Oecologia (2002) 133:441–448
DOI 10.1007/s00442-002-1047-9

ECOPHYSIOLOGY

Sharon M. L. Ewe · L. da S.L. Sternberg

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

Received: 9 October 2001 / Accepted: 17 May 2002 / Published online: 19 September 2002

Abstract *Schinus terebinthifolius* Raddi (Anacardiaceae) is an aggressive invader found in both disturbed and native habitats of Florida. The purpose of this study was to compare *Schinus* water uptake patterns to those of four native species in a disturbed previously farmed area versus a native pineland community. Although neither of the study sites was flooded, soils in both sites were saturated with water at the end of the wet season. Isotopic analysis of stem water showed that almost all the native species in both sites showed a seasonal change in plant water uptake; plants utilized mainly groundwater during the dry season but shifted to a high proportion of soil water during the wet season. In the pineland community, *Schinus* showed no seasonal shift in water uptake source. In the disturbed community, however, *Schinus* was not isotopically distinct from the native species with regard to water source. Despite greater soil water availability in the wet season, predawn water potentials were significantly lower in the wet than in the dry season for native species at both sites. The counterintuitive decrease in water potentials during the wet season in both study sites could be the response of native plants to root flooding. Predawn water potentials of *Schinus* in both study areas however, remained constant across seasons. Predawn and noontime water potential differences were smaller in *Schinus* than in the native species at both sites during the wet season, but this pattern was found only in the disturbed area during the dry season. *Schinus* was most likely less affected by seasonality and more tolerant of root flooding than the native species studied.

Keywords Brazilian pepper · δ^{18}O · Everglades · Water potentials · Stable isotopes · Water source

---

S.M.L. Ewe (✉) · L. da S.L. Sternberg
Department of Biology, University of Miami, Coral Gables,
FL 33124, USA
e-mail: ewe@sms.si.edu
Tel.: +1-772-4656630 ext. 106, Fax: +1-772-4618154

S.M.L. Ewe
Smithsonian Marine Station, 701 Seaway Drive, Fort Pierce,
FL 34949, USA

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, over 900 species are potentially invasive (Ward 1989). One of the areas most threatened by invasive exotic species is the Everglades National Park (ENP). A total of 221 introduced plant species have been recorded in the ENP by Whiteaker and Doren (1989), comprising 23% of the recorded number of plant species present within park boundaries.

At 688,000 ha, the ENP is one 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 May and October (Chen and Gerber 1990).

Unfortunately, over 65% of the original 10,000 km^2 of the marshy Everglades ecosystem has 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 groundwater levels caused by human activities may contribute to the success of invasive exotics within the ENP if native species are less competitive under the new conditions.

One of the most serious biological threats to the Everglades upland ecosystem is *Schinus terebinthifolius* Raddi (hereafter *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 the ENP, *Schinus* is found in hydrologically distinct communities such as upland rock pinelands, sawgrass marshes, and even mangrove forests (Doren and Jones 1997). Attempts to control *Schinus* have ranged from discing, through plant and substrate removal (Koepp 1979), to burning (Loope and Dunevitz 1981), and herbicide treatment (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).

The purpose of this study was to compare water-use 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. We hypothesized that *Schinus* would be less affected by seasonality than native species and thus would be less physiologically constrained by hydroperiod fluctuations.

Materials and methods

Study site

Two adjacent study sites were selected within the 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. 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 the 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. 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 (Ewe, personal observation). Change in substrate characteristic is believed to have prevented native plants from recolonizing this area (Krauss 1987; Dalrymple et al. 1993). Instead of native plant succession after the cessation of farming, the area became a closed, low canopy (4–5 m), dense forest of *Schinus* with an understory of *Ardisia elliptica* (Ewel et al. 1982) and individuals of some weedy native species such as *Baccharis halimifolia*, *Myrica cerifera* and *Metopium toxiferum.* The HID site has relatively low vascular plant species diversity compared to other plant communities within the ENP (Olmsted et al. 1983). Currently the largest stand of *Schinus* within the 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. 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 & 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 generally small and shrubby because of park fire management practices. 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. Litter was removed before collecting surface mineral soil (1–3 cm depth). Single groundwater samples were collected from a well in a nearby pineland (<2 km distant) at the end of the wet

