

TRANSPIRATION AND STOMATAL CONDUCTANCE OF TWO WETLAND MACROPHYTES (*CLADIUM JAMAICENSE* AND *TYPHA DOMINGENSIS*) IN THE SUBTROPICAL EVERGLADES¹

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In the subtropical Everglades, greater than 85% of water input through atmospheric precipitation, the primary source of water to the ecosystem, is lost through evapotranspiration (ET). Two dominant macrophytes that could influence ET rates through transpiration and stomatal control were investigated in a field study: *Cladium jamaicense*, presently the species with the greatest distribution (65%–70%); and *Typha domingensis*, a species increasing in distribution due to eutrophication and hydrological modifications to the ecosystem. Transpiration rates and stomatal conductance of the two species were compared at eutrophic, mesotrophic, and oligotrophic sites throughout an annual wet and dry season of subtropical Florida. *Typha domingensis* possessed higher transpiration and conductance rates ($>11 \text{ mmol m}^{-2} \text{ sec}^{-1}$) than *C. jamaicense* ($<7 \text{ mmol m}^{-2} \text{ sec}^{-1}$; $P < 0.01$), during the winter and spring months when ambient temperatures and vapor pressure were at a minimum. However, rates for the two species converged and were not significantly different during the summer and fall months. Stomatal conductance of *C. jamaicense* remained constant over the range of ambient vapor pressures, but significantly increased in *T. domingensis* with decreasing vapor pressure. Vapor pressure and light were the best predictors of seasonal and diurnal transpiration rates of *T. domingensis*, whereas temperature explained the most variability in *C. jamaicense*. Annual transpiration rates for both species were 1 to 2 $\text{mmol m}^{-2} \text{ sec}^{-1}$ greater at the eutrophic site than at the transitional and oligotrophic sites. Leaf area increased six times in *C. jamaicense* and twofold in *T. domingensis* from the control to nutrient-enriched sites. Results at the leaf scale suggest vegetation shifts and nutrient enrichment have the potential to alter water balances in the Everglades. However, canopy level studies may be necessary to support these conclusions when applied to the larger ecosystem or regional scale.

The Florida Everglades comprises approximately 500,000 ha of subtropical freshwater wetlands, dominated (65%–70%) by the emergent sedge, *Cladium jamaicense* (Loveless, 1959). In recent years, anthropogenic nutrient loading has enhanced phosphorus availability to Everglades vegetation (Koch and Reddy, 1992) contributing to changes in macrophyte species dominance (Davis, 1989). *Typha domingensis*, which is well adapted to enriched conditions (Kadlec, 1987; Grace, 1988) and extended hydroperiods (Grace, 1989), has increased in areal distribution in the Everglades over the last three decades. A dominant species shift from *C. jamaicense* and open water sloughs to dense stands of *T. domingensis* could modify several ecosystem-level processes including evapotranspiration (ET). ET rates are particularly important in south Florida where water demands are high and periodic drought conditions may persist for several consecutive years. Average annual ET (127 cm yr^{-1}) as calculated from pan evaporation accounts for $>85\%$ of water loss from atmospheric inputs (140 cm yr^{-1}), the primary source of water to the Everglades marsh (Gunderson, 1989).

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During the last several decades, the role of emergent and floating aquatic plants on ET rates in wetland ecosystems has stimulated considerable debate. The presence of *Typha* spp. and other macrophytes has been demonstrated to increase ET rates over open water evaporation rates (E/E_o) by up to 450% (Otis, 1914; Penfound and Earle, 1948). This increased water loss may be explained by sensible heat transfer from surrounding nonvegetated surfaces, by a process known as the "oasis" effect, which artificially accelerates transpiration rates in lysimeter studies conducted on dry ground (Van der Weert and Kamerling, 1974; Linacre, 1976). A marked increase in transpiration rates was observed by van Bavel, Fritschen, and Reeves (1963) after cutting the height of sudangrass around a small plot relative to the transpiration rate before cutting, under conditions of high soil-moisture. They concluded, based on this experiment, that both radiative and sensible heat, not physiological factors, control transpiration rates in a highly evaporative environment.

Convective heat transfer to vegetation may significantly increase transpiration in small isolated marshes or along the perimeter of expansive wetlands, overshadowing any physiological control of transpiration under high soil moisture conditions. An increasing body of evidence from large-scale tropical and temperate swamps supports the supposition that the presence of vegetation can decrease evaporation from open water surfaces (Rijks, 1969; Linacre et al., 1970; Munro, 1979; Idso, 1981). Idso (1981) provides several examples of large-scale wetland areas possessing E/E_o ratios less than one: 1) A semiarid African swamp approximately 500 m in width had E/E_o values ranging from 0.38 to 0.81 over a 15-day period (Rijks,

