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Seasonal gas exchange characteristics of *Schinus terebinthifolius* in a native and disturbed upland community in Everglades National Park, Florida

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Abstract

Schinus terebinthifolius Raddi (*Schinus*) is an invasive exotic plant widely found in Florida and Hawaii. This species is found from the upland pinelands to the mangrove forests of Florida. Dense *Schinus* infestations have the capacity to displace native species, reduce species diversity and been shown to reduce faunal use of the community.

The purpose of this study was to determine if gas exchange patterns of *Schinus* were significantly different from native species. This work was part of a larger study to determine if the exotic's physiology contributed to its presence in two upland communities of South Florida. The first was an endemic rock pineland community and the second, a disturbed previously farmed area where *Schinus* was the canopy dominant. *Schinus* gas exchange, leaf nitrogen and carbon stable isotope contents were contrasted with four native species for one wet and dry season.

Schinus tended to have higher assimilation (A), mesophyll conductance (g_m), intrinsic water-use efficiency (WUE) and photosynthetic nitrogen-use efficiency (PNUE) than native species in the pineland site during the wet season but these differences were not statistically significant. There were also no significant differences in conspecific plant responses between the two communities. Seasonal differences were, however, significant for most of the gas exchange parameters at either one or both of the study sites. Wet season A, g_m, nitrogen concentration ([N]), intrinsic WUE, PNUE and carbon stable isotope signatures (δ^{13}C) were higher than the dry season, most likely a consequence of greater water availability within the substrate.

Although differences in gas exchange could contribute to the invasiveness of *Schinus* into native pineland and disturbed upland areas, other aspects of its autoecology also play an important role.

Keywords: Invasive exotic; Everglades; Photosynthesis

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1. Introduction

Since historical times, humans have transported both plants and animals for their own purposes (Gordon and Thomas, 1997). Non-native species have been deliberately imported into the United States for agricultural, commercial, and ornamental purposes. South Florida is a hub for the importation of both plants and animals into the United States (U.S. Congress, 1993) and the high proportion of invasive exotics in peninsular Florida has been attributed to this region's weather and unique island-like biogeography (Elton, 1958). The subtropical

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weather of this peninsula supports both tropical and temperate species and South Florida's relative isolation from continental effects allows many plants and animals to persist after introduction. Together with Hawaii, Florida is one of the two regions of North America most threatened by invasive exotics (Simberloff, 1997).

The most widespread invasive exotic in Florida is *Schinus terebinthifolius* Raddi (*Schinus*), a species found in over 280,000 ha of South Florida (1993 South Florida Water Management Survey as cited in Schmitz et al., 1997). Imported from South America over a 100 years ago, this exotic is now found invading disturbed areas and a variety of native communities, ranging from upland pinelands to mangrove forests. *Schinus* growing in high densities have lowered species diversity and reduced faunal use of invaded areas (Curnutt, 1989).

Although traits such as high growth rates and large annual reproductive outputs (Ewel et al., 1982; Gordon, 1998) have been attributed to this exotic's prevalence in South Florida, it is also possible that *Schinus* ecophysiology, in particular its gas exchange characteristics contribute to its current widespread distribution. Studies have shown that exotics often differ from native species in ways that potentially contribute to their success within introduced habitats (e.g. Weiss and Noble, 1984; Busch and Smith, 1995; Dukes and Mooney, 1999; Yamashita et al., 2000; Horton et al., 2001). The objective of this study was to determine if gas exchange responses of *Schinus* were significantly different from native species in two communities, a native rock pineland community and a disturbed previously farmed area. This study is part of a larger work seeking to understand the differences between *Schinus* and native species, and how these differences possibly contribute to the prevalence of this exotic in South Florida.

A plant's efficiency at assimilating and utilizing resources has implications for its survival, growth and reproductive capacity, particularly in spatially and temporally variable environments (Lambers and Poorter, 1992). Plants with high rates of net carbon assimilation (A) have the potential to grow faster than species with low assimilation. Previous studies have shown that invasive exotics often have higher rates of leaf-level gas exchange than native species (Pattison et al., 1998; Baruch and Goldstein, 1999; Durand and Goldstein, 2001). For example, in the Hawaiian Islands, several exotic species including *Schinus* have higher assimilation than co-occurring native species (Pattison et al., 1998).

