roots were air-dried for 2 months before weighing. Plant RGR was expressed by the equation

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

where W_2 is the biomass at harvest (g), W_1 the initial biomass (g), t_2 the harvest date (month) and t_1 is the start date of experiment (month). The proportions of leaves, stems and roots to total plant biomass were calculated. Root/shoot (R:S) ratios were 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 carbon dioxide (CO_2) was extracted from a 5 mg ground leaf subsample based on the modified methods of Buchanan and Corcoran (1959) and analyzed on an isotope-ratio mass spectrometer (VG Prism, Micromass, Middlebury, England). Leaf carbon isotopic signatures, in per mil units (‰), were determined using the following equation

$$\delta^{13}C = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1,000$$

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 relative to Pee–Dee Belemnite. Leaf carbon isotopic signatures were used as a proxy for integrated plant water-use efficiency (WUE) as $\delta^{13}C$ values have been shown to be positively related to WUE over its lifespan (Farquhar et al. 1982). A second ground up leaf subsample was used for nitrogen analysis using a CN analyzer (NC2100, Carlo Erba, Milan, Italy). Leaf nitrogen content was expressed as a function of leaf area ([N], g N m^{-2} leaf).

Instantaneous gas exchange was measured with a LI-6200 (LiCor, Lincoln, Neb.) on sunny days (PAR >1,000 µmol m^{-2} s^{-1}). Gas exchange was measured between 0900 hours and 1500 hours on 45 randomly selected plants (n=3). The second mature leaf from the growing tip was measured for 60 s using a 390 ml chamber attachment.

Gas exchange from the last two sample days (Julian days 197 and 217) were compared among species to determine plant salinity responses. Intrinsic WUE (µmol CO_2 mol^{-1} H_2O) was calculated by dividing net carbon dioxide 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}). Photo-synthetic nitrogen-use efficiency (PNUE, µmol CO_2 g^{-1} N s^{-1}) was determined by dividing A over [N]. As variance between days was smaller than among species, data from both days were pooled to increase sample size; values from individuals sampled on both dates were averaged before analysis. Between three to five individuals were measured per species for each treatment.

Statistical analysis

For each morphometric parameter, the initial measures (Julian day 77) were normalized to 100%. Changes in $L_\#$, S_{length}, and S_{circ} were analyzed using a repeated-measures analysis-of-variance (ANOVA). For all analyses described above, the probability of Type I error was set at 0.05 (i.e., α=0.05).

Table 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 α=0.05 level (P<0.05)

Change in growth parameters	df, error df	$P_{Treatment}$	df, error df	P_{Time}	df, error df	$P_{(Treatment \times Time)}$
$L_\#$						
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
S_{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
S_{circ}						
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

Plant biomass parameters [RGR ($n=5$), LAR (m^2 kg^{-1}; $n=3$), SLA ($n=3$), and $R{:}S$ ($n=5$)] were 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 ($\alpha=0.05/4$, $P<0.0125$). Significant factors were subsequently analyzed with the Tukey HSD.

Two-factor (treatment and species) ANOVAs were carried out on each gas exchange parameter. Tukey HSD post hoc tests were carried out on factors that were significant. Two-factor ANOVAs were preferred over a single multivariate ANOVA to better isolate treatment and species differences. Significance levels on these ANOVAs were Bonferroni corrected for the number of parameters ($\alpha=0.05/6=0.008$). Additionally, discriminant function (DF) analysis was used to investigate patterns of species responses (A, g_s, g_m, A/g_s, $\delta^{13}C$, [N] and PNUE) at each salinity. *Schinus* was initially excluded from each analysis as to not bias its classification relative to the other species. Instead, values from the exotic were laid onto DF graphs after analysis based on their squared Mahalanobis distance to the centroid. Classification results are also shown in addition to the DF graphs. All data were analyzed using SPSS 8.0 (SPSS, Chicago, Ill.).

