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Photosynthetic light and carbon dioxide response of the invasive tree, *Vochysia divergens* Pohl, to experimental flooding and shading

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Abstract

Vochysia divergens Pohl is considered to be a flood-adapted, light-demanding pioneer species that has been invading grasslands of the Brazilian Pantanal. In these areas, a successful invasion requires an ability to tolerate physiologically wide fluctuations in surface hydrology and shading induced by a dense cover of grasses and other vegetation. We evaluated how flooding and shading affected the photosynthetic performance of *V. divergens* saplings by measuring light-saturated gas exchange (net photosynthetic rate, P_N; stomatal conductance, g_s), and intercellular CO_2 (P_N/C_i) and photosynthetic photon flux density (P_N/PPFD) response curves over a 61-d field experiment. Shading and flooding reduced significantly light-saturated P_N and g_s and affected multiple aspects of the leaf gas exchange response of *V. divergens* to variations in PPFD and CO_2. Flooding influenced the physiology of this species more than shading. Given the success of *V. divergens* at invading and expanding in seasonally flooded areas of the Pantanal, the results were surprising and highlighted the physiological ability of this species to tolerate suboptimal conditions. However, the consistently higher light-saturated P_N and g_s under nonflooded conditions suggested that the invasive success of *V. divergens* might not be related to its physiological potential during flooding, but to situations, when flooding recedes during the dry season and soil water availability is adequate.

Additional key words: Brazilian Pantanal; CO_2 and light-response curves; ecophysiology; invasive plants; tropical wetlands.

Introduction

The distribution and abundance of plant species are strongly influenced by their physiological tolerance of environmental conditions (Heschel *et al.* 2004). However, natural or anthropogenic changes to ecosystems can disproportionally benefit some species, allowing them to become invasive (Mack *et al.* 2000). For example, *Tamarix ramosissima* (tamarisk) is a drought-tolerant species from Eurasia, which may become invasive in desert riparian areas that experience reduced flow (Lite and Stromberg 2005), while *Cortaderia selloana* (pampas grass) may become invasive in Mediterranean-type ecosystems that experience an increase in disturbance

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Abbreviations: C_i – intercellular CO_2 concentration; C_i/C_a – ratio between CO_2 in the intercellular mesophyll spaces and atmospheric CO_2; Chl – chlorophyll; DOY – day of year; FS-F – flooded with full sunlight; FS-NF – nonflooded with full sunlight; g_s – stomatal conductance; J_{max} – light-saturated rate of electron transport; L – light; LCP – light compensation point; P_{max} – photosynthetic rate at light saturation; P_N – net photosynthetic rate; P_N/C_i – photosynthetic response curves to variations in intercellular CO_2 concentration; P_N/PPFD – photosynthetic response curves to variations in PPFD; PPFD – photosynthetic photon flux density; P_{sat} – photosynthetic rate at CO_2 saturation; R_D – dark respiration rate; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; S-F – flooded in shade; S-NF – nonflooded in shade; T_1 – first day of experiment; T_{61} – last day of experiment; TPU – triose-phosphate utilization; V_{cmax} – maximum rate of Rubisco activity; W – water; Φ – apparent quantum yield.

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frequency (Lambrinos 2002). A lesser known example is *Vochysia divergens* Pohl (locally known as cambará), which is reportedly a flood-tolerant, light-demanding pioneer species native to the lowland forest of the Amazon Basin (Pott and Pott 1994, Lorenzi 1998). Over the last 3–4 decades, cambará has spread rapidly in seasonally flooded grasslands of the Brazilian Pantanal, forming extensive monospecific forests (Junk and Nunes da Cunha 2005, Nunes da Cunha *et al.* 2007). Measurements of a growth and seedling establishment and recruitment support the notion that cambará is a light-demanding, flood-tolerant species. For example, seedling establishment was the highest in bare soils, and the growth was limited by shading (Nunes da Cunha and Junk 2004). Additionally, the expansion of *V. divergens* may be limited by multiyear variations in drought stress, and the plant may retreat to wetter areas during times of prolonged drought (Nunes da Cunha and Junk 2004).