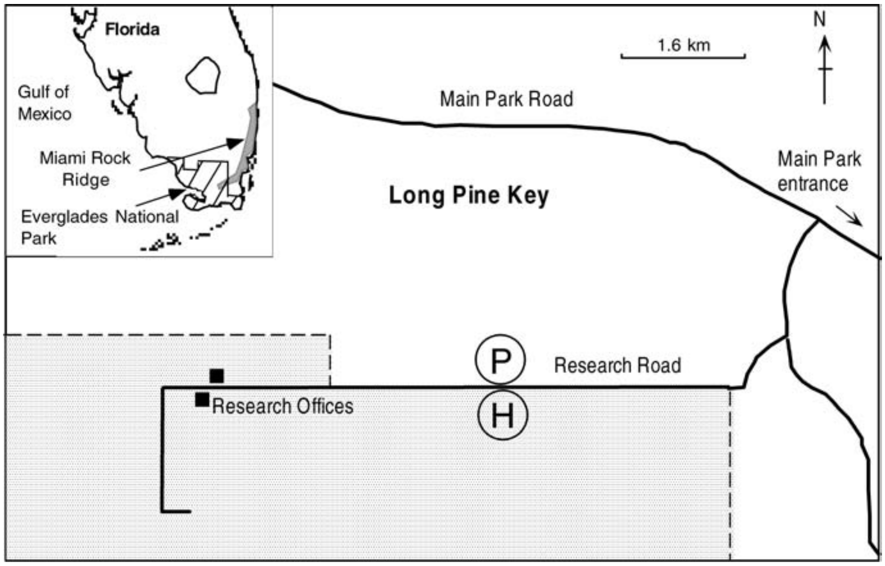

Fig. 1 Study sites (*P* pineland; *H* Hole-in-the-Donut) located within the Long Pine Key (*diagonal lines*) and Hole-in-the-Donut disturbed area (*stippled*) in the Everglades National Park. *Inset* Everglades National Park (*diagonal lines*) on the Miami Rock Ridge (*stippled*) within Florida

(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:

$$\text{Water content}\,(\%) = [(\text{Wet} - \text{Dry soil weight})/\text{Dry soil weight}] \times 100\% \qquad (1)$$

Soil organic content was determined by the following equation:

$$\text{Organic content}\,(\%) = [1 - (\text{Soil weight post} - \text{ashing}/\text{Soil weight pre} - \text{ashing})] \times 100\% \qquad (2)$$

Stable isotope analysis

Small (less than 1 cm in diameter), fully suberized plant stem sections were collected between 0900 and 1100 hours on the sampling dates (2 May 1998, 7 November 1998). Where possible, plant sections distal from the terminal tips and 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 based on 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 units of parts per mil (‰) according to the following equation:

$$\delta^{18}\text{O}\,(‰) = [(R_{\text{sample}}/R_{\text{standard}}) - 1]\,1{,}000 \qquad (3)$$

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

$$\%\ \text{groundwater} = \frac{(\delta_{\text{plant}} - \delta_{\text{soil}})}{(\delta_{\text{ground}} - \delta_{\text{plant}})} \times 100\% \qquad (4)$$

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 potential

Predawn water potentials (PDWP) 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 hours) hours. To measure plant 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, Ore.).

Diel water potential

Water potentials of plant stems were measured at approximately 3-h intervals over a 24-h 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 one-tailed *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 two-factor analysis-of-variance (ANOVA). For species common to both sites, differences among species, across sites, and between seasons were analyzed using a 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, Chicago, Ill.) or Statistix 7.0 (Analytical Software, Tallahassee, Fla.).