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 some leaf loss under high salinity, all individuals survived the experiment. As the trends $L_\#$ and S_{length} were similar (Table 1), only changes in $L_\#$ are shown (Fig. 1). Leaf numbers were significantly different among treatments for *L. racemosa*, *R. punctata* and *R. aculeata* (Table 1, Fig. 1). At low salinity, *L. racemosa* plants were larger and had more leaves than control or high salinity plants (Fig. 1). For *R. punctata* and *R. aculeata* however, both salinity treatments resulted in smaller plants with fewer leaves than the controls (Fig. 1). Plant size and morphology however, did not change in either *R. mangle* or *Schinus*. Leaf lengths and widths, analyzed with MANOVAs, were not significantly different across treat-

Fig. 1 Increases in leaf number (%) for each species from the start of data analysis (growth at start normalized to 100%). Averages of the control (*filled circle*), low salinity (*filled triangle*), and high salinity (*filled square*) treatments are shown with their standard errors. *Asterisks* indicate significant differences among treatments. Symbols with the same letters do not differ significantly at $P>0.05$ by post hoc Tukey HSD
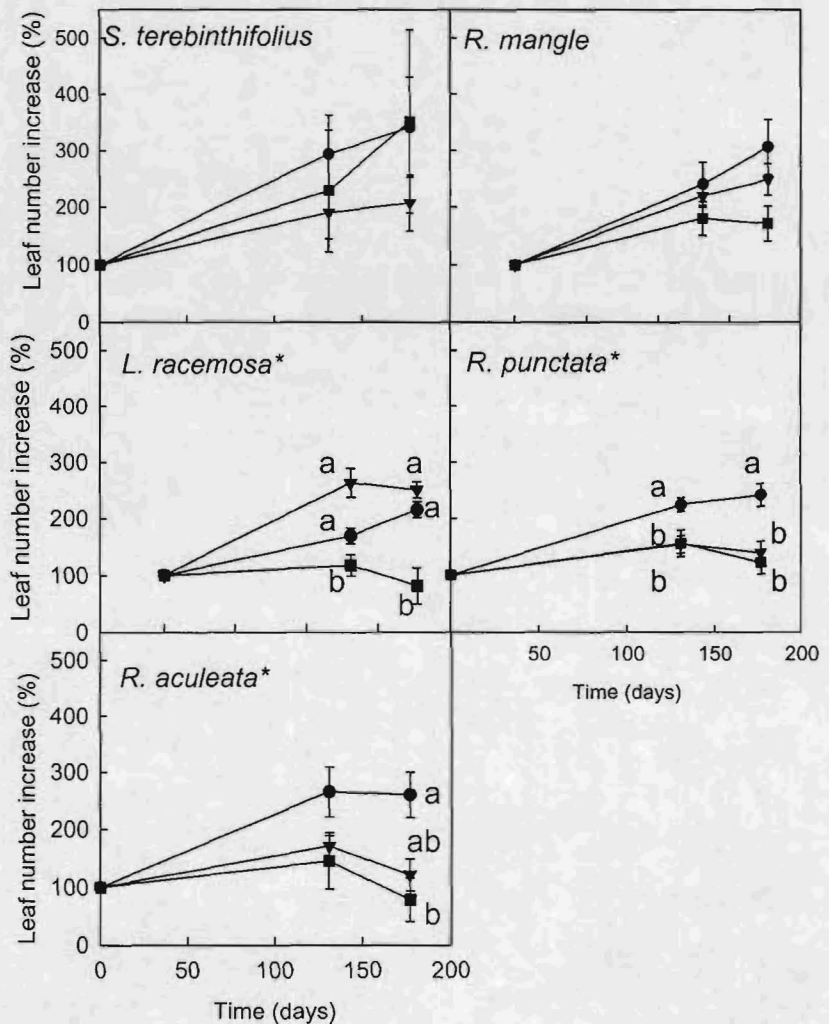
ments or among species at the end of the experiment. Branch number also did not vary significantly with species or treatment.

