The physiological light response of two tree species across a hydrologic gradient in Brazilian savanna (Cerrado)

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Abstract

Tropical savanna ecosystems are extremely diverse and important for global carbon storage. In the state of Mato Grosso, tropical savanna (locally known as the Cerrado), turns from well-drained, upland areas into seasonally flooded areas within the Pantanal; however, the Cerrado and the Pantanal share many common tree species, such as *Vochysia divergens*, a flood-adapted tree native to the Amazon Basin, and *Curatella americana*, a tree, adapted native to the well-drained the Cerrado. We measured the photosynthetic light response of these species in the the Cerrado and the Pantanal over a 1-year period to determine how these species physiologically adjust to these hydrologically distinct habitats. We hypothesized that neither species would experience a significant decline in maximum, light-saturated photosynthetic rate (P_{max}) in their naturalized habitat. Physiological performance of each species was generally higher in the habitat that they were adapted to; however, our data indicated that both species have broad tolerance for seasonal variations in hydrology, allowing them to tolerate seasonal drought during the dry season in the Cerrado, and seasonal flooding during the wet season in the Pantanal. In *V. divergens*, flexible water-use efficiency, higher specific leaf area (SLA), and a greater ability to adjust mass-based P_{max} ($P_{max,m}$) to variations in leaf N and P concentration appeared to be key traits for withstanding prolonged drought in the Cerrado. In *C. americana*, increases in SLA and higher nutrient-use efficiency appeared to be important in maintaining high rates of $P_{max,m}$ in the seasonally flooded Pantanal. Flexibility in physiology and resource-use efficiency may allow these species to survive and persist in habitats with broadly differing hydrology.

Additional key words: ecophysiology, *Curatella americana*, leaf gas exchange, neotropical wetlands, Pantanal, *Vochysia divergens*.

Introduction

Brazilian savanna, locally known as the Cerrado, covers approximately 20–25% of the total land cover of Brazil and is the second largest vegetation type following Amazonian forest (Furley and Ratter 1988). The Cerrado is composed of distinctive physiognomies that vary as a function of height, cover, and/or density of trees

(Goodland 1971, Eiten 1972, Furley and Ratter 1988). In the southern portion of Mato Grosso, the Cerrado converts to the Pantanal, which is the largest wetland in the world with an area of 150,000 km^2 (Haase 1999). Most of the Pantanal is subjected to seasonal flooding, which results from local precipitation patterns, run off to large river systems, and impeded drainage of rain water (da Cunha and Junk 2001, Arieira and da Cunha 2006). While the Pantanal is considered a seasonally flooded form of the Cerrado by some authors, others argue that the Cerrado is a well-drained, upland vegetation, distinct from the Panatanal (Eiten 1972, Haase 1999). However, the upland Cerrado and the Pantanal share many common tree species (Haase 1999) and the Cerrado-Pantanal transition is very dynamic and determined by soil moisture and the duration of flooding (Santos *et al.* 2006).

Both ecosystems represent potentially stressful conditions for leaf gas exchange and physiology. In the Cerrado, the combination of low rainfall and high evaporative demand during the dry season, combined with nutrient-poor and acidic soil, leads to drought stress and nutrient limitation (Franco *et al.* 2005, Bucci *et al.* 2008, Vourlitis and da Rocha 2011). In the Pantanal, persistent flooding during the rainy season can cause declines in physiological performance due to the development of soil anoxia or hypoxia (Parolin *et al.* 2010, Dalmolin *et al.* 2012, Dalmagro *et al.* 2013). Even so, some species have demonstrated the ability to persist in both habitats. For example, *V. divergens* Pohl (commonly known as Cambará) is a flood-adapted pioneer tree species native to the Amazon Basin (Pott and Pott 1994) that is common in both the Pantanal and the Cerrado (Zeilhofer and Schessl 1999, da Cunha and Junk 2001, Junk and da Cunha 2005, Arieira and da Cunha 2006, Junk *et al.* 2006). *C. americana* L. (commonly known as Lixeira) is native to the upland Cerrado (Medina and Francisco 1994, Lorenzi 2002), where flooding is rare (Eiten 1972, Furley and Ratter 1988), but it has been recently observed to be invading large areas in the Pantanal (Santos *et al.* 2006). The mechanism of this invasion is poorly understood; however, Lixeira apparently expands into the Pantanal from the surrounding the Cerrado during times of low water and becomes established before flooding ensues during the wet season (Santos *et al.* 2006).