High levels of photosynthesis at low levels of leaf nitrogen also potentially provide a competitive edge for an exotic co-occurring with native species. Studies (e.g. Field et al., 1983; Bilbao and Medina, 1990; Lambers and Poorter, 1992; Schieving and Poorter, 1999) have shown that plants with high photosynthetic nitrogen-use efficiency (PNUE) often have high growth rates. During limited water availability however, water-use efficiency (WUE) often becomes a more important indicator of a plant's physiological performance than PNUE because intrinsic WUE (A/stomatal conductance (g_s)) provides an estimate of a plant's efficiency in taking up CO_2 versus water loss (Larcher, 1995). In this study, we also measured leaf carbon isotopic ratio ($\delta^{13}C$) to determine plant WUE integrated over the whole growing season. We used $\delta^{13}C$ as a proxy of a plant's seasonal WUE because under water stress, plants discriminate less against ^{13}C during CO_2 uptake resulting in an increase in integrated WUE. Farquhar et al. (1982a,b) have shown a relationship between integrated WUE and carbon stable isotopes both theoretically and empirically.

Here, we test the hypothesis that *Schinus* and native plants in South Florida upland communities had different gas exchange patterns. Specifically, during the dry season when water availability is lowest, is the exotic physiologically more tolerant of the dry conditions than native species? During the wet season when the soil is saturated, does the exotic reflect less physiological stress from an abundance of water and potential root flooding?

2. Methods and materials

2.1. Study sites

Both communities, located in Everglades National Park, were selected because *Schinus* is a community dominant in the disturbed area and is now invading the native pineland community (Ewel et al., 1982; Ewel, 1986; Doren and Jones, 1997). The study sites are located in Everglades National Park, on the Miami Rock Ridge limestone outcrop (Fig. 1). The ridge, a Pleistocene era limestone formation (Hoffmeister,

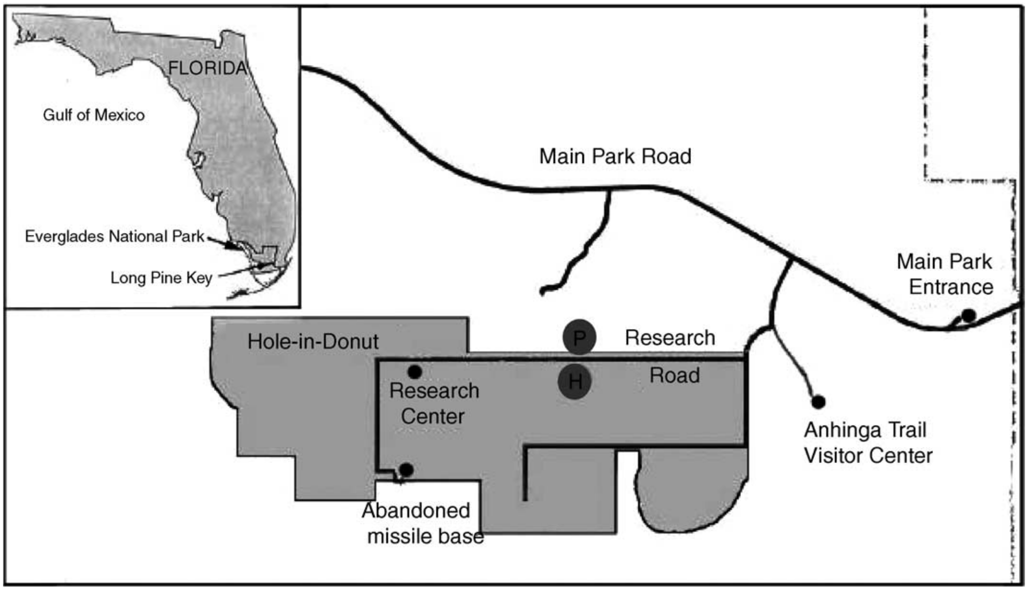

Fig. 1. General study area within Everglades National Park showing the locations of the native pineland community (P) and the *Schinus* dominated disturbed site (H). The shaded area is the 2000 ha previously rock-plowed area known as the Hole-in-the-Donut. Inset: location of Everglades National Park in Florida.

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

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

The first site (LPK), a non-rock plowed area, is now a native pineland community (Fig. 1). At this site, soil is only found in limestone pockets within the bare rock substrate. The community is composed of an open canopy of *Pinus elliottii* var. densa Little & Dorman, with a subcanopy of native species such as *Myrica cerifera* L. (Myricaceae), *Baccharis halimifolia* L. (Asteraceae), *Tetrazygia bicolor* (Mill.) Cogn. (Melastomataceae) and *Metopium toxiferum* (L.) Krug & Urban (Anacardiaceae). The invasive *Schinus* is also a co-dominant species in this site. The main seed source of *Schinus* originates south of the LPK, from the rock-plowed area known as the Hole-in-the-Donut (HID). The second site (HID) is located within the disturbed, previously farmed area. The substrate is a mix of soil and crushed limestone rock that varies in depth from a few centimeters to about 30 cm (Snyder et al., 1990). The canopy dominant in HID is the exotic *Schinus*. A few native species such as *M. cerifera*, *B. halimifolia* and *M. toxiferum* are also found in this site. The canopy in the HID is approximately 5 m tall and is relatively dense compared to the adjacent LPK.