Changes in S_{circ} across treatments were only significant for *R. punctata* and *R. aculeata* where increasing salinity decreased stem size. All *Schinus* and *L. racemosa* showed an increase in S_{circ} over time but *R. mangle* did not increase significantly in girth throughout the sample period (Table 1).

Relative growth rates varied among species but not across treatments. Among species, RGR was highest in *L. racemosa* and *R. punctata* (Fig. 2a). *L. racemosa* growth rates, unlike all other species, was weakly stimulated by low salinity (one-factor ANOVA: $F_{2,9}=4.79$, $P=0.038$) (Fig. 2a). In general, although high salinity reduced RGR in all species (Fig. 2a), the responses of *Schinus* and *R. mangle* were most similar. Neither species, when analyzed with post hoc tests, showed significant reductions in RGR with increasing salinity. LAR (Fig. 2b) differed across treatments ($F_{2,28}=6.21$, $P<0.012$). Despite a trend of decreasing LAR with increasing salinity (Fig. 2b), 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 different across treatments (Table 2) but was significantly different among species

(Table 3). *Schinus* allocated most of its biomass to stems (46.9%) and least to its leaves. *Schinus* only allocated an average 15.4% of its total biomass to leaves while native species allocated an average of 22.7%. *Schinus* LAR however, was not significantly different from most native species across treatments (Fig. 2b).

There was a difference in SLA (Fig. 2c) 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*. At low salinity, *Schinus* SLA was marginally significantly higher than native species (one-factor ANOVA, $F_{4,14}=2.74$, $P=0.067$) indicating thinner leaves than native species. Root:shoot ratios showed no

Table 2 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). Because of non-significance across treatments, fractions for each species regardless of treatment were pooled

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 × Species	8	0.179	8	0.407	8	0.388

Error df=51.

Fig. 2 Averages (± SE) of *Schinus* (*open square*), *R. mangle* (*north-east striped box*), *L. racemosa* (*gray-shaded square*), *R. punctata* (*south-west striped box*), and *R. aculeata* (*filled square*) under control, low, and high salinity treatments. Graphs show: **a** Relative growth rates (RGR), **b** Leaf area ratio (LAR), **c** Specific leaf area (SLA), **d** root/shoot ratios (*R:S*) and **e** leaf nitrogen concentration per leaf area ([N]). 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 above the bars show differences among treatments within species at *P*<0.012 by post hoc Tukey HSD
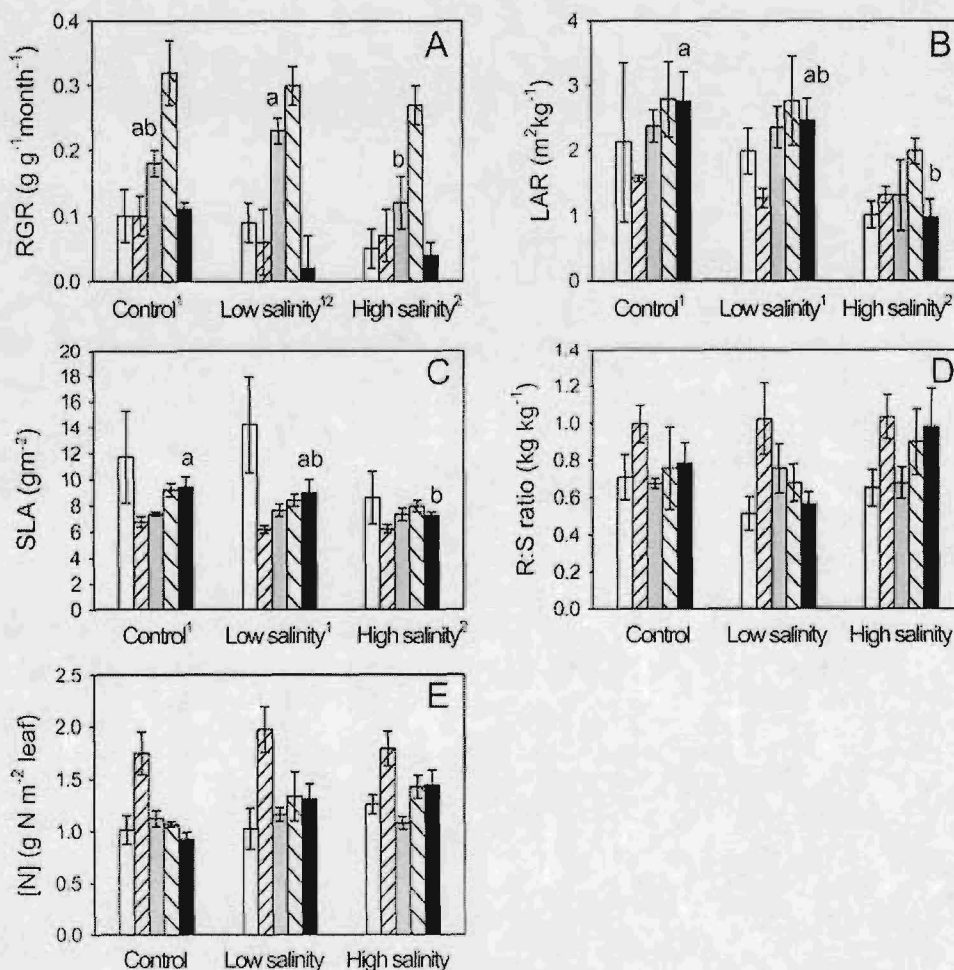
Table 3 Percentage biomass fraction (±SEM) of each plant organ. Values followed by the same letter do not differ significantly at $\alpha=0.05$ by Tukey HSD following the MANOVA