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 × season ($F_{1,\,15}$=0.21, P>0.10). Groundwater levels fluctuated with season, ranging from 0.12 m (7 November 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. 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 isotopic signatures 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 1, Fig. 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 season was approximately 57% (Table 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 1, Fig. 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.

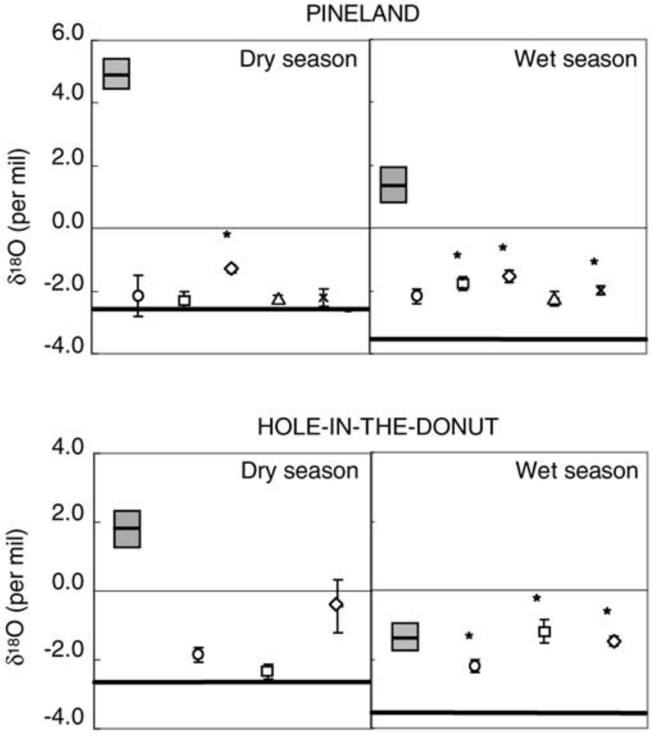

Fig. 2 Oxygen stable isotope signatures of plants from each site during the wet and dry seasons. The *line within the solid gray rectangle* represents the mean isotopic composition of soil water while the *rectangle* represents the standard error of the mean. The *solid thick line* represents the groundwater 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 1). Each species average (± SEM) is denoted as such: *Schinus terebinthifolius* (*circle*), *Myrica cerifera* (*square*), *Baccharis halimifolia* (*diamond*), *Rapanea punctata* (*triangle*) and *Randia aculeata* (*cross*)

Predawn water potential

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 2). Post hoc Bonferroni comparisons showed that significance of the interactions at both sites was attributable to higher PDWP in the native species during the 1998 and 1999 dry seasons compared to the wet season (Fig. 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 native species (Fig. 3) but during the wet season, *Schinus* water potentials were similar to or higher than the native species.

Predawn water potentials of *Schinus, M. cerifera* and *B. halimifolia* in both sites when analyzed in a three-factor ANOVA, showed significant ($P<0.05$) species, site and seasonal differences (Table 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 were lower than those of the dry season in the two native species but not in *Schinus* at either site (Fig. 3). *Myrica cerifera* and *B. halimifolia* in the HID had higher dry season water potentials compared to the LPK; no site differences were observed for *Schinus* (Fig. 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 range (i.e. predawn – midday) of water potentials was calculated to determine the degree of diel change (Fig. 4). Within each study site, two-factor ANOVAs showed differences among species ($P<0.05$) but seasonal differences were only found in the HID ($P<0.05$) (Table 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. 4). In the HID, overall wet season daily extremes were greater than in the dry season.