Rainfall in South Florida is strongly seasonal (Fig. 2). South Florida receives about 75% of its annual rainfall during the wet season. At both study sites, annual rainfall in an average year ranges from 1400 to 1525 mm. The rainy season typically starts late May and ends in early November (Fig. 2). The wet season is followed by a slow dry-down during the winter months and by the end of April, conditions are often extremely dry. Wildfires are prevalent towards the end of the dry season and at the start of the rainy season because of high incidence of lightning (Taylor, 1980). The pineland site is fire-managed by the Park Service and upland areas in Long Pine Key are burned at approximately 2-year intervals. Because of the seasonal availability of rainfall in South Florida,

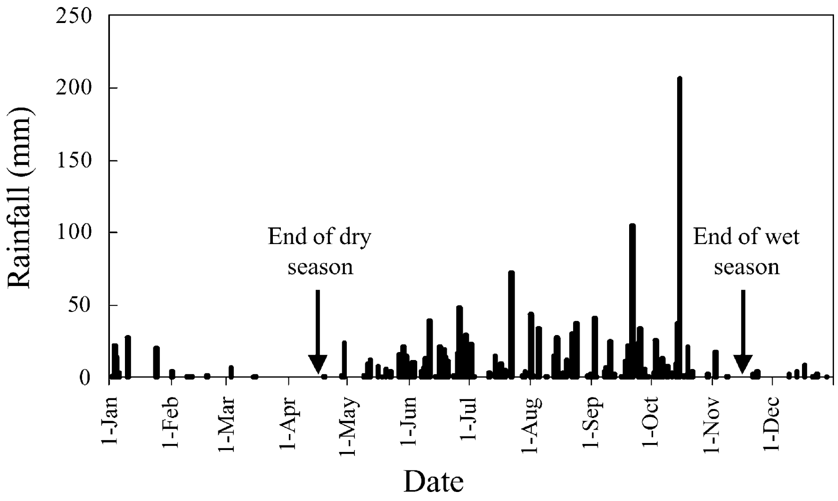

Fig. 2. Daily rainfall totals for 1999 in Long Pine Key, Everglades National Park. Arrows indicate the sampling periods at the end of the dry and wet seasons. (Data courtesy of Everglades National Park at http://www.sfnrc.ever.nps.gov).

groundwater depths range from more than 1.5 m during the dry season to less than 12 cm below ground during the wet season (Ewe, pers. obs.). Although both sites are not flooded during the wet season, soils within the two sites are saturated when water levels are at their highest near the end of the wet season in late October. There was no standing water in the LPK site but shallow pools were observed in the HID within depressions of exposed limestone.

2.2. Species studied

Schinus is a dioecious, shrubby evergreen perennial that grows to approximately 5 m in South Florida. In a closed stand, the plant forms a multi-stemmed tangle of non-abscising branches beneath a dense canopy that precludes understory plant growth (Ewel et al., 1982). *Schinus* litter decomposes quickly so there is very little ground fuel within a mature *Schinus* stand, resulting in poor burning conditions (Ewel, 1986). Unlike some native South Florida communities, a community dominated by mature *Schinus* is not easily controlled by fire (Doren and Whiteaker, 1990; Clark, 1997). *Schinus* resprouts vigorously and once juvenile plants are over 1 m high, mortality from fire decreases significantly (Doren and Whiteaker, 1990).

Gas exchange of the exotic *Schinus* was compared to native species widely found within each community. In the LPK, *Schinus* was compared to four native species, *M. cerifera*, *B. halimifolia*, *Rapanea punctata* (Lam) Lundell (Myrsinaceae) and *Randia aculeata* L. (Rubiaceae). Study species within LPK were mostly small and shrubby because of park fire management practices. Only two other native species (*M. cerifera* and *B. halimifolia*) were compared to *Schinus* in the HID because *R. punctata* and *R. aculeata* were not prevalent within this community. Five individuals per species were sampled every season at each site. Measurements were made at the end of the dry and wet seasons of 1999 (Fig. 2). Different individuals were measured during the dry season than the wet season because the National Park Service burned the initial LPK study plot. Plants in an adjacent pineland and HID section (<800 m distant) from the original plants were sampled during the wet season.