Most research on *V. divergens* invasion has focused on its population dynamics and the effects of invasion on plant communities and soil resources (Junk and Nunes da Cunha 2005, Arieira and Nunes da Cunha 2006, Junk *et al.* 2006, Nunes da Cunha *et al.* 2007, Vourlitis *et al.* 2011). Thus, the physiological aspects of the invasion, such as the potential photosynthetic acclimation to widely varying hydrological and light conditions, are unknown. Understanding how its physiological performance is affected by environmental variations can help elucidate possible mechanisms for its survival in potentially unfavorable environments (McDowell 2002, Sharkey *et al.* 2007). This may be especially true for wetland areas like the Brazilian Pantanal, where periodic flooding is a common phenomenon, and the physiological plasticity is of crucial importance for plant survival. For example, plants exposed to periodic flooding often exhibit a decline in P_N and/or g_s, because hypoxia and/or anoxia which develops during flooding, can cause a reduction in chlorophyll (Chl) and cytokinin synthesis (Zhang *et al.* 2000), accumulation of potentially toxic compounds like ethanol and lactate (de Oliveira and Joly 2010), and an increase in abscisic acid (ABA) concentration (Maurenza *et al.* 2009, Herrera *et al.* 2010). Shading also results in a decline in the gas exchange as plants acclimated to shade have typically lower contents of Chl, proteins, and enzymes related to photosynthesis and ion assimilation (Brooks *et al.* 1996, Griffen *et al.* 2004). Declines in Chl and other photosynthetic proteins and enzymes also significantly reduce leaf respiratory cost and the light compensation point (Penning de Vries 1975), which increases the potential for the survival of plants growing in shaded canopies. Acclimation to shade can take place over daily/weekly timescales; however, the full acclimation may not be possible for the light-demanding species (Griffen *et al.* 2004).

We conducted a short-term field experiment to evaluate the interactive effects of light availability and flooding on the leaf gas exchange of *V. divergens* saplings. We repeatedly measured light-saturated P_N and g_s, and conducted CO_2 (P_N/C_i) and light (P_N/PPFD) response curves to quantify the physical and biochemical limitations to the leaf gas exchange in response to shading and flooding. Two hypotheses were tested: (*1*) based on the fact that *V. divergens* is considered light-demanding, we expected that plants grown under full-sunlight would have a higher rate of P_N; and (*2*) given that *V. divergens* is considered flood-tolerant, we expected that flooding would not significantly affect its gas exchange.

Materials and methods

Experimental design: About one-year-old *V. divergens* trees (saplings) were collected during the dry season from the Pantanal in an invaded area ($n = 60$ trees). At the time of harvest, the saplings were about 30 cm tall, with 20–30 leaves per plant and a trunk diameter ≤ 3 cm. Plants were growing in the shaded understory of a dense canopy of bunchgrasses (*Gymnopogon spicatus* Spreng.), trees (*Curatella americana* L.), and herbaceous shrubs (*Mimosa pellita* H. *et* B.).

The collected saplings were transferred to a shade house at the Federal University of Mato Grosso, transplanted into 8 L pots containing native soil, placed under shade corresponding to the situation under the grass canopy in the field, where they were harvested, and left to recover for about 3 months until they showed good health, which was assessed as the production of new green leaves. The shade house was covered with a cloth that attenuated about 78% of the ambient light, which was similar to that observed in forest canopies of the Pantanal (Biudes 2008), and transmitted wavelengths longer than 600 nm, which was similar to those transmitted by a typical plant canopy (Holmes and Smith 1977).

Surviving plants (28 out of the initial 60) were randomly allocated to one of 4 treatment groups ($n = 7$ plants per group): flooded plants exposed to full sunlight (FS-F); flooded plants exposed to simulated understory shade (S-F); nonflooded plants exposed to full sunlight (FS-NF), and non-flooded plants exposed to simulated understory shade (S-NF). Simulated flooding was accomplished by placing each 8 L pot into a larger 10 L pot filled with water, and the water level was maintained every other day to a level of 4 cm above the soil. NF plants were manually irrigated every other day. Shaded plants were left within the shade house, while the plants exposed to full sun were placed outside the shade house. This design led to an unfortunate spatial segregation of shaded and unshaded plants. For this reason, the physical location of plants inside and outside the shade house was altered daily to minimize the potential for spatial variations in microclimate to interact with the light treatment.

Treatments were initiated on 246th day of the year (September 3, hereafter referred to as T_1) and continued until 307th day of the year (November 3, hereafter referred to as T_{61}), corresponding to a 61-d experimental period. Climatologically, this was during the dry- to wet-season transition, when mean daily temperature was typically 28°C and relative humidity 60%. However, maximum daytime temperatures can exceed 38°C and relative humidity can be only 40% (Biudes 2008).