Table 1 Percent groundwater usage (± SEM) by plant species in both study sites during the dry and wet seasons. Asterisks (*) indicate significant difference either 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	93.7±19.3	5	72.0±10.9
Myrica cerifera	5	95.6±7.9	5	63.5±9.4*
Baccharis halimifolia	5	82.4±3.9	5	59.1±8.9*
Rapanea punctata	5	95.2±3.4	5	73.6±10.2
Randia aculeata	4	94.6±7.6	5	67.3±5.9*
Hole-in-the-Donut				
Schinus terebinthifolius	5	82.3±10.4	5	38.6±18.7*
Myrica cerifera	5	93.8±11.2	5	11.6±16.1*
Baccharis halimifolia	5	50.4±35.2	5	5.98±10.0*

Table 2 Two-factor ANOVAs of predawn water potentials for plants in the Long Pine Key pineland and Hole-in-the-Donut disturbed site

	Long Pine Key pineland				Hole-in-the-Donut			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
Species	4	18.399	9.427	0.000	2	20.456	14.653	0.000
Season	2	61.036	31.274	0.000	2	30.891	22.128	0.000
Species × Season	8	9.775	5.009	0.000	4	6.600	4.728	0.004
Error	60	1.952			36	1.396		

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

	Predawn water potential (MPa)				Diel water potential (MPa)			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
Species	2	39.282	23.876	0.000	2	4.198	35.960	0.000
Site	1	19.182	11.659	0.001	1	0.023	0.197	0.659
Season	2	69.324	42.136	0.000	1	0.008	0.065	0.800
Species × Site	2	3.153	1.916	0.155	2	0.227	1.947	0.154
Species × Season	4	20.362	12.376	0.000	2	0.135	1.159	0.322
Site × Season	2	2.304	1.401	0.253	1	0.907	7.765	0.008
Species × Site × Season	4	4.405	2.678	0.038	2	0.291	2.495	0.093
Error	72	1.645			48	0.117		

Fig. 3 Predawn water potentials (± 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 *black 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 (*P* <0.05)

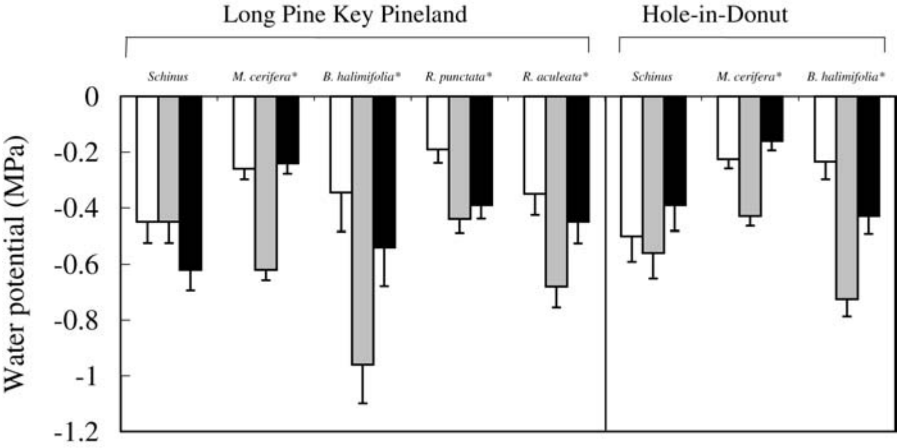

Fig. 4 Wet and dry season predawn-midday water potential differences (± SEM) of *Schinus terebinthifolius* (*clear*), *Myrica cerifera* (*shading 1*), *Baccharis halimifolia* (*shading 2*), *Rapanea punctata* (*shading 3*) and *Randia aculeata* (*shading 4*) in the Long Pine Key pineland (LPK) and Hole-in-the-Donut (HID) sites. Values followed by the same letter within a site do not differ significantly at the *P*<0.05 level using a post-hoc Bonferroni comparison of means after analysis with a two-factor ANOVA