2.3. Gas exchange measurements

Gas exchange was measured on a portable gas exchange system (LI-6200, LiCor, Logan, Utah) with a 390 ml chamber attachment. Measurements were made between 930 and 1600 h, starting after dew had evaporated from leaf surfaces and ending when light levels on sample leaves were less than 1000 μmol $m^{-2} s^{-1}$. One site was measured per day at the end of a dry (12 and 14 April 1999) and wet (16 and 17 November 1999) season. For each plant, the second fully expanded leaf from the tip of an east-facing lateral branch exposed to full sunlight was sampled. Attempts were made to measure the same leaf throughout the day. In the case where leaves were damaged or became detached during sampling, other leaves of similar locations at the same or adjacent branches were used.

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

2.4. Leaf area, carbon isotope ratios and nitrogen content

Gas exchange has been shown to decrease with increasing leaf age (Kitajima et al., 1997). Therefore, general patterns of leaf development in the focal species were noted throughout the study period. Leaf production of all study species was observed to be seasonal; leaves were produced towards the end of the dry season and production continued throughout the wet season. Young leaves produced at the end of the wet season continued to mature despite onset of the dry season. An attempt was made to measure leaves of similar age. There was no overlap of leaves produced one season being sampled the following season.

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

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

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

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

A second set of subsamples of the collected and processed leaves were used for nitrogen analyses. In the dry season, leaf nitrogen concentration (g N g^{-1} leaf) was analyzed using the Kjedahl method; wet season leaves were analyzed using an elemental analyzer (Carlo Erba NC2100, ThermoFinnigan Italia S.p.A., Milan, Italy). As the Kjedahl technique volatilizes ammonia (<1% total leaf N) in the sample (Binkley and Vitousek, 1989), a correction factor was applied to the Kjedahl values. This correction factor was determined by re-analyzing some dry season leaf samples on the elemental analyzer and obtaining the average ratio of Kjedahl/elemental analyzer nitrogen concentrations. Nitrogen contents were reported on a leaf area basis ([N], g N m^{-2} leaf) by dividing nitrogen concentration by SLA. Photosynthetic nitrogen-use efficiency was determined from dividing A by [N].

2.5. Statistical analyses

Homogeneity of variances and normality of data for each species was confirmed using Levene's Test of Equality of Error Variances and the Shapiro–Wilks normality test, respectively. For each site, seven variables (A, [N], g_s, g_m, A/g_s, $\delta^{13}C$, PNUE) were analyzed with a two-factor (species and season) multivariate analysis-of-variance (MANOVA). All MANOVAs were carried out using SPSS 8.0 (SPSS Inc., Chicago, IL). Factors that were significant were further analyzed by post-hoc Bonferroni pairwise comparisons of means tests ($\alpha = 0.05$); interactions between factors were analyzed using a Tukey HSD post-hoc interaction effects tests using Statistica 5.5 (Statsoft Inc., Tulsa, Oklahoma). A three-factor (species, season and site) MANOVA was used to compare the same seven parameters for species common to both sites. For each MANOVA, significance (*P*-value) is reported for Pillai's Trace (test of multivariate significance) and each variable. Average power for all factors in the multivariate analyses was 0.834.

3. Results

Although there were trends of some gas exchange parameters being higher in *Schinus* compared to the native species, *Schinus* gas exchange was not statistically different from most native species both seasons sampled. Assimilation (*A*) differed over seasons at the LPK (Table 1) as wet season *A* was higher in most species sampled compared to the dry season (Table 2). Average dry season *A* in the LPK ranged from 4.7 to 9.1 μmol CO_2 m^{-2} s^{-1} while wet season values ranged from 6.8 to 11.8 μmol CO_2 m^{-2} s^{-1}. There was a species × season interaction (Table 1) in *A* that was also reflected in g_m ($=A/c_i$) (Table 2). The interactions in both *A* and g_m were caused by the absence of a seasonal *A* difference in *B. halimifolia* and *R. punctata* at the LPK (Table 2). In the HID, g_m was highest in *Schinus*, followed by *B. halimifolia* and *M. cerifera* (Table 2). Although there were no significant seasonal effects on g_m at either site (Table 1), most species had higher g_m during the wet season compared to the dry (Table 2). This seasonal difference was significant when compared to species common to both sites (Table 3).