Light-saturated rates of leaf gas exchange: Light-saturated leaf gas exchange was measured using a portable photosynthesis system (*LI-6400*, *LI-COR Bioscience*, Lincoln, NE, USA). Between T_1 and T_{61}, light-saturated P_N and g_s were measured 19 times (approximately every 3 days) on 7 plants per treatment group. For each measurement, a single, fully expanded leaf per plant, typically the fourth or fifth leaf from the apex, which was free of chlorosis and/or disease symptoms, was exposed to 1,000 μmol(photon) m^{-2} s^{-1} PPFD, a chamber temperature of 28°C, a CO_2 concentration of 400 μmol(CO_2) mol^{-1}, and a relative humidity of 60%. The PPFD level of 1,000 μmol(photon) m^{-2} s^{-1} was chosen to allow comparisons of light-saturated leaf gas exchange between shaded and unshaded plants, while the humidity and temperature conditions were consistent with ambient humidity and temperature conditions, respectively.

P_N/C_i and P_N/PPFD response curves: In addition to measuring rates of light-saturated leaf gas exchange, photosynthetic response curves to variations in intercellular CO_2 concentration (P_N/C_i) and photosynthetic photon flux density (P_N/PPFD) were performed twice over the experimental period ($n = 3$ plants per a treatment combination) to determine how experimental flooding and shading affected the CO_2 fixation and radiation use dynamics of *V. divergens* saplings. P_N/C_i and P_N/PPFD response curves were made on T_1 and T_{61}. A total of 24 P_N/PPFD and P_N/C_i response curves were made, and for each response curve, measurements were made on a single, fully expanded leaf per plant, typically the fourth or fifth leaf from the apex, which was free of chlorosis and/or disease symptoms as described above.

For each P_N/C_i curve, the leaf was placed in the *LI-6400* chamber and exposed to a CO_2 concentration of 400 μmol(CO_2) mol^{-1}, PPFD of 1,000 μmol(photon) m^{-2} s^{-1}, a chamber temperature of 28°C, and a relative humidity of 60%. After 15 min of acclimation, the CO_2 concentration was adjusted in the following order: 400, 300, 250, 200, 150, 100, 50, 400, 400, 450, 500, 600, 700, 800, 1,000; and 1,200 μmol(CO_2) mol^{-1}. For each P_N/PPFD curve, the same leaf used for the P_N/C_i curve was acclimated to a CO_2 concentration of 400 μmol(CO_2) mol^{-1} and maintained at a chamber temperature of 28ºC and a relative humidity of 60%. After 15 min of acclimation, PPFD varied between 0 and 2,000 μmol (photon) m^{-2} s^{-1} in decreasing order 2,000; 1,500; 1,250; 1,000; 800, 500, 250, 100, 50, 25, and 0 μmol(photon) m^{-2} s^{-1}. CO_2 assimilation was recorded after each change in CO_2 concentration or PPFD when the coefficient of variation for P_N was $\leq 0.3\%$.

Data analysis: A repeated-measures analysis of variance (*ANOVA*) was used to determine if variations in light-saturated P_N and g_s were significantly ($p<0.05$) affected by time, flooding, and shading. P_N/C_i curve parameters were calculated using the Farquhar *et al.* (1980) photosynthesis model and corrected to 25°C using coefficients previously reported by Harley *et al.* (1992) and Sharkey *et al.* (2007). The main equations of this photosynthesis model are:

$$P_N = min\left\{P_c, P_j, P_p\right\} - R_D \tag{1}$$

$$P_c = V_{cmax}\,\frac{C_i - \Gamma^*}{C_i + K_c\,(1 + O/K_o)} \tag{2}$$

$$P_j = J_{max}\,\frac{C_i - \Gamma^*}{4\,C_i - 8\,\Gamma^*} \tag{3}$$

$$P_p = 3\ \mathrm{TPU} \tag{4}$$

where O is the molar concentration of O_2 at Rubisco [μmol(O_2) mol^{-1}]; Γ^* is the CO_2 compensation point in the absence of mitochondrial respiration [μmol(CO_2) mol^{-1}]; min{} denotes "the minimum of"; P_c, P_j, and P_p are the rates of Rubisco-limited CO_2 fixation, ribulose-1,5-bisphosphate (RuBP) regeneration, and triose-phosphate utilization (TPU), respectively [μmol(CO_2) m^{-2} s^{-1}]; V_{cmax} is the maximum rate of Rubisco activity [μmol(CO_2) m^{-2} s^{-1}]; K_c and K_o are the Michaelis-Menten coefficients of Rubisco activity for CO_2 and O_2, respectively [μmol mol^{-1}]; and J_{max} is the light-saturated rate of electron transport [μmol(CO_2) m^{-2} s^{-1}].