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

differences across treatments ($F_{2,53}=1.12$, $P>0.012$) (Fig. 2d). There were species differences in R:S ratios ($F_{4,53}=3.22$, $P=0.019$), but no interaction between treatment and species ($F_{8,53}=0.519$, $P>0.012$). *Schinus* R:S ratios were not different from most native species but were lower than *R. mangle* (which allocated almost 50% of its total biomass to roots) (Table 3). Leaf [N] (Fig. 2e) was significantly different across treatments ($F_{2,53}=3.64$, $P<0.05$) and among species ($F_{4,53}=13.28$, $P<0.05$) but there were no interactions 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. 2e).

Gas exchange and stable isotopes

Examination of the individual gas exchange variables (A, g_s, g_m) showed that all parameters decreased at the highest salinity. Assimilation rates were significantly lower at high salinity than low salinity and control treatments (Fig. 3a). Although A differed significantly among treatments ($F_{2,44}=11.44$, $P<0.008$) and species ($F_{4,44}=4.98$, $P<0.008$) there was no interaction between the two factors ($F_{8,44}=1.97$, $P>0.008$). *Schinus* had the lowest A of all species, significantly lower than *R. aculeata* and *R. mangle* (which had the highest overall A) (Fig. 3a). Individual species' one-factor ANOVAs showed that differences between treatments 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 (Fig. 3b) was different among treatments ($F_{2,44}=4.93$, $P=0.012$) but not species ($F_{4,44}=2.40$, $P>0.008$). There was however a significant interaction between both factors ($F_{8,44}=3.11$, $P<0.008$). Post hoc tests showed that significance in the interaction was from *R. mangle* ($P<0.01$) and *R. aculeata* ($P<0.01$) (Fig. 3b). Stomatal conductance in *R. mangle* was highest at 8 ppt relative to the other treatments while in *R. aculeata*, g_s was significantly lower at both salinity treatments (Fig. 3b). Mesophyll conductance (Fig. 3c) was different among treatments ($F_{2,44}=6.18$, $P<0.008$) but not among the five species compared ($F_{4,44}=3.40$,