Some general patterns of consistent differences were observed in several parameters at both study sites. First, species differences were observed for [N] and PNUE (Table 1). *M. cerifera* at both sites consistently had the highest wet season [N] of all species compared (Table 2). Comparison of leaf [N] for the three species common to both sites showed *M. cerifera* to have the highest [N] followed by *Schinus* and *B. halimifolia*. *Schinus* [N] at both sites was similar to all native species except *M. cerifera* in LPK (Table 2). An opposing pattern was observed for PNUE. The rank order of annual PNUE in the LPK, from lowest to highest average values were: *R. aculeata* < *M. cerifera* < *R. punctata* < *B. halimifolia* < *S. terebinthifolius* (Table 2). In the HID, *M. cerifera* had lower PNUE than either *Schinus* or *B. halimifolia* (Table 2). During the dry season at this site, *M. cerifera* PNUE was over 50% less than *Schinus* or *B. halimifolia*. For species common to both sites, differences among species (Table 3) were a consequence of *M. cerifera* PNUE being lower than either *Schinus* ($P < 0.01$) or *B. halimifolia* ($P < 0.01$).

Second, seasonal differences were significant for both [N] and A/g_s at both sites (Table 1). Leaf [N] and

Table 1
Significance (*P*-values) for two MANOVAs

Site	Parameters	Species	Season	Species × Season
Long Pine Key	Pillai's Trace	0.000	0.000	0.183
	A (μmol CO_2 m^{-2} s^{-1})	0.085	**0.015**	**0.018**
	g_m (m s^{-1} × 10^{-5})	0.076	0.102	**0.019**
	[N] (g N m^{-2} leaf)	**0.001**	**0.000**	0.060
	PNUE (μmol CO_2 g N^{-1} s^{-1})	**0.001**	0.938	0.269
	A/g_s (μmol CO_2 mol H_2O^{-1})	0.076	**0.006**	0.518
	$\delta^{13}C$ (‰)	**0.013**	**0.008**	0.226
	g_s (mol CO_2 m^{-2} s^{-1})	0.154	0.662	0.106
Hole-in-Donut	Pillai's Trace	0.001	0.000	0.393
	A (μmol CO_2 m^{-2} s^{-1})	0.300	0.185	0.299
	g_m (m s^{-1} × 10^{-5})	**0.044**	0.199	0.483
	[N] (g N m^{-2} leaf)	**0.004**	**0.001**	0.604
	PNUE (μmol CO_2 g N^{-1} s^{-1})	**0.044**	0.820	0.415
	A/g_s (μmol CO_2 mol H_2O^{-1})	0.443	**0.000**	0.136
	$\delta^{13}C$ (‰)	0.720	0.069	0.897
	g_s (mol CO_2 m^{-2} s^{-1})	0.260	**0.007**	0.583

Seven variables (*A*, g_m, [N], PNUE, A/g_s, $\delta^{13}C$ and g_s) were analyzed for species and seasonal differences at each of the study sites. Values in bold represent $P < 0.05$.

Table 2
Species average (±S.E.M.) for each season

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

The parameters measured are: A (μmol CO_2 m^{-2} s^{-1}); g_m (m s^{-1} × 10^{-5}); [N] (g N m^{-2} leaf); PNUE (μmol CO_2 g N^{-1} s^{-1}); g_s (μmol CO_2 mol H_2O^{-1}); $\delta^{13}C$ (‰); and g_s (mol H_2O m^{-2} s^{-1}) at both sites. Values followed by the same letter do not differ significantly between species within a site.

intrinsic WUE in both the LPK and HID were significantly higher in the wet season than in the dry (Table 2). On average, wet season A/g_s was 130% greater than the dry season in the LPK and approximately 203% greater in HID. Within each site, no differences were observed among species (Table 1) but across sites, comparisons of *Schinus*, *M. cerifera* and *B. halimifolia* showed significance for season, site, species × season and season × site (Table 3). Season × site differences resulted from higher HID wet season A/g_s compared to the LPK (Table 2). Overall, *Schinus* had the highest wet season A/g_s among the three species common to both sites (Table 2).

Long-term WUE as measured by $\delta^{13}C$ signatures reflected seasonal trends similar to A/g_s. There was a significant correlation between A/g_s and $\delta^{13}C$ for all plants in the LPK (Pearson correlation = 0.445, $P = 0.02$) and HID (Pearson correlation = 0.339, $P = 0.08$). Species differences were found in $\delta^{13}C$ signatures for plants in the LPK but not HID (Table 1). Species differences in the LPK were caused by lower $\delta^{13}C$ values ($P < 0.05$) in *R. aculeata* when compared to *Schinus* or *M. cerifera* while seasonal differences were caused by higher wet season $\delta^{13}C$ values compared to the dry season (Table 2). Despite a similar trend, this pattern was not significant for plants in the HID.