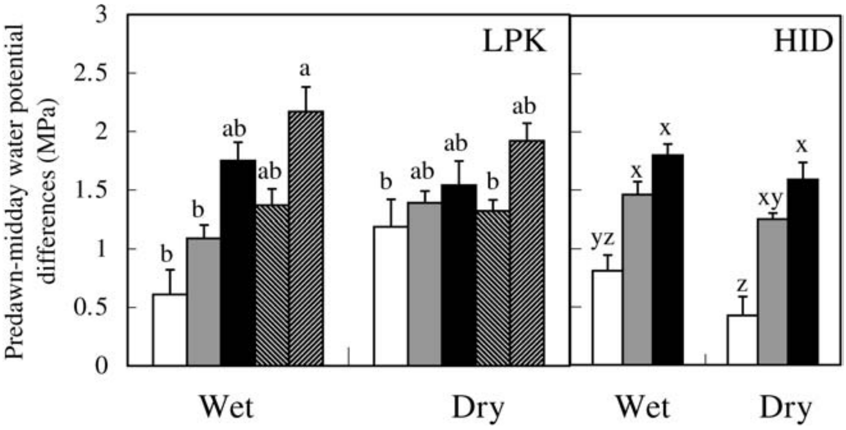

Table 4 Two-factor ANOVAs of species and season differences in daily extremes of diel water potentials at the Long Pine Key pineland site and Hole-in-the-Donut disturbed site

	Long Pine Key				Hole-in-the-Donut			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
Species	4	1.871	13.128	0.000	2	3.034	39.934	0.000
Season	1	0.068	0.480	0.492	1	0.540	7.107	0.014
Species × Season	4	0.318	2.228	0.083	2	0.026	0.336	0.718
Error	40	0.143			24	0.086		

For the three species sampled in both sites (*Schinus*, *M. cerifera* and *B. halimifolia*), a three-factor ANOVA (Table 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* had the smallest diel changes of all species at both sites for the two seasons compared (Fig. 4).

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. 2), probably because of greater evaporative rates at the soil surface under the open canopy of the pineland. It is well known that evaporation results in enriched surface soil water $\delta^{18}O$ signatures (Walker and Brunel 1990).

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. 2) agree with the findings of Ewe et al. (1999) from a nearby pineland. 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 seen for *Schinus*. In the HID site, all species including the exotic exhibited significant ground to soil water use shift compared to the pineland species. From the dry to wet season, plant groundwater usage decreased from an average of 75% to 19% (approximately 56% total uptake) in the HID site while groundwater usage only decreased from 92% to 67% in the pineland. Significant seasonal soil water usage shift in the HID site compared to the LPK site was most likely because of greater 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. The disturbed soil layer in the HID potentially is an adequate rooting substrate for plants, hence the reduced need to access deeper groundwater as shown by $\delta^{18}O$ data (Table 1). Groundwater $\delta^{18}O$ most likely does not differ between the sites as both study areas are less than 200 m apart. Groundwater $\delta^{18}O$ from data of Ewe et al. (1999) showed a difference of 0.3‰/km in the wet season and 0.2‰/km during the dry season.

Unlike the Ewe et al. (1999) study, plant PDWP in the wet season at the LPK site did not reflect increased water availability by an increase in PDWP (Fig. 3). Instead, despite greater soil water content during the wet season, all native species actually showed a decrease in predawn water potentials (Fig. 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 caused by 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), research (e.g. Kozlowski and Pallardy 1984; Reid and Bradford 1984) has 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 often have decreased gas exchange capacity and lowered water potentials, caused by leaf stomatal closure, when their roots are flooded (Naidoo 1983, 1985; Reid and Bradford 1984; Kozlowski and Pallardy 1984). These responses could be from root hypoxia (Jackson and Drew 1984), lowered root hydraulic conductance (Davies and Flore 1986; Else et al. 2001), increased abscisic acid concentrations (Kozlowski and Pallardy 1984; Zhang and Davies 1987), signaling from as yet undetermined chemical cues (Else et al. 1995, 2001), and/or secondary effects caused by flooding such as accumulation of toxic plant and microbial metabolites (Jackson and Drew 1984; Kozlowski 1997). 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) between seasons. If the above hypothesis of root flooding 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 the 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 roots tolerant of flooding that regenerate after death of the original root system (Hook 1984). During the wet season, *Schinus* also had the smallest diel differences of all species at both sites (Fig. 4). This finding is consistent with the hypothesis that *Schinus* is less affected by flooding than the native species.