Fig. 3 Leaf: **a** assimilation (A), **b** stomatal conductance (g_s), **c** mesophyll conductance (g_m), **d** intrinsic water-use efficiency (A/g_s), **e** photosynthetic nitrogen-use efficiency (PNUE) and **f** carbon isotope signatures ($\delta^{13}C$). The *bars* show averages (± SEM) for *Schinus* (*open square*), *R. mangle* (*north-east striped box*), *L. racemosa* (*gray-shaded square*), *R. punctata* (*south-west striped box*), and *R. aculeata* (*filled square*) 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 above bars* show within-species treatment differences at $P<0.008$ by post hoc Tukey HSD
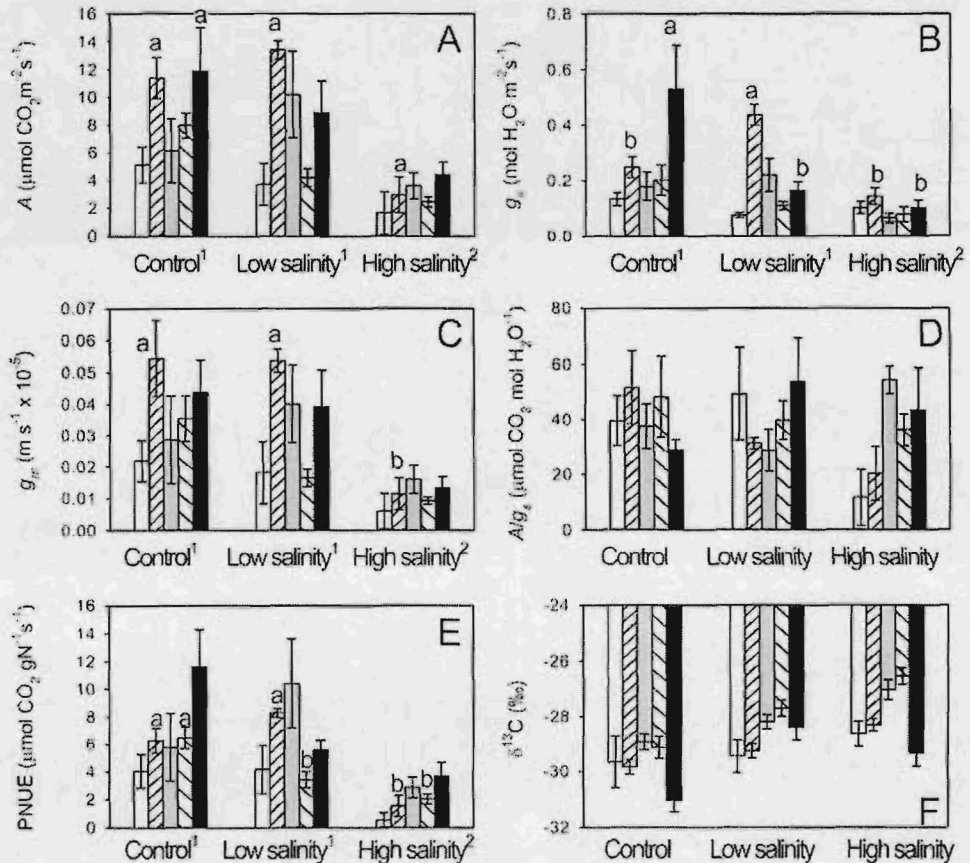
$P>0.008$). There was also no interaction between factors ($F_{8,44}=0.80$, $P>0.008$). Mesophyll conductance was significantly lower in the high salinity treatment than in the other two treatments (Fig. 3c). *Schinus* grown in freshwater had g_m approximately 4-fold that of plants grown at high salinity.

Intrinsic WUE (Fig. 3d) showed no significant differences among treatments ($F_{2,44}=0.58$, $P>0.008$) or species ($F_{4,44}=0.82$, $P>0.008$) although *Schinus* showed a trend of decreasing A/g_s with increasing salinity. Photosynthetic nitrogen-use efficiency (Fig. 3e) was significantly different across 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 growing in high salinity compared to 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. 3e). Carbon isotopic signatures (Fig. 3f) were not significantly different either among species ($F_{4,60}=2.27$, $P>0.008$) or treatments ($F_{2,60}=2.65$, $P>0.008$) although in most native species, there was a trend towards greater $\delta^{13}C$ values with increasing salinity (Fig. 3f).