The P_N/PPFD response was calculated using the rectangular-hyperbolic equation by Long and Hallgren (1993):

$$P_N = \left[\frac{\Phi\ \mathrm{PPFD} + P_{max} - \sqrt{(\Phi\ \mathrm{PPFD} + P_{max})^2 - 4\ \Phi\ P_{max}\ \Theta}}{2\,\Theta}\right] - R_D$$

where Φ is the apparent quantum yield [μmol(CO_2) μmol(PPFD)$^{-1}$]; PPFD is the photosynthetic photon flux density [μmol(photon) m^{-2} s^{-1}]; P_{max} is the photosynthetic rate at light saturation [μmol(CO_2) m^{-2} s^{-1}]; Θ is the curve convexity (dimensionless), and R_D is the dark respiration rate [μmol(CO_2) m^{-2} s^{-1}]. A 2-way *ANOVA* was used to assess whether variations in the P_N/C_i or P_N/PPFD parameters were significantly affected by flooding or shading.

Results

Light-saturated P_N and g_s: Flooding significantly reduced the P_N ($F_{1,24}$ = 240.40, $p<0.001$) and g_s measured at 1,000 µmol(photon) m^{-2} s^{-1} PPFD ($F_{1,24}$ = 73.79, $p<0.001$) over the 61-d experiment (Fig. 1). At T_1, P_N ranged between 7.9–12.7 µmol(CO_2) m^{-2} s^{-1} across all flooding and light treatments, but at T_{61}, the P_N of plants exposed to flooding was less than half of the P_N of plants exposed to normal irrigation, resulting in a significant flooding *vs.* time interaction ($F_{18,367}$ = 3.67, $p<0.001$; Fig. 1*A*). Similar results were obtained for g_s, and plants exposed to flooding had g_s, which was 2–4 times lower than plants exposed to normal irrigation ($F_{1,24}$ = 73.79, $p<0.001$; Fig. 1*B*).

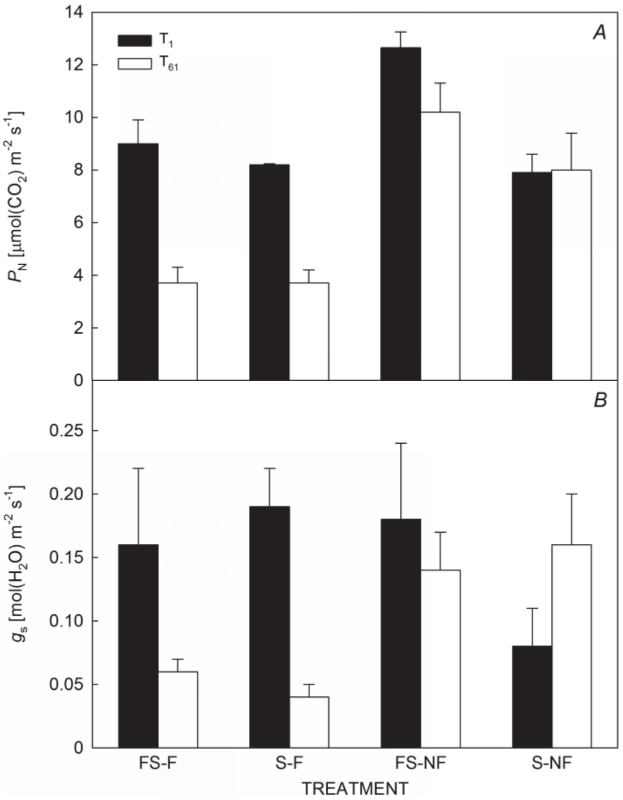


Fig. 1. (*A*) Net photosynthetic rate (P_N) and (*B*) stomatal conductance (g_s) of *Vochysia divergens* saplings exposed to shading (S) or full sunlight (FS), and flooding (F) or normal irrigation (NF) during the first (T_1; *black bars*) and last (T_{61}; *white bars*) days of the experiment. Mean ± SE (n = 7 plants per treatment combination).