Stomatal conductance (g_s) was seasonally different in the HID but not significantly different among species at both sites (Table 1). All HID species had lower g_s in the wet season compared to the dry

Table 3
Results (P-values) of a three-factor MANOVA for the three species (*Schinus*, *R. punctata* and *R. aculeata*) common to both sites

Parameters	Species	Season	Site	Species × Season	Species × Site	Season × Site	Species × Season × Site
Pillai's Trace	0.000	0.000	0.027	0.047	0.829	0.061	0.407
A (μmol CO_2 m^{-2} s^{-1})	0.188	**0.003**	0.083	0.097	0.946	0.180	**0.013**
g_m (m s^{-1} × 10^{-5})	**0.014**	**0.009**	**0.040**	0.240	0.791	0.337	**0.017**
[N] (g N m^{-2} leaf)	**0.000**	**0.000**	0.897	0.405	0.801	0.747	0.328
PNUE (μmol CO_2 g N^{-1} s^{-1})	**0.002**	0.858	0.960	0.211	0.927	0.840	0.382
A/g_s (μmol CO_2 mol H_2O^{-1})	**0.022**	**0.000**	**0.002**	**0.038**	0.488	**0.002**	0.644
$\delta^{13}C$ (‰)	0.692	**0.014**	0.695	0.584	0.886	0.698	0.685
g_s (mol CO_2 m^{-2} s^{-1})	**0.044**	**0.015**	0.810	**0.046**	0.981	0.066	0.387

Values in bold are significant at $\alpha = 0.05$.

(Table 2). Wet season values ranged from an average of 140–245% lower in the wet season than dry season for *M. cerifera* and *Schinus*, respectively. There were differences between the three species common to both sites (Table 3), a result of higher g_s in *B. halimifolia* compared to *M. cerifera*.

4. Discussion

Overall, *Schinus* seasonal gas exchange patterns were not significantly different from most native species (Table 2). A comparative ecophysiological study by Schierenbeck and Marshall (1993) on the invasive vine showed that photosynthetic rates of the exotic were not significantly different from its native congener (*L. sempervirens*) although maximum g_s and WUE of the exotic were often higher than the native. Some invasive exotics co-occurring with native species had higher A, WUE and PNUE than native species (Busch and Smith, 1995; Pattison et al., 1998; Durand and Goldstein, 2001), but *Schinus* in this study did not show this trend consistently at both sites. In this study, although *Schinus* gas exchange was not statistically different from most native species, it was however worth noting that *Schinus* had the highest wet season g_m, A/g_s, $\delta^{13}C$ and PNUE in the LPK (Table 2). Additionally, where species differences among *Schinus*, *M. cerifera* and *B. halimifolia* were significant (Table 3), *Schinus* had the highest g_m, A/g_s and PNUE.

Studies have shown (e.g. Mooney et al., 1978; Lambers and Poorter, 1992) plant PNUE to be positively correlated with growth. Post-hoc tests indicated *Schinus* PNUE to be similar to all native species except *R. aculeata* in the LPK. However, average PNUE was higher in *Schinus* compared to native species, indicating potentially higher growth rates compared to most native species.

Plants in both sites showed increased [N] and A/g_s from dry to wet season (Table 2). Higher [N] could result from greater nitrogen mobility in the soils during the wet season. Koch and Snedaker (1997) have shown high ammonium concentrations in Everglades marsh porewater. It is possible that soils in the LPK, which were adjacent to freshwater marshes, had higher nitrogen contents during the wet season when there was more water within the soils. *M. cerifera* had the highest [N] at both sites (Table 2), most likely because of its nitrogen-fixing ability (Tomlinson, 1980). This high [N] in *M. cerifera* at the HID contributed to its low PNUE (Table 2).

Assimilation was higher in most species in the wet season compared to the dry season while the opposite trend was true for g_s, resulting in greater A/g_s during the wet season. This finding implied that the plants were utilizing water more effectively during the wet season. The indication of the wet season being more favorable to LPK plants in terms of gas exchange was also reflected in the g_m of *Schinus*, *M. cerifera* and *R. aculeata*. Higher g_m in the wet season than the dry indicated greater carboxylation efficiency in these plants. In comparing the three species common to both sites, *Schinus* had higher A/g_s than either *M. cerifera* or *B. halimifolia* (Table 2) during the wet season, indicating that the exotic was physiologically more efficient at water use than native species.

Carbon stable isotope signatures (i.e. integrated WUE) represent a pattern of water use integrated over the growth and development of a leaf. A theoretical inverse relationship between $\delta^{13}C$ and a plant's c_i has been shown by von Caemmerer and Farquhar (1981); greater $\delta^{13}C$ is a function of low c_i, and is sometimes caused by low g_s relative to assimilation. A positive relationship between $\delta^{13}C$ and WUE has been empirically demonstrated for many crop and tree species (e.g. Farquhar and Richards, 1984; Hubick et al., 1986; Sun et al., 1996). In this study, we also showed a relationship between integrated and intrinsic WUE. The data further support a long-term relationship between A versus $\delta^{13}C$ that indicates a greater capacity for plant productivity during the wet season.