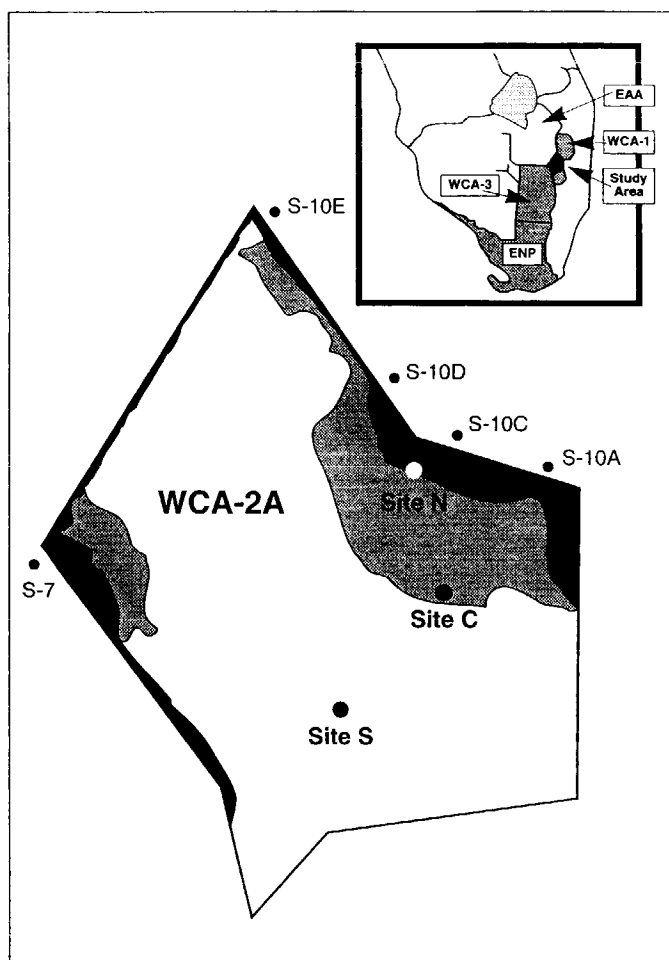


Fig. 1. The Everglades ecosystem is depicted in the upper illustration which includes the Everglades Agricultural Area (EAA), Water Conservation Areas (WCA) 1, 2, 3, and Everglades National Park (ENP). The study area, WCA-2A, and the three sampling sites: northern site (Site N), central site (Site C), and southern site (Site S), are shown in detail on the lower left. The two shaded areas and white region in WCA-2A represent three major vegetation classes (South Florida Water Management District, unpublished data) digitized from a 1987 supervised spot satellite image: the blackened region is classified as primarily monotypic stands of *Typha domingensis*, the shaded area represents a mixed community of *Typha domingensis* and *Cladium jamaicense* sawgrass prairie and aquatic sloughs, and the white background consists primarily of *Cladium jamaicense* sawgrass prairie and aquatic sloughs. Major surface water inflow structures (S-10A, S-10C, S-10D, S-10E, and S-7) are indicated.

1969); 2) vegetated prairie potholes in North Dakota had E/E_o ratios of 0.7 and 0.8 when compared to open water surfaces for 2 years (Munro, 1979); and 3) a 3,000-ha Australian swamp had evaporation rates that were approximately one-third of rates measured in a nearby 240-ha lake during a dry period. After heavy rain, lake evaporation was reduced to similar levels to those recorded in the swamp. Anderson and Idso (1987) found that two aquatic species with planate floating leaves had E/E_o ratios less than unity and hypothesized that minimum atmospheric turbulence and stomatal regulation reduced potential evaporation.

Vegetation may influence ET rates in expansive wet-

lands by feedback mechanisms. For example, several thousand hectares of transpiring leaves would be expected to influence the flux of heat and vapor from an evaporative surface, in this case the canopy. Also, vegetation structure and density modify aerodynamics of the airstream above the canopy and thus influence microclimatological gradients controlling rates of ET. In continuously flooded wetlands with no apparent soil-moisture deficit, vegetation is thought to provide little or no direct control on ET (van Bavel, Fritschen, and Reeves, 1963). Thus equations most widely being used to estimate ET are based entirely on meteorological data and disregard species composition or stomatal resistance of the transpiring vegetation. Physiological parameters such as stomatal conductance may be more important in semiarid, tropical, and subtropical wetlands where precipitation is highly seasonal. Although vegetation may have important effects on wetland water fluxes, information is minimal on the factors that control transpiration and stomatal conductance under in situ conditions, and few direct measurements of transpiration rates and stomatal resistance for wetland species exist in the literature (Giurgevich and Dunn, 1981, 1982; Lafleur, 1988). Wetland species that encompass thousands of contiguous hectares, such as *C. jamaicense* in the Florida Everglades, would be of particular importance.

In the present study, transpiration and stomatal conductance rates of *C. jamaicense*, which currently has the greatest distribution in the Everglades, and *T. domingensis*, a species which is increasing in distribution due to anthropogenic activities, were measured in the field under mesic and hydric soil conditions through a wet and dry season of south Florida. Transpiration rates, stomatal conductance, and leaf area indices (LAI) were also compared between the two species along an established nutrient gradient. Regression analysis was used to determine which climatological factors were most important in explaining the seasonal and diurnal changes of stomatal conductance and transpiration rates in the two species.

MATERIALS AND METHODS

Study sites—The present Everglades ecosystem is subdivided into separate hydrological units encompassed within the Water Conservation Areas (WCA-1, WCA-2, WCA-3) in the northern Everglades basin and the Everglades National Park (ENP) to the south (Fig. 1). In this study, three sites were chosen along a soil-porewater phosphorus gradient in WCA-2 (Fig. 2): a northern site (N), a central site (C), and a southern site (S). Soil and water nutrient concentrations at the three sites are further described in Koch and Reddy (1992). Stands of *C. jamaicense* and *T. domingensis*, in close proximity to each other, were selected from each of the three sites to facilitate nearly simultaneous transpiration measurements and to standardize, as much as possible, environmental conditions such as solar radiation, relative humidity (RH), and air temperature.

Steady state porometer—A steady state porometer (LI-COR, LI-1600M) was used to measure water loss from transpiring leaves. This method measures the flow rate

of dry air (<2% RH) necessary to maintain a constant relative humidity (nulled to ambient RH) inside a cuvette which has been clamped onto a transpiring leaf. Care was taken during sampling to ensure all leaves were completely dry before any readings were taken. A narrow leaf sensor head was employed during all measurements exposing 1 cm² of leaf area to the dry air stream. Leaf temperature (± 0.7 °C) and cuvette temperature (± 0.5 °C) as well as cuvette relative humidity ($\pm 3\%$) were also recorded (leaf relative humidity was assumed to be 100%). Leaf transpiration rate (E_i ; mmol cm⁻² sec⁻¹) is related to the volumetric flow rate according to LI-COR (1989). Stomatal conductance (g_i) is calculated directly from the measured values of relative humidity, leaf and air temperature, and flow rate using the equation described in Cowan (1977) and LI-COR (1989).