Discriminant function analysis of gas exchange properties

In the control (Fig. 4), *Schinus* was not significantly different from native species along both axes. At 0 ppt, DF 1 explained approximately 83.4% of the total variation; A and PNUE were the most significant variables (i.e., they had the largest canonical coefficients). DF 2 explained 14.1% of the variability, the largest coefficients being g_s and g_m. *Schinus* was the most dispersed of all species indicating higher variability of all parameters in this species relative to native species. Classification of *Schinus* group membership showed the exotic was classified

evenly in all other species groups (Table 4). All native species were classified correctly except one *R. punctata* which was incorrectly classified as *R. aculeata* at both 0 ppt and 15 ppt (Table 4). At low salinity (8 ppt), there was still significant overlap of most species along both axes. The only exception was *R. mangle* along DF 1. *Schinus* was classified in all groups except *R. mangle* (Table 4). Under high salinity, there was increasing separation among species along DF1 (A and g_s). There was little overlap of *Schinus* with *R. punctata* and *R. aculeata* and no overlap at all between the exotic and *L. racemosa* (Fig. 4). Most of the *Schinus* individuals were classified as *R. mangle* (Table 4).

Discussion

Our general findings concur with previous studies on plant responses to salinity (Allen et al. 1997; Naidoo et al. 2002; Sohan et al. 1999). Morphology (Fig. 1), growth (Fig. 2), biomass allocation (Table 2) and gas exchange (Fig. 3) responses were affected by salinity but patterns of species responses varied among parameters measured. In this study, salinity significantly affected many aspects of morphology in most native species but not *Schinus* (Fig. 1). *Schinus* and *R. mangle* were not significantly affected by salinity while *L. racemosa* was actually stimulated by low salinity. Although growth in some halophytes is promoted at low and intermediate salinities (Ball and Pidsley 1995; Khan and Aziz 2001), most plants will show a reduction in growth with increasing salinity (Asch et al. 2000; Warwick and Bailey 1997). Decreasing growth and changes with morphology with increasing salinity have been well documented in glycophytic species (Fung et al. 1998; Plaut et al. 2000). Growth of both *R. punctata* and *R. aculeata* were maximum in freshwater and decreased with increasing salinity (Fig. 2a).
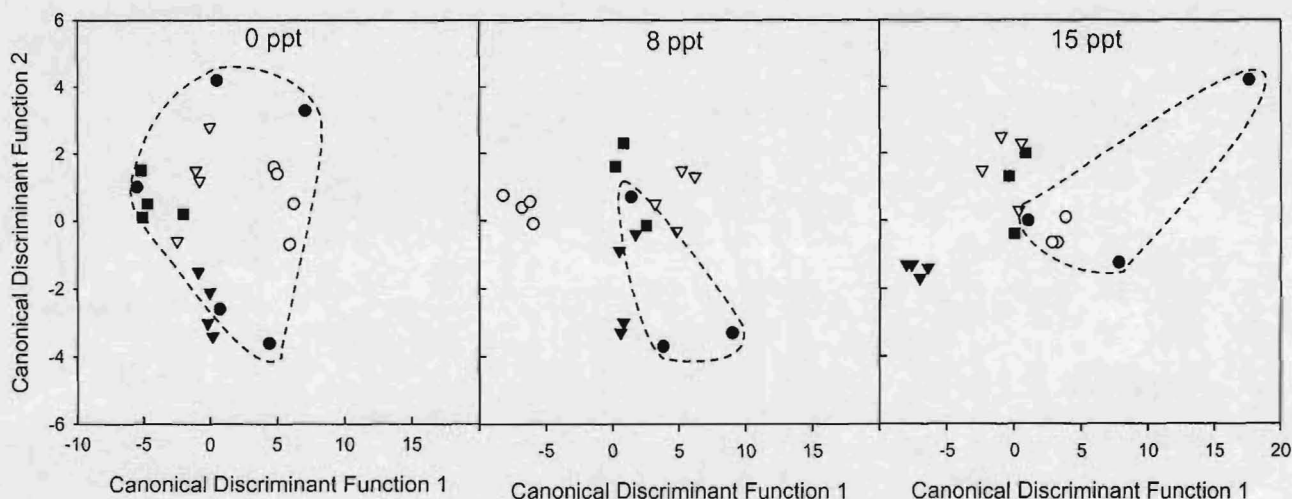