Generally, species able to invade and persist in novel habitats often share characteristics associated with the maximization of carbon (C) gain, such as high leaf area production, maximum photosynthetic rate, and specific leaf area (Funk 2008). Furthermore, high phenotypic and physiological plasticity are key features that allow species to expand their distribution into areas with substantially different resource availability. Plants that invade seasonally flooded areas must be able to tolerate long periods of hypoxia and/or anoxia (Armstrong *et al.* 1994, Maurenza *et al.* 2009) and high concentrations of toxic products (McKevlin and McKee 1993, Jackson and Colmer 2005) to be successful (Fernández 2006). In contrast, species adapted to humid regions, which invade dry areas, must be able to tolerate periodic drought and/or have root systems that can exploit deep water reserves (Hall *et al.* 1996, Lite and Stromberg 2005).

Several studies have focused on growth, population, and community dynamics of *V. divergens*, and to a much lesser extent, *C. americana*, in their naturalized environments (Junk and da Cunha 2005, Ariera and Cunha 2006, Junk *et al.* 2006, da Cunha *et al.* 2007, Dalmolin *et al.* 2012, Dalmagro *et al.* 2013), however, little is known about the ecophysiological aspects of the *V. divergens* and *C. americana* invasion. Understanding the effects of spatial and environmental variation on physiological performance can help elucidate possible mechanisms for survival in potentially unfavorable conditions (McDowell 2002, Sharkey *et al.* 2007, Wright *et al.* 2001, Domingues *et al.* 2007). Thus, the aim of this study was to evaluate how rates of leaf gas exchange of *V. divergens* and *C. americana* are influenced by seasonality in the upland (well-drained) Cerrado and the seasonally flooded Pantanal. Specifically, rates of leaf gas exchange of *V. divergens* and *C. americana* were measured as a function of photosynthetic photon flux density (PPFD) to see how the physiological light response varied in these hydrologically distinct habitats. Photosynthetic light curves were utilized because light is often limiting for seedlings and saplings invading in the Cerrado and the Pantanal due to shading by canopy trees and/or bunch grasses (da Cunha and Junk 2004, Dalmolin *et al.* 2012). We hypothesized that neither species experiences a significant decline in leaf physiological performance, such as P_{max}, in its naturalized habitat because of its ability to expand outside of its native range.

Materials and methods

Site and species descriptions: The study was conducted between May 2009 and April 2010 in the upland Cerrado and the Pantanal in Mato Grosso, Brazil (Table 1). The Pantanal site is located approximately 160 km SSW from Cuiabá and 60 km SE from Poconé, Mato Grosso (16º39'50"S, 56º47'50"W) at an elevation of 116 m a. s. l. The study site is located within the Reserva Particular do Patrimônio Natural (RPPN) of the Serviço Social do Comércio (SESC) – Pantanal, which is a federally protected nature reserve. Vegetation is characterized as a mixed forest-grassland, with *V. divergens* and *C. americana* as the common tree species, and a herbaceous understory composed of grass [*Gymnopogon spicatus* (Spreng.) Kuntze] and herbaceous perennials (*Mimosa pellita* H. *et* B.). The soil texture was primarily a sandy–clay loam (Vourlitis *et al.* 2011). Research in the Cerrado

Table 1. Site characteristics for the Pantanal (seasonally flooded forest) and the Cerrado (nonflooded forest). Sources for data: †Vourlitis 2011, ‡Zeilhofer 2006, §Antunes Jr. 2011.