Contrary to expectation, these plant water potential data demonstrate that the wet season may stress the native species more than the dry season in our two study sites. Although there is no information on root depth or architecture of plants growing in the Everglades HID and pineland areas (because of the rocky substrate), this study provides indirect evidence for *Schinus* rooting deeper than that native species during the wet season and a variable rooting depth for the natives depending on the season.

Findings from this study support the hypothesis that *Schinus* water relations are less affected by seasonality than that of native species, as was observed in the saline transition zone of coastal southwest Florida (Ewe and Sternberg, in press). Invasion of exotics into the Long Pine Key pinelands of the Everglades National Park may have been inadvertently facilitated by human manipulation of water levels in South Florida. The water uptake patterns observed in the native and exotic plants sampled suggest that the exotic may be favored over native species that are being physiologically stressed via belowground flooding during the wet season.

Acknowledgements We wish to thank Drs. David Janos and Stewart Schultz, as well as the two anonymous reviewers for their comments. This is a University of Miami Tropical Biology Contribution no. 651 and the Smithsonian Marine Station at Fort Pierce Contribution no. 533.

References

Chen E, Gerber JF (1990) Climate. In: Myers RL, Ewel JJ (eds) Ecosystems of Florida. University of Central Florida Press, Orlando, Fla. pp 11–34

Dalrymple NK, Dalrymple GH, Fanning KA (1993) Vegetation of restored rock-plowed wetlands of the East Everglades. Restor Ecol 1:220–225

Davies FS, Flore JA (1986) Flooding, gas exchange, and hydraulic root conductivity of highbush blueberry. Physiol Plant 67: 545–551

Doren RF, Jones DT (1997) Management in Everglades National Park. In: Simberloff D, Schmitz DC, Brown TC (eds) Strangers in paradise: impact and management of nonindigenous species in Florida. Island, Washington D.C. pp 275–286

Doren RF, Whiteaker LD, Molnar G, Sylvia D (1990) Restoration of former wetlands within the Hole-in-the-Donut. In: Webb FJ Jr (ed) Proceedings of the seventeenth annual conference on wetlands restoration and creation. 10–11 May 1990. Hillsborough Community College, Plant City, Fla. pp 33–50

Doren RF, Whiteaker LD, Rochefort R (1991) Seasonal effects on herbicide basal bark treatment of *Schinus terhebinthifolius*. In: Center TD (ed) Proceedings of the symposium on exotic pest plants: 2–4 November 1988, University of Miami, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida. United States Department of the Interior, Washington D.C. pp 115–129

Else MA, Davies WJ, Malone M, Jackson MB (1995) A negative hydraulic message from oxygen-deficient roots of tomato plants? Influence of soil flooding on leaf water potential, leaf expansion, and synchrony between stomatal conductance and root hydraulic conductivity. Plant Physiol 109:1017–1024

Else MA, Coupland D, Dutton L, Jackson MB (2001) Decreased root hydraulic conductivity reduces leaf water potential, initiates stomatal closure and slows leaf expansion in flooded plants from castor oil (*Ricinus communis*) despite diminished delivery of ABA from the roots to shoots in xylem sap. Physiol Plant 111:46–54

Epstein S, Mayeda T (1953) Variations of O-18 content of water from natural sources. Geochim Cosmochim Acta 42:213–224

Ewe SML, Sternberg LdaSL, Busch DE (1999) Water-use patterns of woody species in pineland and hammock communities of South Florida. For Ecol Manage 118:139–148

Ewe SML, Sternberg LdaSL. Water utilization patterns of the invasive exotic *Schinus terebinthifolius* and native species in two coastal plant communities. J Ecol (in prep)

Ewel JJ, Ojima DS, Karl DA, Debusk WF (1982) *Schinus* in successional ecosystems of Everglades National Park. South Florida Research Center Report No. T-676. National Park Service, Everglades National Park, Homestead, Fla.