Transpiration and conductance measurements—Leaf E_i and g_i measurements ($N = 10$) were taken at each of the three sites in January, March, May, August, September, and November through the dry and rainy seasons of 1990. In addition, E_i measurements ($N = 10$) were taken hourly from 08:00 to 18:00 at Site C on 3 June 1991. Each site was sampled on consecutive days over a 3-day period. To facilitate comparisons between sites and species, only cloudless days were chosen for measurements. During bimonthly sampling, readings were taken from ten randomly selected leaves of both *C. jamaicense* and *T. domingensis* at 10:00, 12:00, and 14:00 hours, alternating between species after five leaves were measured. Leaves were slowly and carefully clamped to prevent damage to cells and release of intercellular material. Once leaves were in the cuvette, a steady state condition was generally achieved within 5 to 15 seconds. No readings were taken if steady state conditions were not met within a 30-second time period. Photosynthetic photon flux density (PPFD; $\mu\text{mol sec}^{-1} \text{m}^{-2}$) was measured with a quantum sensor concomitant with gas exchange measurements. Before readings, air temperature, wind speed, and direction were recorded for each time period.

A preliminary test was conducted to determine the E_i of the adaxial and abaxial surfaces of leaves from both *C. jamaicense* and *T. domingensis* (March 1990). Simultaneous readings were taken from two steady state porometers to determine potential variance between the two meters and differences in E_i and g_i between sides of the leaf surface.

Leaf area—Five 0.25-m² plots of both monotypic *T. domingensis* and *C. jamaicense* stands were randomly selected at each site to estimate leaf area for each species and site. All aboveground tissue was grouped by individual plants. Leaves were then cut to the soil surface and subsequently transported to the laboratory. Sites were sampled from 23 March to 22 April 1991, thus allowing all leaf area measurements to be taken immediately after sampling to ensure an accurate representation of the standing green live leaf tissue before browning occurred. Individual leaves were measured for total length and then were examined for dead and other nonphotosynthetic (brown) areas, which were removed. The remaining sample was then measured for green length, maximum width,

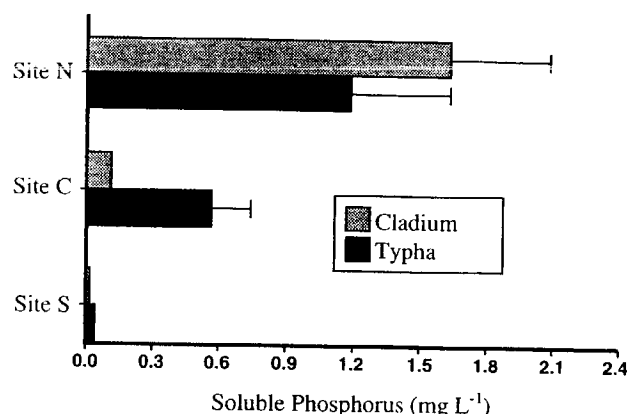


Fig. 2. Mean seasonal (January, May, July, and October 1990) interstitial phosphorus concentrations (0–30 cm) within stands of *Typha domingensis* and *Cladium jamaicense* at the northern, central, and southern sites (Koch and Reddy, 1992).

and live leaf surface area. All measurements were made using a LI-COR LI-3000A portable area meter and the LI-3050A transparent belt conveyor.

Statistical analyses—Statistical analyses including the determination of means, standard errors, analysis of variance, stepwise regression, *t*-tests, and tests for data normality were performed using the SAS statistical package, version 6.03 (SAS, 1988). Multiple mean comparisons were tested using Duncan's multiple range test; values reported are significantly different at the $P < 0.05$ level unless otherwise stated. Stepwise regression analysis was used to determine the controlling factors of monthly and diurnal transpiration rates for the two species. Residuals were tested for normal distributions according to the Shapiro-Wilks test.

RESULTS

Preliminary tests—No significant differences were found for E_i between the two porometer units ($P < 0.05$). In addition, flow rates, cuvette and leaf temperature, relative humidity, and PPFD measurements were not significantly different between porometers. Simultaneous readings of adaxial and abaxial sides of the leaves were not significantly different between porometers; however, g_i rates for *T. domingensis* were three times greater than *C. jamaicense* (Table 1).

Seasonal transpiration and conductance—During the monthly sampling, *T. domingensis* E_i showed greater variation than *C. jamaicense* to the time of day when measurements were taken (Fig. 3). Mean monthly E_i of *T. domingensis* were significantly higher at 12:00 and 14:00 hours compared to 10:00 hour at all sites ($P < 0.05$). *Cladium jamaicense* had a similarly lower 10:00 E_i at site S, but no significant time effect was observed at sites N and C. Although g_i tended to increase during the day from 303 to 360 mmol m⁻² sec⁻¹ in *T. domingensis* and decrease from 230 to 196 mmol m⁻² sec⁻¹ in *C. jamaicense*,