Despite differences in substrate structure, there were no site differences in most gas exchange responses among the three species common to both sites (Table 3). It is possible that the degree of soil saturation affected all species equally during the wet season regardless of substrate type. Studies have shown that plants are most affected by flooding during their growing season (Kozlowski, 1984). The wet season is the primary growing season for almost all plant species in this seasonal environment. Although the ground was saturated at both sites during the wet season, there were no signs of outward damage to the plant such as wilting or chlorosis (Ewe, pers. obs.). In fact, most species appeared to be responding positively to the increased water availability.

Among all species compared, *Schinus* gas exchange patterns appear to be most similar to *B. halimifolia*. Both *Schinus* and *B. halimifolia* are invasive exotics in parts of Australia (Panetta and McKee, 1997; Land Protection, 2001). A congener of *M. cerifera*, the nitrogen-fixer *M. faya* is an invasive on the infertile volcanic areas in Hawaii (Vitousek and Walker, 1989). All species were chosen based on their prevalence within the community as we felt it necessary to understand the gas exchange of species that could potentially be out-competed by the exotic. It is possible that the lack of statistical difference between *Schinus* and natives is because of the species selected, where the most robust and weedy species have been contrasted.

5. Conclusion

Schinus gas exchange patterns were not significantly different from native species. However, during the wet season (i.e. the period of active growth) at the LPK for these species, *Schinus* had the highest g_m, A/g_s, $\delta^{13}C$ and PNUE. Thus, *Schinus* gas exchange characteristics could confer the exotic physiological advantages over native species. Further studies with other species and more replicates will be necessary to assert this conclusion.

References

Baruch, Z., Goldstein, G., 1999. Leaf construction cost, nutrient concentration and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia 121, 183–192.

Bilbao, B., Medina, E., 1990. Nitrogen-use efficiency for growth in a cultivated African grass and a native South American pasture grass. J. Biogeogr. 17, 421–425.

Binkley, D., Vitousek, P., 1989. Soil nutrient availability. In: Pearcy, R.W., Ehleringer, J., Mooney, H.A., Rundel, P.W. (Eds.), Plant Physiological Ecology: Field Methods and Instrumentation. Chapman & Hall, London, England, pp. 75–96.

Buchanan, D.L., Corcoran, E.J., 1959. Sealed tube combustions for the determination of ^{14}C and carbon isotopes. Anal. Chem. 31, 1635–1638.

Busch, D.E., Smith, S.D., 1995. Mechanisms associated with the decline of woody species in riparian ecosystems of the southwestern U.S. Ecol. Monogr. 65, 347–370.

Clark, D., 1997. Management techniques: physical control. In: Amy, F. (Ed.), Brazilian Pepper Management Plan for Florida. A Report from the Florida Exotic Pest Plant Council's Brazilian Pepper Task Force. Florida Exotic Pest Plant Council, West Palm Beach, FL, pp. 13.

Curnutt, J.L., 1989. Breeding bird use of a mature stand of Brazilian pepper. Florida Field Nat. 17, 53–76.

Doren, R.F., Jones, D.T., 1997. Management in Everglades National Park. In: Simberloff, D., Schmitz, D.C., Brown, T.C. (Eds.), Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida. Island Press, Washington, DC, pp. 275–286.

Doren, R.F., Whiteaker, L.D., 1990. Effects of fire on different size individuals of *Schinus terebinthifolius*. Nat. Area J. 10, 107–113.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends Ecol. Evol. 14, 135–139.

Durand, L.Z., Goldstein, G., 2001. Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126, 345–354.

Elton, C.S., 1958. The ecology of invasions by plants and animals. Wiley, New York, NY.

Ewel, J.J., 1986. Invasibility: lesons from South Florida. In: Mooney, H.A., Drake, J.A. (Eds.), Ecology of Biological invasions of North America and Hawaii. Springer, New York, NY, pp. 214–230.

Ewel, J.J., Ojima, D.S., Karl, D.A., DeBusk, W.F., 1982. *Schinus* in Successional Ecosystems of Everglades National Park. South Florida Research Center Report No. T-676. National Park Service, Everglades National Park, Homestead, FL.

Farquhar, G.D., Ball, M.C., von Caemmerer, S., Roksandic, Z., 1982a. Effect of salinity and humidity on $\delta^{13}C$ value of halophytes-evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. Oecologia 58, 121–124.

Farquhar, G.D., O'Leary, M.H., Berry, J.A., 1982b. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9, 121–137.