Florida Exotic Pest Plant Council (2001) List of Florida's most invasive species. http://www.fleppc.org/99list.htm. Cited 31 July 2001

Frank JH, McCoy ED, Hall HG, O'Meara GF, Tschinkel WR (1997) Immigration and introduction of insects. In: Simberloff D, Schmitz DC, Brown TC (eds) Strangers in paradise: impact and management of nonindigenous species in Florida. Island, Washington D.C. pp 75–99

Hook DD (1984) Adaptations to flooding with fresh water. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, Orlando, Fla. pp 265–294

Jackson MB, Drew MC (1984) Effects of flooding on growth and metabolism of herbaceous plants. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, Orlando, Fla. pp 47–128

Koepp WP (1979) The status of *Schinus* manipulation in Everglades National Park: In: Workman RW (ed) Technical proceedings of techniques for control of *Schinus* in South Florida: a workshop for natural area managers. Sanibel-Captiva Conservation Foundation, Sanibel, Fla. pp 45–51

Kozlowski TT (1997) Responses of woody plants to flooding and salinity. Tree Physiol Monogr 1:1–29. http://heronpublishing.com/tp/monograph/kozlowski.pdf Cited 28 February 2002

Kozlowski TT, Pallardy SG (1984) Effects of flooding on water, carbohydrate and mineral relations. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, Orlando, Fla. pp 165–193

Krauss P (1987) Old field succession in Everglades National Park, Report SFRC-87/03. South Florida Research Center, Everglades National Park, Homestead, Fla.

Lodge TE (1994) The Everglades handbook: understanding the ecosystem. Delray Beach, St. Lucie Press, Fla.

Loope LL, Dunevitz VL (1981) Impact of fire exclusion and invasion of *Schinus terebinthifolius* on limestone rockland pine forests of southeastern Florida (Report T645). South Florida Research Center, Everglades National Park, Homestead, Fla.

Naidoo G (1983) Effects of flooding on leaf water potential and stomatal resistance in *Bruguiera gymnorrhiza* (L.) Lam. New Phytol 93:369–376

Naidoo G (1985) Effects of waterlogging and salinity on plant water relations and on the accumulation of solutes in three mangrove species. Aquat Bot 22:133–143

Olmsted I, Robertson WBJ, Johnson J, Bass OLJ (1983) The vegetation of Long Pine Key, Everglades National Park (Report SFRC-83/05). South Florida Research Center, Everglades National Park, Homestead, Fla.

Reid D, Bradford KJ (1984) Effects of flooding on hormone relations. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, Orlando, Fla. pp 195–219

Schmitz DC, Simberloff D, Hofstetter RH, Haller W, Sutton D (1997) The ecological impact of nonindigenous plants. In: Simberloff D, Schmitz DC, Brown TC (eds) Strangers in paradise: impact and management of nonindigenous species in Florida. Island, Washington, D.C. pp 39–61

Snyder JR, Herndon A, Robertson WB Jr (1990) South Florida rockland. In: Myers RL, Ewel JJ (eds) Ecosystems of Florida. University of Central Florida Press, Orlando, Fla. pp 230–278

Sokal RR, Rohlf RJ (1998) Biometry: the principles and practice of statistics in biological research. W.H. Freeman, New York

Stephens JC (1974) Subsidence of organic soils in the Florida Everglades- a review and update. In: Gleason PJ (ed) Environments of south Florida: present and past. Memoir 2: Miami Geological Society. Miami Geological Society, Miami, Fla. pp 352–361

Walker CD, Brunel J-P (1990) Examining evapotranspiration in a semi-arid region using stable isotopes of hydrogen and oxygen. J Hydrol 118:55–75

Ward DB (1989) How many plant species are native to Florida? Palmetto 9:3–5

White WC, Cook ER, Lawrence JR, Broeker WS (1985) The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. Geochim Cosmochim Acta 49:237–246

Whiteaker LD, Doren RF (1989) Exotic plant species management strategies and list of exotic species in prioritized categories for Everglades National Park, Report SER-89/04. US Department of the Interior, National Park Service, Homestead, Fla.

Zhang J, Davies WJ (1987) ABA in root and leaves of flooded pea plants. J Exp Bot 38:649–659