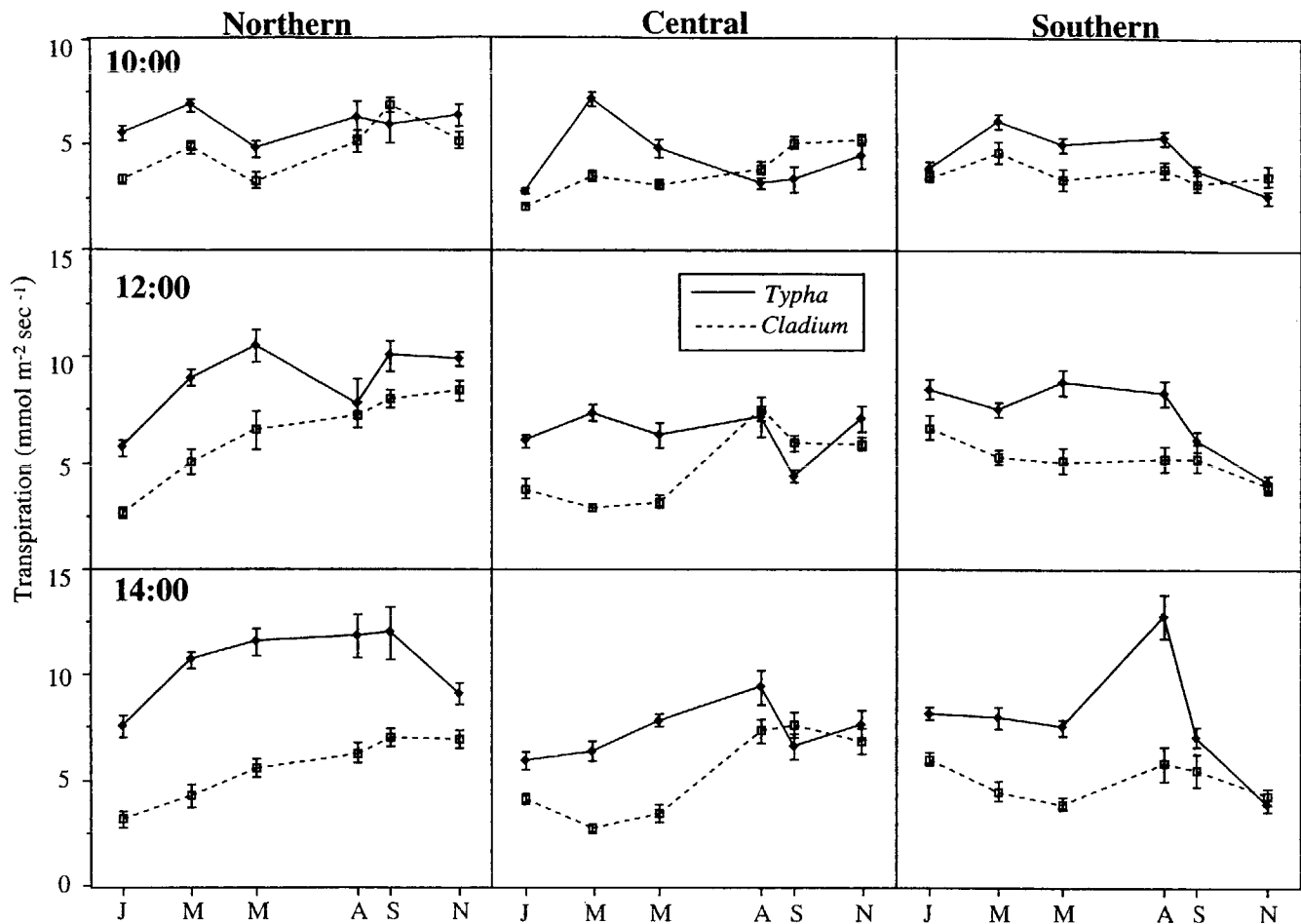


Fig. 3. Seasonal changes in transpiration rates ($\text{mmol m}^{-2} \text{sec}^{-1}$) of *Typha domingensis* and *Cladium jamaicense* measured at 10:00, 12:00, and 14:00 hours at the northern, central, and southern sites. Means are given with \pm standard error of the mean ($N = 10$).

mean monthly g_i did not significantly change as a function of time for either species or sites (Fig. 4).

Minimal differences between E_i and g_i readings during the three time periods are probably due to midday mea-

TABLE 1. Simultaneous measurements of *Cladium jamaicense* and *Typha domingensis* adaxial (T) and abaxial (B) leaf surfaces at Site C (March 1990).

Side	Species	Stomatal conductance ^a		Transpiration	
		(cm sec^{-1})	($\text{mmol m}^{-2} \text{sec}^{-1}$)	($\mu\text{g cm}^{-2} \text{sec}^{-1}$)	($\text{mmol m}^{-2} \text{sec}^{-1}$)
B	<i>Cladium</i>	0.29 ± 0.26	117 ^b —	4.24 ± 0.34	2.36 ± 0.19
T	<i>Cladium</i>	—	152 ± 12	—	2.72 ± 0.21
B	<i>Typha</i>	1.05 ± 0.09	426 ^b —	12.49 ± 0.77	6.94 ± 0.43
T	<i>Typha</i>	—	364 ± 24	—	6.36 ± 0.45

^a Stomatal conductance is reported in different units due to the definition and calculation of conductance between the LI-1600C (cm sec^{-1}) and LI-1600M ($\text{mmol m}^{-2} \text{sec}^{-1}$; LI-COR, 1989).

^b Velocity units were converted to molar units for comparison according to: $g_{m,m} = g_v (P/RT_i)$ where $g_{m,m}$ and g_v are stomatal conductance in molar and velocity units, respectively; P = barometric pressure in Pa; R = gas constant ($8.314 \text{ Pa m}^3 \text{mol}^{-1} \text{K}^{-1}$); and T_i is leaf temperature.

surements on cloudless days. At 10:00, PPFD was on average ($1,281 \mu\text{mol sec}^{-1} \text{m}^{-2}$) only 300 to 500 $\mu\text{mol sec}^{-1} \text{m}^{-2}$ lower than at 12:00 ($1,500 \mu\text{mol sec}^{-1} \text{m}^{-2}$) and 14:00 ($1,552 \mu\text{mol sec}^{-1} \text{m}^{-2}$) hours. Other climatological changes in the canopy over the three measurement periods included a 10% higher relative humidity and 2 C cooler temperature at 10:00 compared to 12:00 and 14:00 hours. Between 12:00 and 14:00 hours, only a 3% decrease in relative humidity and 1 C increase in temperature were observed.

During the first 3 months of sampling, January, March, and May, *T. domingensis* had significantly higher E_i and g_i than *C. jamaicense* at site N and C ($P < 0.01$; Figs. 3, 4). At the most nutrient-enriched site, *T. domingensis* E_i and g_i at 14:00 hour were higher than *C. jamaicense* over the entire year ($P < 0.01$; Figs. 3, 4). At site S, E_i were only significantly different between species in August at 10:00 hour, May and August at 12:00 hour, and from January to August at 14:00 hour ($P < 0.01$; Fig. 3). The greatest differences in E_i between the two species were observed when temperature, water levels, and ambient vapor pressure (e_a) were lowest during a drought from January to May 1990 (Figs. 3, 5). However, rates were similar between the two species when water levels and temperature increased in July (Figs. 3, 5).