Parameter	Unit	Ecosystem Cerrado	Pantanal
Dominant plant species		*Curatella americana,* *Vochysia divergens,* *Qualea parvilhora,* *Qualea grandiflora*	*Vochysia divergens,* *Curatella americana,* *Gymnopogon spicatus,* *Mimosa pellita*
pH		5.7	4.7[†]
Leaf area index	[$m^2 m^{-2}$]	3.4	3.5[†]
Soil organic matter	[$g dm^{-3}$]	18.7	10.3[†]
Total soil nitrogen	[$g kg^{-1}$]	0.8	-
Total soil phosphorus	[$mg dm^{-3}$]	3.5	2.8[†]
Soil type (parent material)		Litólicos distróficos[§]	Gleyic Solonetz[‡]
Annual rainfall	[mm]	1,491	1,608
Mean annual temperature	[°C]	26.1	26.7
Mean annual relative humidity	[%]	72.4	76.2
Mean annual vapor pressure deficit	[kPa]	1.1	0.9

was conducted in the Cuiaba Basin at the Fazenda Miranda, located 15 km SSE of Cuiaba, Mato Grosso, Brazil (15º43'51"S, 56º04'17"W). The vegetation is a mix of grasses and trees; typical tree species include *C. americana, Qualea grandiflora* Mart., *Qualea parvifolia* Mart., *Caryocar brasiliense* Cambess., *Terminalia argentea* Mart. & Zucc, and *V. divergens*. The research area is on flat terrain at an elevation of 181 m above sea level. The soil is a dystrophic red–yellow latosol locally known as a Solo Concrecionário Distrófico (RADAMBRASIL 1982) with a rocky, sandy–clay loam texture (Vourlitis *et al.* 2013).

Both sites experience an average annual rainfall of 1,420 mm and temperature of 26.5ºC, and rainfall is strongly seasonal with a dry season extending from May to September (Vourlitis and da Rocha 2011). In the Pantanal, the flat topography causes extensive flooding during the wet season (da Cunha and Junk 2001), and average flood height is typically 1–2 m in depth during the peak of the wet season (da Cunha and Junk 2004).

C. americana is a tree species native to the Brazilian Cerrado and reaches 6–10 m in height (Medina and Francisco 1994, Lorenzi 2002). It has a semideciduous phenology with leathery leaves, which have a lifespan of about 10 months (Dalmolin *et al.* 2012). *V. divergens* is an evergreen tree native to the Amazon Basin and can reach a height of 25–28 m (Pott and Pott 1994). Leaves are glossy and dark green, with a life span of 8–9 months (Dalmolin *et al.* 2012) and they are produced regularly throughout the year, but with a break in the flooding period (*ca*. December–March).

Climatology: Both sites have micrometeorological towers for measuring temporal variations in radiation, temperature, and humidity. At Fazenda Miranda, meteorological measurements were made on a 35 m tall tower located at the main study site, while in the Pantanal, meteorological measurements were made on a 40 m tall tower located within 2 km of the study site. At both sites, net radiation (R_N) was measured above the canopy using a net radiometer (*NR–LITE, Kipp & Zonen*, Delft, The Netherlands). Air temperature (T_{air}) and vapor pressure were measured at the top of each tower using a relative humidity sensor (*HMP–35, Vaisala, Inc.*, Helsinki, Finland), and the atmospheric vapor pressure deficit (VPD) was calculated as the difference between saturation and actual vapor pressure. Precipitation was measured using a tipping–bucket rainfall gauge (*TE525MM, Texas Electronics, Inc.*, Dallas, TX, USA). Micrometeorological sensor output was measured every 30–60 s using a solid-state datalogger (*CR1000* or *CR10X*, Campbell *Scientific, Inc.,* Logan, UT, USA) and data were averaged over 15–30 min intervals.