Farquhar, G.D., Richards, R.A., 1984. Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. Aust. J. Plant Physiol. 11, 539–552.

Field, C., Merino, J., Mooney, H.A., 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia 60, 384–389.

Gordon, D.R., 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecol. Appl. 8 (4), 975–989.

Gordon, D.R., Thomas, K.P., 1997. Florida's invasion by nonindigenous plants: history, screening and regulation. In: Simberloff, D., Schmitz, D.C., Brown, T.C. (Eds.), Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida. Island Press, Washington, DC, pp. 21–37.

Hoffmeister, J.E., 1974. Land from the sea the geologic story of south Florida. University of Miami, Coral Gables, FL.

Horton, J.L., Kolb, T.E., Hart, S.C., 2001. Leaf gas exchange characteristics differ among Sonoran Desert riparian species. Tree Physiol. 21, 233–241.

Hubick, K.T., Farquhar, G.D., Shorter, R., 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (Arachis) germplasm. Aust. J. Plant Physiol. 13, 803–816.

Kitajima, K., Mulkey, S.S., Wright, S.J., 1997. Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. Am. J. Bot. 84, 702–708.

Koch, M.S., Snedaker, S.C., 1997. Factors influencing *Rhizophora mangle* L. seedling development in Everglades carbonate soils. Aquat. Bot. 59, 87–98.

Kozlowski, T.T., 1984. Responses of woody plants to flooding. In: Kozlowski, T.T. (Ed.), Flooding and Plant Growth. Academic Press, Orlando, FL, pp. 129–159.

Lambers, H., Poorter, H., 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv. Ecol. Res. 23, 187–261.

Land Protection, 2001. Groundsel bush (*Baccharis halimifolia*). Queensland Government Natural Resources and Mines Pest Series, Queensland, Australia.

Larcher, W., 1995. Physiological Plant Ecology. Springer, Berlin.

Mooney, H.A., Ferrar, P.J., Slatyer, R.O., 1978. Photosynthetic capacity and carbon allocation patterns in diverse growth forms of Eucalyptus. Oecologia 36, 103–111.

Panetta, F.D., McKee, J., 1997. Recruitment of the invasive ornamental, '*Schinus terebinthifolius*', is dependent upon frugivores. Aust. J. Ecol. 22, 432–438.

Pattison, R.R., Goldstein, G., Ares, A., 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117, 449–459.

Schierenbeck, K.A., Marshall, J.D., 1993. Seasonal and diurnal patterns of photosynthetic gas exchange for *Lonicera sempervirens* and *L. japonica* (Caprifoliaceae). Am. J. Bot. 80, 1292–1299.

Schieving, F., Poorter, H., 1999. Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. New Phytol. 143, 201–211.

Schmitz, D.C., Simberloff, D., Hofstetter, R.H., Haller, W., Sutton, D., 1997. The ecological impact of nonindigenous plants. In: Simberloff, D., Schmitz, D.C., Brown, T.C. (Eds.), Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida. Island Press, Washington, DC, pp. 39–61.

Simberloff, D., 1997. The biology of invasions. In: Simberloff, D., Schmitz, D.C., Brown, T.C. (Eds.), Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida. Island Press, Washington, DC, pp. 3–17.

Snyder, J.R., Herndon, A., Robertson, W.B.J., 1990. South Florida Rockland. In: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida Press, Orlando, FL, pp. 230–278.

Sun, Z.J., Livingston, N.J., Guy, R.D., Ethier, G.J., 1996. Stable carbon isotopes as indicators of increased water use efficiency and productivity in white spruce ('Picea glauca' (Moench) Voss) seedlings. Plant Cell Environ. 19, 887–894.

Taylor, D.L., 1980. Summary of fires in Everglades National Park and Big Cypress National Preserve, 1979. Report T-595. South Florida Research Center, National Park Service, Homestead, FL.

Tomlinson, P.B., 1980. The Biology of Trees Native to Tropical Florida. Harvard University Press, Allston, MA.

U.S. Congress, 1993. Harmful Non-Indigenous Species in the United States, OTA-F-565. U.S. Government Printing Office, Washington, DC.

Vitousek, P., Walker, L., 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecol. Monogr. 59, 247–266.

von Caemmerer, S., Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376–387.

Weiss, P.W., Noble, I.R., 1984. Status of coastal dune communities invaded by *Chrysanthemoides monilifera*. Aust. J. Ecol. 9, 93–98.

Yamashita, N., Ishida, A., Kushima, H., Tanaka, N., 2000. Acclimation to sudden increase in light favoring invasive over native trees in subtropical islands, Japan. Oecologia 125, 412–419.