P_N/C_i and P_N/PPFD response curves: There were no significant differences between the P_N/C_i curves at T_1 (Table 1), but at T_{61}, flooding caused a significant reduction in V_{cmax} and J_{max} (Fig. 2, Table 1). Leaves exposed to flooding conditions had 2-fold lower rates of V_{cmax} and J_{max} than leaves exposed to nonflooding conditions (Table 1). In fact, flooded plants at T_{61} had such a low P_N at high C_i (Fig. 2*B*) that it was impossible to calculate a CO_2 saturated rate of assimilation (P_{sat}) or the limitation of P_N due to TPU using the Farquhar *et al.* (1980) model (Fig. 2*B*, Table 1).

In contrast, P_N/PPFD curves for the water and light treatments differed significantly at T_1 and T_{61}, although patterns varied over time (Fig. 3, Table 2). At T_1, P_{max} and LCP were significantly higher in plants exposed to full sunlight (Fig. 3*A*, Table 2). Similarly, R_D at T_1 was significantly lower in flooded plants, and there was a significant light *vs.* water (L *vs.* W) interaction, because S-F plants had the lowest rate of R_D of all treatment combinations (Fig. 3*A*, Table 2).

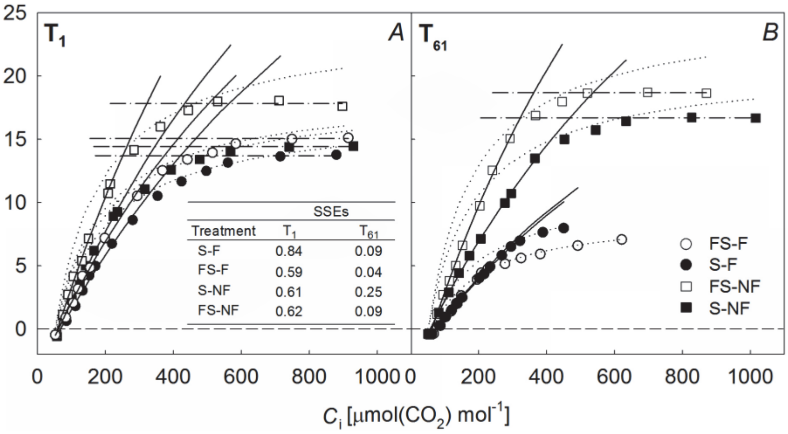
At T_{61}, the initial differences in P_{max} between flooded and normally irrigated plants increased, and the plants exposed to flooding had on average 3–4 times lower P_{max} than the plants exposed to normal irrigation (Fig. 3*B*, Table 2). Φ declined significantly in response to shading and flooding (Fig. 3*B*, Table 2). In contrast, the significantly lower R_D observed for flooded plants at T_1 was not observed at T_{61}, and instead R_D was significantly lower in the plants exposed to shading (Fig. 3*B*, Table 2). The effects of shading on the LCP at T_1 became larger at T_{61}, and the full-sun plants had a 2-fold higher LCP [21.41 ± 0.77 µmol(photon) m^{-2} s^{-1}] than the plants growing under shade [14.85 ± 1.83 µmol(photon) m^{-2} s^{-1}] (Fig. 3*B*, Table 2). There was also no significant L *vs.* W interaction on LCP at T_{61} (Table 2), indicating the initial influence of flooding on the shading-induced decline in the LCP was negligible by the end of the experiment.

Discussion

Vochysia divergens is considered to be a light-demanding pioneer species that is adapted to flooding (Pott and Pott 1994, Lorenzi 1998); however, our results indicated that flooding affected physiological performance more than shading. In particular, the decrease in flooded plants was probably due to a concomitant decline in g_s (Fig. 1). Flooding typically leads to a reduction of water absorption by roots and, consequently, to a decrease in g_s (Kozlowski 1984, Parolin 2001, Maurenza *et al.* 2009). Strong stomatal control can be considered a survival mechanism for plants in flooded conditions, because water loss by transpiration cannot be counterbalanced by absorption. As the soil becomes hypoxic or anoxic in response to flooding, roots may alter their metabolism from aerobic respiration to fermentation, resulting in a decline in proton translocation and a reduction in ATP (Kozlowski 1984). There may be also a buildup of lactic acid (Crawford 1992, de Oliveira and Joly 2010) and, as