Fig. 4 Canonical discriminant function analyses of the gas exchange parameters for each species at three different salinities. The *symbols* show *Schinus* (*filled circle*), *R. mangle* (*open circle*), *L. racemosa* (*filled down triangle*), *R. punctata* (*open down triangle*), and *R. aculeata* (*filled square*) at each salinity. The *dotted lines* outline the distribution of *Schinus* values

Table 4 For cross validation of group membership, native individuals were reclassified into groups (i.e., species) based on their discriminant function values after discriminant analysis. Within each treatment, most plants were correctly reclassified. As *Schinus* was initially excluded from the analysis, classification of *Schinus* individuals into native species groups indicates the similarity of *Schinus* to these species

	Predicted classification				
	R. mangle	*L. racemosa*	*R. punctata*	*R. aculeata*	Total individuals
Control (0 ppt)					
Schinus	1	2	1	1	5
R. mangle	4	0	0	0	4
L. racemosa	0	4	0	0	4
R. punctata	0	0	3	1	4
R. aculeata	0	0	0	4	4
Low salinity (8 ppt)					
Schinus	0	1	1	1	3
R. mangle	4	0	0	0	4
L. racemosa	0	3	0	1	4
R. punctata	0	0	4	0	4
R. aculeate	0	0	0	3	3
High salinity (15 ppt)					
Schinus	2	0	0	1	3
R. mangle	4	0	0	0	4
L. racemosa	0	4	0	0	4
R. punctata	0	0	3	1	4
R. aculeata	0	0	0	3	3

Leaf area appears to be one of the first plant traits to be affected by salinity (Munns and Termaat 1986); plants unable to tolerate saline conditions often have fewer and smaller leaves because salt affects leaf expansion (Aspinall 1986; Marcelis and van Hooijdonk 1999). The two glycophytes, *R. punctata* and *R. aculeata*, were the only species to have fewer (Fig. 1) and smaller (Fig. 2b) leaves with higher salinity.

SLA of the exotic was also higher than all native species across treatments, indicating thinner leaves (Fig. 2b). High growth rates have been shown in plants with high SLA (Lambers and Poorter 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 (Figs. 2, 3). This is most likely explained by *Schinus'* biomass allocation patterns. Potential advantages that could have been derived from high SLA in *Schinus* were offset by the fact that (1) the exotic invested most of its biomass in stems and (2) had [N] similar to native species. This resulted in the exotic having a similar leaf area and most likely similar rubisco contents/leaf area as well as comparable CO_2 assimilative capacities with native species. Two ecological observations are derived from the findings above. First, thinner leaves of cheaper carbon costs could potentially provide *Schinus* with a competitive edge over the native species. Baruch and Goldstein (1999) have shown that leaf construction costs of thin leaves are lower than thick leaves in some exotic Hawaiian species, possibly contributing to the invasive ability of these species. Second, in *Schinus*, the greater allocation to stems allowed this plant to grow taller than native species across all treatments. Higher rates of stem growth potentially provide the exotic with a significant advantage in competition for light.

When comparing *Schinus* and *R. mangle*, two species with very similar RGR across treatments (Fig. 2a), one finds that different traits contributed to the patterns observed. Although both species had almost similar LAR (Fig. 2b) in the control and high salinity treatments, the exotic had higher SLA (Fig. 2c) than *R. mangle* while the mangrove had higher [N] than the exotic (Fig. 2e). Despite contrasting leaf allocation and assimilation strategies (i.e., thin leaves, low [N] and A in the exotic as opposed to thicker, higher [N] and A leaves) the overall RGR (Fig. 2a) of both species was similar across treatments.