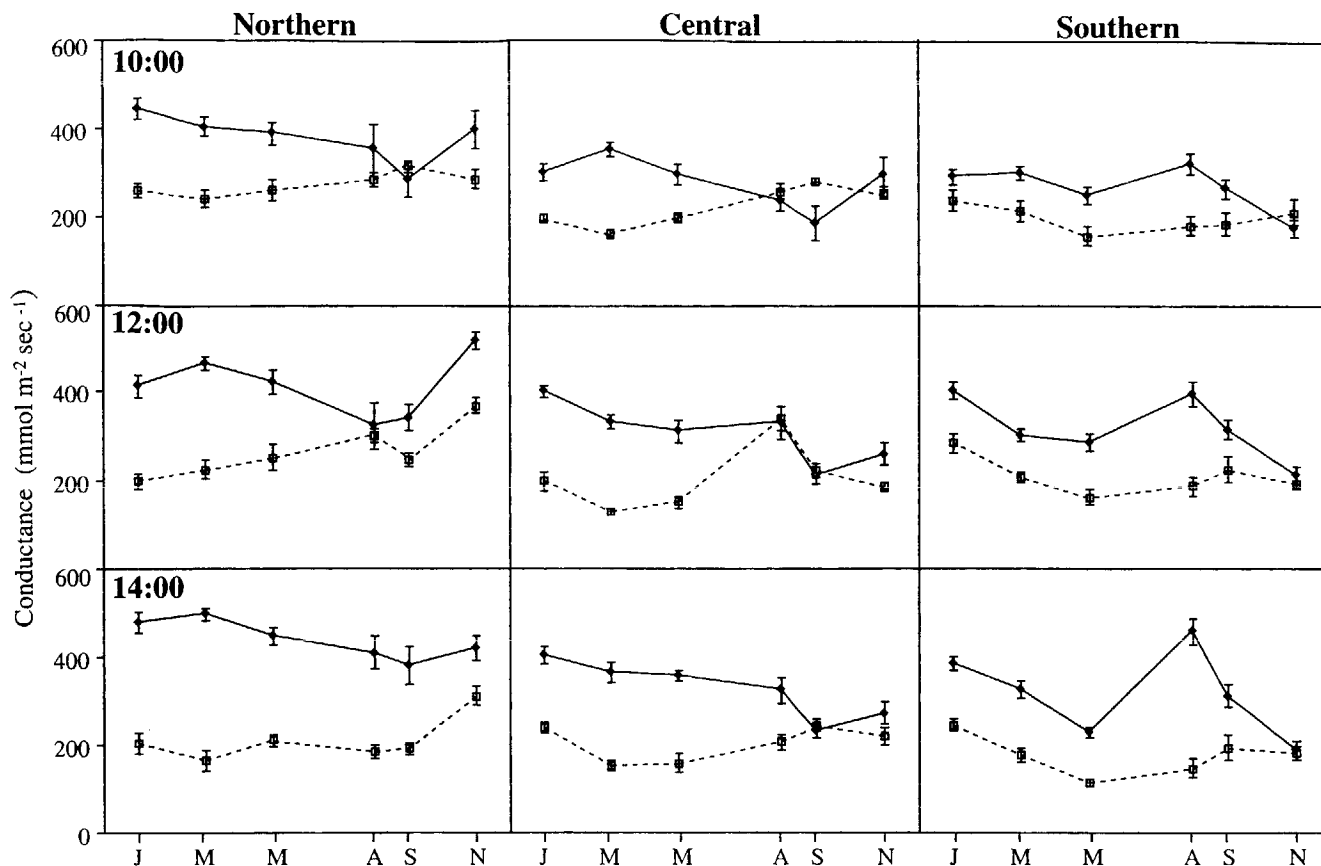


Fig. 4. Seasonal changes in stomatal conductance rates ($\text{mmol m}^{-2} \text{sec}^{-1}$) of *Typha domingensis* and *Cladium jamaicense* measured at 10:00, 12:00, and 14:00 hours at the northern, central, and southern sites. Means are given with \pm standard error of the mean ($N = 10$).

Stepwise regression analyses—Monthly transpiration rates in *C. jamaicense* were a function of cuvette temperature and e_a with leaf temperature and PPFD not incorporated into the linear model at $P < 0.15$ (Table 2). By comparison, e_a and PPFD accounted for the greatest amount of monthly E_t variability in *T. domingensis*, with cuvette and leaf temperature explaining less than 10% and 5%, respectively (Table 2).

Diurnal changes in *C. jamaicense* and *T. domingensis* E_t and g_l as a function of fluctuating light, temperature, and e_a , are illustrated in Fig. 6. Dominant factors controlling monthly E_t in each species also controlled diurnal E_t (Table 2). Diurnal changes in cuvette temperature explained 75% of the variability in E_t of *C. jamaicense*, with only 6% accounted for by e_a . In contrast, e_a accounted for 64% of the variability in diurnal E_t for *T. domingensis* with PPFD explaining 18%.

Over the range of observed e_a , g_l remained constant in *C. jamaicense* with no significant slope (Fig. 7). Despite the presence of high variability, g_l significantly increased in *T. domingensis* with decreasing e_a (slope = -48 , $P = 0.03$; Fig. 7).

Leaf area—*Cladium jamaicense* leaf surface area (m^2 leaf area per m^2 marsh; $N = 5$ plots) decreased twofold from the northern ($6.10 \pm 0.21 \text{ m}^2 \text{ m}^{-2}$) to the central site ($3.77 \pm 0.65 \text{ m}^2 \text{ m}^{-2}$) and sixfold from the northern to the southern site ($0.86 \pm 0.18 \text{ m}^2 \text{ m}^{-2}$). No significant

differences in leaf area between site C and S (3.94 ± 0.78 and $3.21 \pm 0.40 \text{ m}^2 \text{ m}^{-2}$, respectively) were found for *T. domingensis*, but site N had a greater leaf area ($5.78 \pm 0.46 \text{ m}^2 \text{ m}^{-2}$) than the other two sites.

To provide a nondestructive method for future estimates of live leaf surface area (LLSA), the following variables were examined using linear models, maximum leaf width (MLW), green leaf length (GLL), and total leaf length (TLL). The MLW, GLL, and TLL explained 92% of the variability in *C. jamaicense* live leaf surface area with the greatest percentage (84%) explained by MLW (model: $\text{LLSA} = -57.4 + 0.21[\text{TLL}] + 0.46[\text{GLL}] + 45.87[\text{MLW}]$; $N = 915$). The MLW, GLL, and TLL also explained 92% of the LLSA variability for *T. domingensis*; however, GLL was the most important variable accounting for 81% of the variation (model: $\text{LLSA} = -54.5 + 0.06[\text{TLL}] + 1.22[\text{GLL}] + 25.75[\text{MLW}]$; $N = 585$).