Leaf gas exchange: We randomly selected five plants of *C. americana* and *V. divergens* from each habitat for repeated measures of the photosynthetic light response. Photosynthetic light response curves were generated using a portable photosynthesis system (*LI-6400, LI-COR Bioscience*, Lincoln, NE, USA). Measurements were made monthly during one year, from May 2009 to April 2010, except for August and November 2009 due to instrumental problems. Leaves were placed in the *LI-6400* chamber, which was adjusted to provide 400 µmol(CO_2) mol^{-1}, 28ºC block temperature, and a relative humidity of 60% in order to minimize the heterogeneity of the stomata. After 15 min of acclimation to these conditions, *LI-6400* was adjusted to vary the active photosynthetic photon flux density (PPFD) in the following order: 2,000; 1,500; 1,250; 1,000; 800, 500, 250, 100, 50, 25, 0 µmol(quantum) $m^{-2} s^{-1}$. Area-based net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were calculated using the standard *LI-6400* software.

Leaf physical and chemical determinations: After each light-response measurement, leaves were removed and their fresh leaf area was measured with a portable leaf area meter (*CI-202, CID Inc.*, Camas, WA, USA). Leaves were then dried at 70ºC until reaching constant mass, and weighed by an analytical balance (*AG 200, GEHAKA*, São Paulo, SP, Brazil). Specific leaf area (SLA) was calculated by dividing the one-sided fresh leaf area by the leaf dry mass (DM). Dried material was then ground and analyzed for N and P concentration. Leaf N concentration was determined using micro-Kjedahl digestion and distillation method (Golterman *et al.* 1978), and P concentration was determined by colorimetric analysis using vitamin C method (Braga and DeFelipo 1974).

Data analysis and modeling: Area-based photosynthetic data were fitted to a model that estimated net CO_2 assimilation (P_N) as a function of PPFD:

$$P_N = \frac{\Phi\,\text{PPFD} + P_{max} - [(\Phi\,\text{PPFD} + P_{max})^2 - 4\,\Phi\,\theta\,\text{PPFD}\,P_{max}]^{0.5}}{2\,\theta} - R_D$$

(1)

where Φ – the maximum quantum yield [μmol(CO_2) μmol(PPFD)$^{-1}$], P_{max} – the maximum area-based rate of light-saturated P_N [μmol(CO_2) m^{-2} s^{-1}], and θ – the dimensionless convexity of the curve (Prioul and Chartier 1977). Nonlinear least squares regression was used to estimate the model coefficients (θ, Φ, and P_{max}). Maximal

Results

Climatology during the measurement period: Micro-meteorological variables varied seasonally but there were no major differences between the ecosystems during the May 2009–April 2010 study period (Fig. 1). Monthly average T_{air} increased from a minimum of 22–23ºC in June to 27.5–28.5ºC in October and remained above 26ºC thereafter (Fig. 1*A*). VPD increased from about 0.8 kPa at the end of the rainy season (May–June) to a peak of 1.7 kPa in August in the Cerrado and 1.35 kPa in September in the Pantanal (Fig. 1*B*). The seasonal pattern of R_N was similar to that observed for air temperature, and it was low during the dry season and high during the wet season despite more frequent cloud cover (Fig. 1*C*). In the wet season, R_N in the Cerrado showed a decrease during December, but over the annual cycle, average R_N was the same for the Cerrado (10.39 ± 0.20 MJ m^{-2} s^{-1}) and the Pantanal (10.38 ± 0.14 MJ m^{-2} s^{-1}) (Fig. 1*C*). Total rainfall was approximately 1,590 mm in the Pantanal and 1,585 mm in the Cerrado during the measurement period; it was about 170 mm higher than the long-term (30 year) mean for this region (Vourlitis and da Rocha 2011). In general, both sites experienced a dry season (precipitation < 100 mm) in May–September 2009 in the Cerrado and in May–October 2009 in the Pantanal and again in April 2010 at both sites (Fig. 1*D*). Water level was above the ground surface in the Pantanal

stomatal conductance (g_{smax}) and C_i were calculated using the portable photosynthesis system software, while area-based dark respiration (R_D) was calculated when PPFD = 0 μmol(quantum) m^{-2} s^{-1}. Mass-based maximum photosynthetic rate ($P_{max,m}$) and dark respiration (R_{Dmass}) rates were calculated by multiplying area-based rates by SLA. Using Eq. 1, the light-compensation point (LCP) was calculated as the value of PPFD where $P_N = 0$ (Prioul and Chartier 1977). The intrinsic water-use efficiency (WUE$_i$) was calculated as the ratio of area-based P_N and g_s, while N (NUE)- and P (PUE)-use efficiency were calculated as the ratio of area-based P_N and the area-based N and P concentration, respectively.