Table 1. Mean (± 95% confidence interval; $n = 3$ plants per treatment combination) saturated rate of net photosynthesis (P_{sat}), the maximum rate of carboxylation (V_{cmax}), the maximum rate of electron transport (J_{max}), triose-phosphate utilization (TPU), and the dark respiration rate (R_D) derived from P_N/C_i response curves measured at the beginning (T_1) and end (T_{61}) of a 61 day, fully-factorial field experiment, where *V. divergens* saplings were exposed to varying light (shaded *vs.* full-sun) and water (flooded *vs.* nonflooded) treatments. The results of a 2-way *ANOVA* (*F*-statistics with 1 effect and 5 error degrees of freedom), where light (L) and water (W) treatments were treated as fixed effects, are also shown. $^{**}p \leq 0.01$. Mean values in the same row with different letters are significantly different ($p < 0.05$).

Time	Parameters	Flooded		Nonflooded		*F*-statistics (1,5)		
		Shade	Full sun	Shade	Full sun	L	W	L *vs.* W
T_1	P_{sat} [μmol(CO$_2$) m^{-2} s^{-1}]	14.4 ± 4.1^A	15.3 ± 6.1^A	15.1 ± 0.1^A	17.9 ± 2.4^A	0.6	0.5	0.2
	V_{cmax} [μmol(CO$_2$) m^{-2} s^{-1}]	37.1 ± 8.0^A	31.0 ± 7.8^A	38.2 ± 0.5^A	48.4 ± 10.5^A	0.2	4.0	3.2
	J_{max} [μmol(CO$_2$) m^{-2} s^{-1}]	48.7 ± 12.1^A	41.7 ± 14.7^A	54.5 ± 1.8^A	66.4 ± 13.3^A	0.1	4.3	1.7
	TPU [μmol(CO$_2$) m^{-2} s^{-1}]	3.8 ± 1.0^A	4.0 ± 1.4^A	4.0 ± 0.1^A	4.7 ± 0.7^A	0.7	0.7	0.7
	R_D [μmol(CO$_2$) m^{-2} s^{-1}]	0.6 ± 0.1^A	0.6 ± 0.2^A	0.6 ± 0.1^A	0.7 ± 0.1^A	0.1	0.5	0.1
T_{61}	P_{sat} [μmol(CO$_2$) m^{-2} s^{-1}]	-	-	16.7 ± 5.7^A	18.7 ± 5.3^A	0.2	-	-
	V_{cmax} [μmol(CO$_2$) m^{-2} s^{-1}]	22.2 ± 4.7^A	15.5 ± 7.1^A	36.8 ± 15.2^{AB}	50.4 ± 3.3^B	0.5	25.2^{**}	4.2
	J_{max} [μmol(CO$_2$) m^{-2} s^{-1}]	30.8 ± 7.8^A	25.7 ± 5.2^{AB}	55.4 ± 18.6^{AC}	71.6 ± 11.0^C	0.7	28.3^{**}	2.6
	TPU [μmol(CO$_2$) m^{-2} s^{-1}]	-	-	4.3 ± 1.4^A	5.0 ± 1.0^A	0.5	-	-
	R_D [μmol(CO$_2$) m^{-2} s^{-1}]	0.6 ± 0.1^A	0.5 ± 0.1^A	0.4 ± 0.2^A	0.9 ± 0.5^A	2.7	0.2	4.5

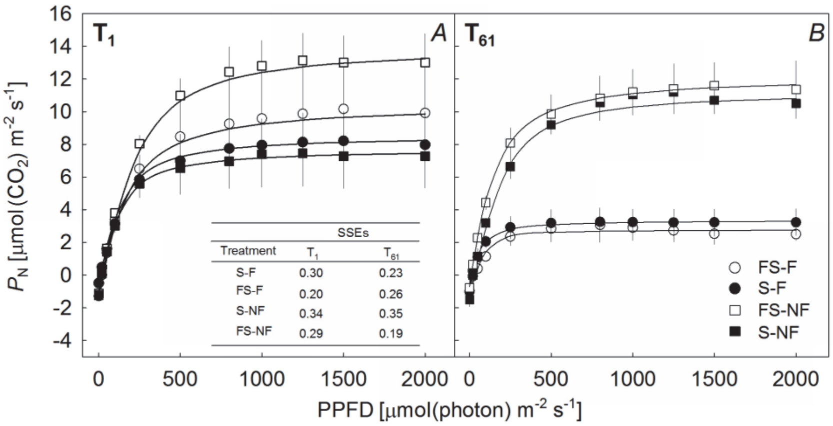


SSEs		
Treatment	T_1	T_{61}
S-F	0.84	0.09
FS-F	0.59	0.04
S-NF	0.61	0.25
FS-NF	0.62	0.09