Plant $R:S$ ratios have also been shown to be affected by salinity whereby salinity tolerant plants show a reduction in $R:S$ ratios while salinity intolerant plants have greater $R:S$ from decreased shoot growth (Bayuelo-Jiminez et al. 2003; Cheeseman and Wickens 1986; Seemann and Critchley 1985). Salinity did not affect $R:S$ ratios of any of the study plants (Fig. 2d). It is possible that the slow, weekly increase in salinity allowed the plants time to acclimate to higher salt levels, resulting in the lack of biomass allocation responses.

Most gas exchange parameters were affected by higher salinity relative to control and low salinity treatments. Although not significant, both mangrove species had higher A, g_s, and g_m (Fig. 4a–c) at low salinity relative to the control and low salinity treatments. These findings concur with other researchers (Lin and Sternberg 1992; Naidoo and von Willert 1999; Naidoo et al. 2002; Tuffers et al. 2001) who have shown that many halophytic species growing in low salinity have greater A than when grown under either high salinity or control conditions because of salt requirement in maintaining low osmotic potentials for water uptake and optimal growth. Gas exchange in both glycophytic species however, decreased with increasing salinity. At high salinity, gas exchange in glycophytes was

most likely limited because of cells being biochemically disrupted by the presence of salts (Munns 1993).

Unlike the study of Baruch and Goldstein (1998), which showed greater daily A in C3 invasive exotics relative to native Hawaiian species, *Schinus A* in this study was not significantly different from native species (Fig. 3a). Plants with greater A have been shown to have greater nitrogen concentrations (on a mass basis) and SLAs (Reich 1993), which could 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 had the capacity to increase leaf PNUE. Instead, *Schinus'* consistently low gas exchange resulted in similar intrinsic WUE (Fig. 3d) and PNUE (Fig. 3e) between the exotic and most of the native species.

Assessment of all gas exchange parameters with DF analyses (Fig. 4) however, indicated that in freshwater and at low salinity, *Schinus* was not significantly different from all species; at high salinity, *Schinus* gas exchange was most similar to *R. mangle*. This indicates possible salt tolerance characteristics in the exotic. Further evidence of *Schinus'* tolerance of salinity was also seen in its $\delta^{13}C$ signatures (Fig. 3f). The isotopic data supported the instantaneous A measures as *Schinus* was the only species to not show a $\delta^{13}C$ response across treatments. Native species showed slight increases $\delta^{13}C$ signatures with higher salinity, indicating a positive relationship between integrated WUE and salinity. Long-term WUE of the exotic however, appeared to be buffered from salinity increases to a greater degree than the native species.

These gas exchange findings support the results of comparative field studies of *Schinus* and native species from both freshwater upland Everglades (Ewe and Sternberg 2003) and brackish mangrove areas (Ewe and Sternberg, in preparation). Field data show that *Schinus* gas exchange was similar to the native species in freshwater and at low salinity levels.

Plants that express high phenotypic plasticity are believed to have the capability of being successful invaders (Kutsch and Kappen 1991; Vickery 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). The morphologic parameters of *Schinus* do not appear to be very plastic in response to salinity, unlike its gas exchange parameters where at higher salinities, *Schinus* start to resemble *R. mangle* (Fig. 4). Plasticity in gas exchange of this exotic may confer this species an advantage in invading South Florida ecosystems.

Schinus may be more ecologically tolerant of salinity relative to native glycophytes as many of its morphological characteristics were not affected by salinity. This tolerance potentially can confer an advantage to *Schinus* over native glycophytes in transition zones where salinity fluctuates seasonally and spatially. The results reported here are consistent with previous field observations of water uptake by *Schinus* (Ewe and Sternberg, accepted not yet published) which shows the exotic to be less influenced by salinity compared to native glycophytes.

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