DISCUSSION

Seasonal E_t from all three sites averaged $4.97 \text{ mmol m}^{-2} \text{sec}^{-1}$ for *C. jamaicense*, approximately 1.5 times lower than E_t of *T. domingensis*, $6.97 \text{ mmol m}^{-2} \text{sec}^{-1}$. Seasonal E_t of both *C. jamaicense* and *T. domingensis* fell within the upper range of annual E_t from salt marsh macrophytes and woody wetland species, integrating over 10-hour days. Annual E_t of three salt and brackish marsh species, *Spartina alterniflora*, *Juncus roemerianus*, and

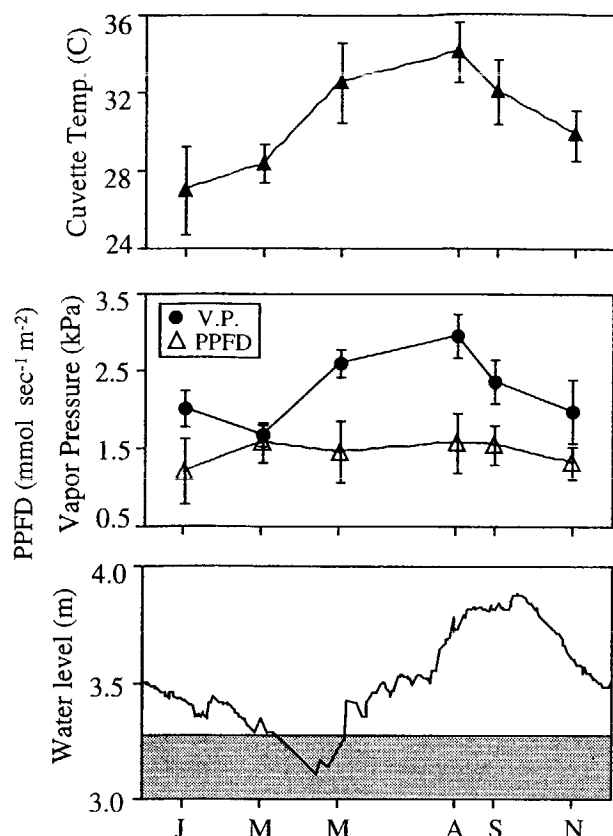


Fig. 5. Average (10:00, 12:00, and 14:00 hours) cuvette temperature (C), vapor pressure (kPa), and light (PPFD) with standard deviations ($N = 18$) measured in association with transpiration readings at the northern, central and southern sites. Average daily water levels recorded continuously at the southern site from January to December 1990; shaded region shows water levels dropping below the soil surface in May.

Spartina cynosuroides ranged from 0.42 to 2.58, 1.19 to 2.70, and 2.05 to 5.60 $\text{mmol m}^{-2} \text{sec}^{-1}$, respectively (Giurgevich and Dunn, 1981, 1982). Kramer (1969) measured midsummer transpiration rates for *Ilex glabra* (2.49 $\text{mmol m}^{-2} \text{sec}^{-1}$), *Myrica cerifera* (1.67 $\text{mmol m}^{-2} \text{sec}^{-1}$), and *Godonia lasianthus* (2.74 $\text{mmol m}^{-2} \text{sec}^{-1}$) growing in pots near soil field capacity in full sun conditions. Compared to the above E_i rates, south Florida E_i rates were high, partially due to annual averages being based on three cloudless midday measurements. However, diurnal rates for the two species from 08:00 to 19:00 hours in June were also high, 5.30 and 5.68 $\text{mmol m}^{-2} \text{sec}^{-1}$ for *C. jamaicense* and *T. domingensis*, respectively. These data suggest that wetland macrophytes growing in subtropical conditions may maintain higher E_i than those previously reported for temperate regions. Since diurnal measurements were not taken during winter months and only cloudless days were sampled, annual averages are considered by the authors to be approaching $E_{i\text{max}}$ for the two species under subtropical climatic conditions.

Temperature was an important variable regulating E_i of *C. jamaicense*. Under field conditions, both tall and short forms of *S. alterniflora* and *J. roemerianus* also exhibited higher E_i during the warmer summer months in a tidal Georgia salt marsh (Giurgevich and Dunn, 1982). However, the differences between mean daily winter and summer temperatures were approximately 11 to 27 C in Georgia, whereas temperatures maintained a higher range from 22 to 29 C in the present study. Giurgevich and Dunn (1981) found that increasing temperatures from 15 to 40 C did not significantly modify E_i in *S. alterniflora*, but *S. cynosuroides* E_i showed a steady increase in response to elevated temperatures. Temperature-dependent growth patterns, potentially related to higher E_i , have been reported in *Cladium mariscus*, a temperate European species that is morphologically and anatomically similar to *C. jamaicense* (Conway, 1938). However, E_i may not

TABLE 2. Seasonal (a) and diurnal (b) leaf transpiration rates of *Cladium jamaicense* and *Typha domingensis* as a function of cuvette temperature, vapor pressure, leaf temperature, and photosynthetic photon flux density (PPFD), as determined by stepwise multiple regression.

Variable	Cladium				Typha				
	Partial R^2	F	df	P	Partial R^2	F	df	P	
Seasonal									
Cuvette temp.	0.30	22.2	52	0.0001	0.07	5.5	52	0.0229	
Vapor pressure	0.14	12.2	52	0.0010	0.22	26.9	52	0.0001	
Leaf temp.	ns ^a				0.04	5.9	52	0.0192	
PPFD	ns				0.30	22.7	52	0.0001	
Overall F test:					Overall F test:				
R^2				0.44	R^2				0.64
$F_{2,51}$				19.6	$F_{4,49}$				21.34
P				<0.0001	P				<0.0001
Diurnal									
Cuvette temp.	0.75	29.3		0.0003	ns				
Vapor pressure	0.06	2.8		0.1312	0.64	17.6		0.0019	
Leaf temp.	ns				ns				
PPFD	ns				0.18	8.4		0.0179	
Overall F test:					Overall F test:				
R^2				0.81	R^2				0.81
$F_{2,11}$				18.6	$F_{2,11}$				19.41
P				<0.0006	P				<0.0005

^a ns = variable not significant ($P > 0.15$).