Multivariate analysis of variance (*MANOVA*) was used to determine whether there were differences in Φ, P_{max}, R_D, LCP, g_{smax}, C_i, WUE$_i$, NUE, and PUE per unit area as a function of ecosystem (Pantanal *vs.* Cerrado) and time (T). *MANOVA* was used because many of these physiological variables are highly correlated. In the event of a significant E × T interaction, a one-way analysis of variance was used to determine whether significant differences were due to E and/or T.

Linear regression was used to analyze the dependence of mass-based $P_{max,m}$ and R_{Dmass} on specific leaf area SLA and leaf nutrient concentration (N$_{mass}$ and P$_{mass}$). Data were grouped in the case of no significant differences between ecosystems.

in May 2009 and again between late-December and April 2010, and seasonal flooding lagged behind the onset of the wet season by approximately 1–2 months (Fig. 1*D*). Peak flooding was approximately 150 cm, which is comparable to the average peak flood stage reported for the Pantanal (da Cunha and Junk 2004).

Variation in leaf morphology and N and P concentration: Leaf N concentration was significantly higher in the Cerrado for both species and there were significant variations in leaf N concentration over time in *C. americana* (Fig. 2*A,B*). Leaf N concentration of *C. americana* generally increased during the dry season in May–August and declined during the dry–wet season transition (Fig. 2*A,B*). In contrast, ecosystem differences in leaf P concentration were negligible for both species; however, seasonal variations were statistically significant and consistent in both species (Fig. 2*C,D*). Leaf P concentration increased during the dry season in August-September and reached a peak during the dry–wet season transition in September–October, but it declined thereafter and remained low throughout most of the wet season in December–February.

The leaf N/P ratio in *V. divergens* was significantly higher in the Cerrado (Fig. 2*E*) but no differences were observed in *C. americana* between the Cerrado and the
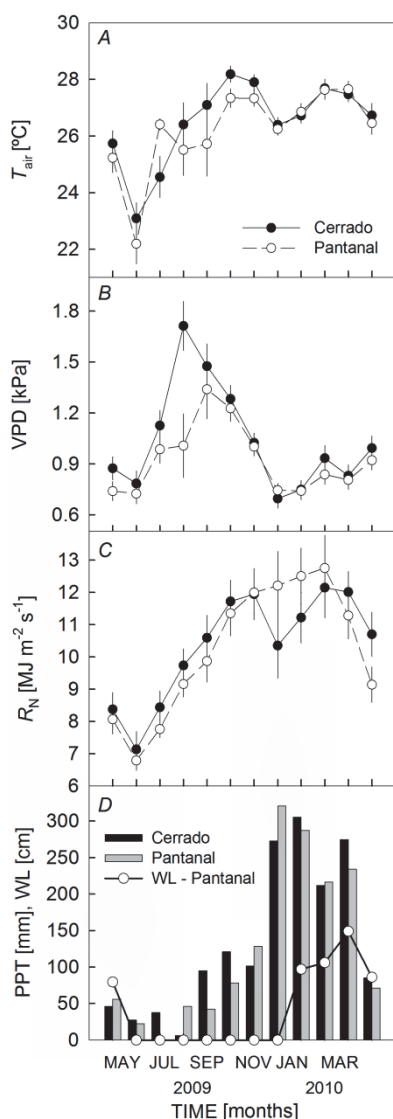
Fig. 1. Mean (± 1 SD) monthly (*A*) air temperature, (*B*) atmospheric vapor pressure deficit, (*C*) net radiation for the Pantanal (*open circles, dashed lines*) and the Cerrado (*solid circles, solid lines*), and (*D*) accumulated monthly rainfall for the Pantanal (*shaded bars*) and the Cerrado (*dark bars*) and water level above ground for the Pantanal (*open circles, solid lines*) during the May 2009–April 2010 study period. Data were obtained from a micrometeorological towers installed at each study site.