Fig. 2. Net photosynthetic rate (P_N) *vs.* intercellular CO$_2$ concentration (C_i) curves for *Vochysia divergens* saplings exposed to shading (*closed symbols*), full sunlight (*open symbols*), flooding (*circles*), or normal irrigation (*squares*) measured at the beginning (T_1) and the end (T_{61}) of a 61-d experiment. *Solid lines* indicate the limitation imposed by the photosynthetic rate of Rubisco carboxylation (P_c), *dotted lines* indicate the limitation imposed by the photosynthetic electron transport (P_j), and the *dot-dashed lines* indicate the rate of photosynthesis limitation imposed by the use of triose phosphate (P_P) calculated using the Farquhar *et al.* (1980) photosynthesis model. The inserted table shows the sum squared error (SSEs) adjustments of all curves. Mean ($n = 3$ plants per treatment combination).

a result, cytoplasm acidification (Drew 1997), which leads to a reduction in the permeability and hydraulic conductivity of roots and an increased synthesis of ABA (Wilkinson and Davies 2002). A decline in water uptake, coupled with an increase in ABA, could be responsible for the decline in light-saturated g_s observed for *V. divergens* saplings exposed to experimental flooding (Kozlowski 1984, Maurenza *et al.* 2009).

The decline in P_N in flooded plants was coincident with a reduction in RuBP carboxylation capacity (V_{cmax}) and RuBP regeneration (expressed as the maximum rate of electron transport, J_{max}). A reduction in V_{cmax} is usually attributed to a decreased amount of Rubisco (Jacob *et al.* 1995, Nakano *et al.* 1997), and sometimes to its low activation state (Sage *et al.* 1989). The mechanism for J_{max} reduction, however, is less clear, because the RuBP regeneration capacity is determined by various biochemical processes in electron transport (von Caemmerer and Farquhar 1981) and the Calvin cycle (Sudo *et al.* 2003). P_N/PPFD curves indicated that flooding caused a significant reduction P_{max} and Φ. These reductions might be due to a reduction in Chl concentration as a result of waterlogging (Mielke and Schaffer 2010), because plants subjected to hypoxia or anoxia often experience an increase in the activities of oxidase and chlorophyllase that are responsible for Chl degradation (Sena Gomes and Kozlowski 1988, Zhang *et al.* 2000, Jacomino *et al.* 2003).



	SSEs	
Treatment	T_1	T_{61}
S-F	0.30	0.23
FS-F	0.20	0.26
S-NF	0.34	0.35
FS-NF	0.29	0.19

Fig. 3. Net photosynthetic rate (P_N) *vs.* photosynthetic photon flux density (PPFD) curves for *Vochysia divergens* saplings exposed to shading (*closed symbols*), full sunlight (*open symbols*), flooding (*circles*), or normal irrigation (*squares*) measured at the beginning (T_1) and the end (T_{61}) of a 61-d experiment. Lines were fit to these data using the rectangular-hyperbolic equation by Long and Hallgren (1993). The inserted table shows the sum squared error (SSEs) adjustments of all curves. Mean (*n* = 3 plants per treatment combination).

Table 2. Mean (± 95% confidence interval; *n* = 3 plants per treatment combination) maximum rate of net photosynthesis (P_{max}), apparent quantum yield (Φ), maximum rate of electron transport (J_{max}), dark respiration rate (R_D), and the light compensation point (LCP) derived from P_N/PPFD curves measured at the beginning (T_1) and end (T_{61}) of a 61 day, fully-factorial field experiment, where *V. divergens* saplings were exposed to varying light (shaded *vs.* full-sun) and water (flooded *vs.* nonflooded) treatments. The results of a 2-way *ANOVA* (*F*-statistics with 1 effect and 5 error degrees of freedom), where light (L) and water (W) treatments were treated as fixed effects, are also shown. $^{*}p \leq 0.05$, $^{**}p \leq 0.01$. Mean values in the same row with different letters are significantly different ($p < 0.05$).