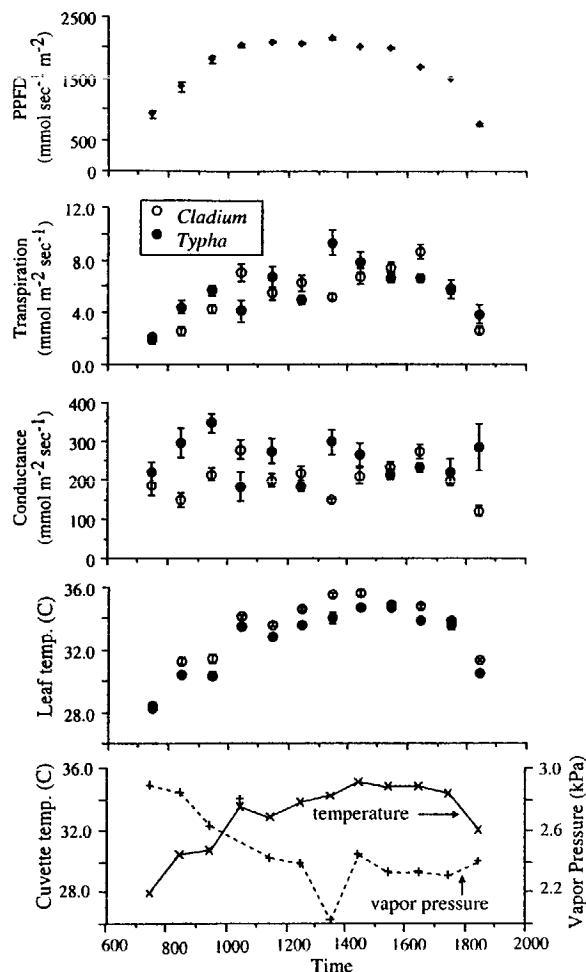


Fig. 6. Hourly readings of photosynthetic photon flux density (PPFD), transpiration rates, stomatal conductance, leaf temperature, and ambient temperature and vapor pressure from 08:00 to 19:00 hours during a diurnal survey at the central site. Cuvette temperature and vapor pressure did not significantly vary between species during any time of measurement and therefore are presented as a single measurement. Means are given with \pm standard error of the mean for Fig. 5 ($N = 10$).

be equated to carbon gain or growth. For example, although *J. roemerianus* had higher E_i in the summer, high temperatures ($> 25^\circ\text{C}$) produced suboptimal conditions for photosynthesis, thereby reducing water-use efficiencies (Giurgevich and Dunn, 1982). No photosynthetic rate measurements were taken for *C. jamaicense* or *T. domingensis* in this investigation; however, they should be considered for future studies to analyze the effect of seasonal E_i on carbon balances in the two species.

Leaf stomatal conductance is an important factor controlling E_i , particularly under arid conditions with high soil and atmospheric water deficits (Burrows and Milthorpe, 1976). Conductance based on molar units is purported to be less dependent on temperature and pressure (Cowan, 1977); however, conductance has been reported for many years in the literature using velocity units (cm sec^{-1}). For convenience in this discussion, our molar estimates of g_{lm} are converted to velocity units (g_{lv}) according to the following equation:

$$g_{lm} = g_{lv}(P/RT_1)$$

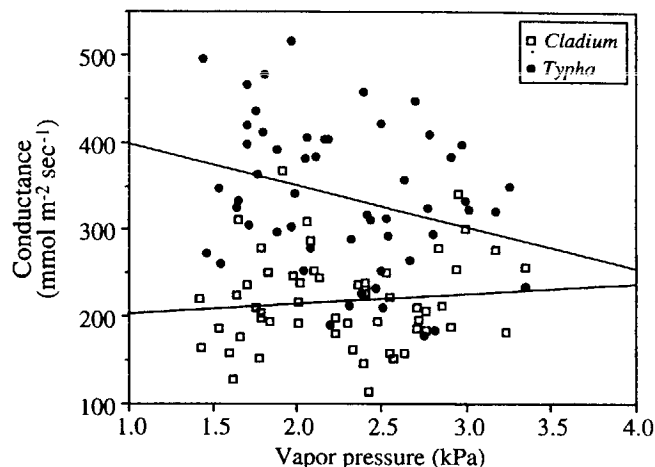


Fig. 7. Relationship between stomatal conductance and vapor pressure for *Cladium jamaicense* and *Typha domingensis* from monthly measurements at the northern, central, and southern sites.

where P = barometric pressure in Pa, R = gas constant ($8.314 \text{ Pa m}^3 \text{ mol}^{-1} \text{ K}^{-1}$), and T_1 is leaf temperature (K). Over the range of leaf temperatures observed in this study, 23 to 38°C , g_i changed only a fraction of a mm sec^{-1} . Therefore, average leaf temperature, 30°C , was used for the following rate conversions. Average seasonal g_i for all sites were 0.54 cm sec^{-1} ranging from 0.28 to 0.92 for *C. jamaicense* and 0.84 cm sec^{-1} ranging from 0.44 to 1.28 for *T. domingensis*. Although climatic conditions are significantly different in the subarctic marshes studied by Lafleur (1988), the sedge, *Carex paleacea* and three woody species, *Alnus rugosa*, *Salix bebbiana*, and *Salix discolor*, had daily maximum g_i between 0.76 and 0.61 falling within the upper and median ranges of *C. jamaicense* and *T. domingensis*, respectively. The only reported $g_{i\text{max}}$ higher than those found in this study were measured from tropical trees in Nigeria ($1.00 \text{ mol m}^{-2} \text{ sec}^{-1}$; Grace, Okali, and Fasehun, 1982).