Time	Parameters	Flooded		Non-flooded		*F*-statistics (1,5)		
		Shade	Full sun	Shade	Full sun	L	W	L *vs.* W
T_1	P_{max} [μmol(CO$_2$) m^{-2} s^{-1}]	9.1 ± 2.7^{A}	12.0 ± 3.0^{AB}	9.0 ± 2.1^{A}	15.1 ± 2.5^{B}	9.9^{**}	1.1	1.2
	Φ [μmol(CO$_2$) μmol(PPFD)$^{-1}$]	0.04 ± 0.1^{A}	0.06 ± 0.01^{A}	0.06 ± 0.01^{A}	0.05 ± 0.01^{A}	0.6	0.6	1.8
	R_D [μmol(CO$_2$) m^{-2} s^{-1}]	0.3 ± 0.1^{A}	1.3 ± 0.3^{B}	1.4 ± 0.1^{B}	1.1 ± 0.4^{B}	5.6	11.1^{*}	20.6^{**}
	LCP [μmol(photon) m^{-2} s^{-1}]	10.1 ± 4.2^{A}	22.7 ± 1.5^{B}	22.0 ± 0.5^{B}	20.1 ± 5.7^{B}	6.5^{*}	4.9	11.8^{*}
T_{61}	P_{max} [μmol(CO$_2$) m^{-2} s^{-1}]	4.3 ± 1.6^{A}	3.8 ± 0.9^{A}	13.0 ± 1.6^{B}	12.9 ± 1.4^{B}	0.2	99.9^{**}	0.1
	Φ [μmol(CO$_2$) μmol(PPFD)$^{-1}$]	0.05 ± 0.01^{A}	0.03 ± 0.01^{B}	0.07 ± 0.01^{C}	0.05 ± 0.01^{A}	10.2^{*}	8.8^{*}	0.3
	R_D [μmol(CO$_2$) m^{-2} s^{-1}]	1.0 ± 0.8^{A}	1.0 ± 0.2^{A}	0.8 ± 0.3^{A}	1.5 ± 0.4^{AB}	9.0^{*}	3.4	1.0
	LCP [μmol(photon) m^{-2} s^{-1}]	19.7 ± 10.1^{A}	34.5 ± 3.7^{B}	11.4 ± 4.4^{A}	31.5 ± 11.0^{AB}	12.0^{**}	1.3	0.3

In contrast, the photosynthetic capacity of *V. divergens* plants appeared to be affected minimally by light availability; however, an increase in Φ and a decrease in R_D and LCP were observed for the plants exposed to shade regardless of water regime. Reductions in the LCP for leaves acclimated to shade were likely related with the reduction in R_D. Plants acclimated to shade have typically lower concentrations of Chl and other proteins and enzymes related to photosynthesis and ion assimilation, which significantly reduces leaf respiratory cost (Penning de Vries 1975, Griffen *et al*. 2004).

In conclusion, our results suggest that shading and flooding significantly affected multiple aspects of the PPFD and CO_2 response of *V. divergens* leaf gas exchange, but flooding was stronger at limiting the photosynthetic capacity of this species. These results were surprising, given *V. divergens* was thought to be a light-demanding, flood-tolerant plant that has been successful at invading seasonally flooded grasslands of the Pantanal. However, the ecological success of *V. divergens* might not be related to its physiological potential during flooding but during the intervening times, when flooding recedes and there is adequate soil moisture. P_N of normally irrigated plants was substantially higher than that reported for other tree species of the Brazilian cerrado (Vourlitis and da Rocha 2010), and the dry season P_N of *V. divergens* was typically higher than that reported for other trees of the Pantanal (Dalmagro, UFMT, unpublished data), indicating a high potential for C gain under nonflooded conditions. While the water content of surface (0–10 cm) soil at the study site is typically low during the dry season (Vourlitis *et al.* 2011), there is an evidence that *V. divergens* is deeply rooted and it has access to deep water sources during the dry season due to the consistently high rates of evapotranspiration measured in cambará monocultures during the dry season (Sanches *et al*. 2011) and the ability of cambará to redistribute reached nutrients to the soil surface (Haase 1999, Vourlitis *et al*. 2011). The access to deep water reserves likely allows substantial C gain to continue during the 4–5 month dry season, when there is often no measurable rainfall. High capacity for C gain during the driest part of the year might be a key reason for the success of flood-adapted species, such as *V. divergens*, to invade and persist in the Pantanal.

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