Averaging over the season and sites, *T. domingensis* showed a 19% increase in g_i from the morning (10:00) to afternoon reading (14:00) in contrast to a 15% decrease in g_i in *C. jamaicense*. A decline in g_i from morning to afternoon was also observed in *J. roemerianus* (0.64 to 0.28) and *S. alterniflora* (0.28 to 0.15), with the afternoon suppression of g_i attributed to stomatal closure in response to decreasing xylem water potential (Giurgevich and Dunn, 1982). Increases in CO_2 may have also been a factor in decreased g_i in *C. jamaicense*, but no midday depression in photosynthesis was observed in salt marsh species (Giurgevich and Dunn, 1982).

Cladium jamaicense was found to maintain a similar g_i over the range of e_a encountered, providing evidence for greater stomatal resistance of this species under various atmospheric vapor conditions and soil moisture regimes, compared to *T. domingensis*. Lafleur (1988) observed a twofold decrease in the range of the g_i with increasing vapor pressure deficits ($\text{VPD} = e_{\text{sat}} - e_a$) less than approximately 1.2 kPa in four wetland species from a subarctic marsh. Although water levels dropped below the soil surface during May of 1990 in the Everglades and may have caused soil moisture stress, VPD was never

below 1.3 kPa during this study. A lack of VPD over the year, >1.3 kPa, may explain the consistent values of g_i in *C. jamaicense* over seasonal fluctuations in e_a . In spite of minimal VPD, g_i increased in *T. domingensis* under lower e_a , suggesting soil water deficits associated with low e_a may have resulted in a decreased resistance of leaves to water loss. In the Everglades, *T. domingensis* is limited in spatial distribution, primarily to deep, locally enriched, alligator holes which infrequently dry out. The apparent restriction of *T. domingensis* to deeper habitats may be associated with the inability of this species to regulate stomatal resistance ($1/g_i$) as soil water stress increases, in addition to nutrient limitations. Johnson and Caldwell (1975) found tundra species, *Dupontia* and *Deschampsia*, that were limited to wet sites, have significantly higher photosynthetic and g_i rates compared to two more widely distributed species, *Carex* and *Geum*. However, higher photosynthetic activity of the more flood-tolerant species was offset by their inability to maintain high photosynthetic capacities and stomatal resistance ($1/g_i$) as water deficits increased. Thus, we hypothesize that slow growth rates (Davis, 1989) and stomatal control of *C. jamaicense* may be adaptive strategies for maintaining internal water balances under the low nutrient and highly variable hydrological regimes encountered in the Everglades.

Life history strategy, in addition to physiological adaptations to environmental conditions, may explain the observed differences in E_i rates between *T. domingensis* and *C. jamaicense*. Davis (1989) showed that *T. domingensis* possesses faster whole plant turnover rates of 11 to 96 weeks, compared to *C. jamaicense*, 28 to 370 weeks, and therefore, *T. domingensis* plants tend to be younger on average. Twofold faster annual leaf turnover rates were also observed for *T. domingensis* by Davis (1989). Younger leaves with higher productivity and growth rates may have higher E_i than older leaves. Wong, Cowan, and Farquhar (1979) correlated plant photosynthetic capacities and periods of maximum growth directly to g_i . The observed August 14:00 hour peak in E_i at site S probably resulted from new leaf tissue growth after this site was burned by a lightning-induced fire in June 1990. Plant heights at site S were similar to preburn conditions for both species 8 weeks postburn (personal observation). Fire is important in the Everglades for recycling limiting nutrients (Steward and Ornes, 1975) and therefore may also increase E_i by stimulating plant productivity and growth.

Transpiration rates and g_i seemed to be partially influenced by nutrient availability. The largest discrepancies of E_i between the two species occurred at the most nutrient-enriched site. Photosynthetic capacities and g_i have been shown to be regulated by N and P availability and soil water potential (Wong, Cowan, and Farquhar, 1979). Both *T. domingensis* and *C. jamaicense* exhibit higher growth rates under nutrient enrichment (Davis, 1989), suggesting eutrophication may influence E_i . Also, *T. domingensis* growth and productivity rates are characteristically high (McNaughton and Fullem, 1970; Davis, 1989), and therefore may possess higher transpiration rates than historically dominant Everglades flora such as *C. jamaicense*.

Nutrient enrichment has also been shown to increase aboveground biomass leading to a greater LAI and rates of ET (DeBusk and Ryther, 1983; Snyder and Boyd, 1987). Canopy structure may influence Everglades marsh

ET in several ways, including extinction of light through the canopy, reflectance of light in the canopy based on leaf angle and density, aerodynamics of the overlying air mass (aerodynamic resistance), and a feedback mechanism from E_i that minimizes VPD and temperature gradients, particularly during the winter and spring dry season.

Earlier studies of ET overestimated canopy aerodynamic resistance resulting in an underestimate of the influence of stomatal conductance (Jarvis and McNaughton, 1986). Recently, due to the successful implementation of the Penman-Monteith equation in determining crop water requirements (Smith et al., 1991), attention has been given to the role of canopy resistance in calculations of ET. Changes in LAI and stomatal conductances due to species changes and nutrient enrichment found in this study may have a significant effect on canopy resistance (r_c) according to the equation (Smith et al., 1991):

$$r_c = R_i / 0.5 \cdot LAI$$

where R_i = stomata resistance of a single leaf (sec m^{-1}). However, based on available regional models, net radiation and average temperature, rather than changes in canopy conductances, are demonstrated to be the dominant factors controlling transpiration on landscape scales (Jarvis and McNaughton, 1986). Vapor pressure and temperature gradients at the leaf-air vs. canopy-air boundary layers can be quite disparate, particularly in grassland biomes, but canopy structure and conductance may also have a significant influence on the overlying boundary temperature and vapor gradients. Thus, further studies are needed, employing weather stations in the marsh interior and additional canopy measurements, to relate transpiration and stomatal conductance results at the leaf scale to effects at the larger, regional scales. Results from the present study suggest that vegetation and nutrient enrichment could potentially have a significant effect on water loss in the Everglades and other large contiguous wetland ecosystems.

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