Pantanal (Fig. 2*F*). Both species exhibited significant variations in the N/P ratio over time, with the highest values in the dry season and a consistent decline into the wet season. *V. divergens* had an N/P ratio >15 in the Cerrado, which is considered the threshold for colimitation of N and P (Koerselman and Meuleman 1996), while *V. divergens* had an N/P ratio of 13–14 during the wet season in December–March in the Pantanal (Fig. 2*E*). Similarly, *C. americana* had a N/P ratio > 15, until January 2010, regardless of ecosystem, and values of 11–12 in February and March 2010 (Fig. 2*F*). Both

species exhibited rapid increases in the N/P ratio during the wet–dry season transition in April 2010 in both the Cerrado and the Pantanal.

Both species showed significant differences in SLA between ecosystems, but in opposite ways, with higher values in *V. divergens* in the Cerrado and higher values in *C. americana* in the Pantanal (Fig. 2*G,H*). Seasonal variations were also statistically significant for both species; however, temporal variations were more consistent in *C. americana* than *V. divergens*. *V. divergens* in the Pantanal exhibited peak SLA during the dry–wet season transition in October, while *V. divergens* in the Cerrado exhibited peaks in SLA during the dry season and at the end of the 2010 wet season in April (Fig. 2*G*). *C. americana* exhibited an increase in SLA during the dry season in July–September; however, peak SLA was observed in September in the Cerrado and October in the Pantanal (Fig. 2*H*). These variations in SLA between ecosystems and seasons resulted in a significant ecosystem *vs.* time interaction for both species (Fig. 2*G,H*).

Photosynthetic light-response (P_N/PPFD) curves: The P_N/PPFD response of both species was well described by the hyperbolic model (Eq. 1) and the coefficient of determination values (r^2) ranged from 0.86 to 0.93 in *V. divergens* (Fig. 3*A,C*) and from 0.83 to 0.98 in *C. americana* (Fig. 3*B,D*). In general, *V. divergens* showed no major differences in the shape of the P_N/PPFD curve over seasonal time scales (Fig. 3*A,C*), while *C. americana* had a greater seasonal variation between ecosystems in photosynthetic light saturation, mainly during the dry season (Fig. 3*B,D*). The light response of *C. americana* in the Cerrado was similar to that in the Pantanal during the peak of seasonal flooding, indicating that the P_N/PPFD response of *C. americana* was not significantly altered by flooding.

MANOVA results revealed a significant ecosystem (E) and time (T) effects on gas exchange and resource-use efficiency, and a significant E *vs.* T interaction (Table 2), which necessitated the use of one-way *ANOVA* to distinguish the factor (E and/or T) that was significantly altering each variable. *V. divergens* showed no significant differences in P_{max} between ecosystems and seasons (Fig. 4*A*), while *C. americana* exhibited significantly higher rates of P_{max} in the Cerrado (Fig. 4*B*).

When P_{max} was converted to $P_{max,m}$ using SLA, a different pattern emerged, where *V. divergens* had a significantly higher $P_{max,m}$ in the Cerrado, primarily because of a higher $P_{max,m}$ at the end of the dry season (Fig. 4*C*), while *C. americana* had similar rates of $P_{max,m}$ in the Cerrado and the Pantanal (Fig. 4*D*). Both species exhibited higher rates of $P_{max,m}$ at the end of the dry season and during the dry–wet season transition, while *V. divergens* also had a peak in $P_{max,m}$ at the end of the wet season in April 2010 (Fig. 4*C,D*).

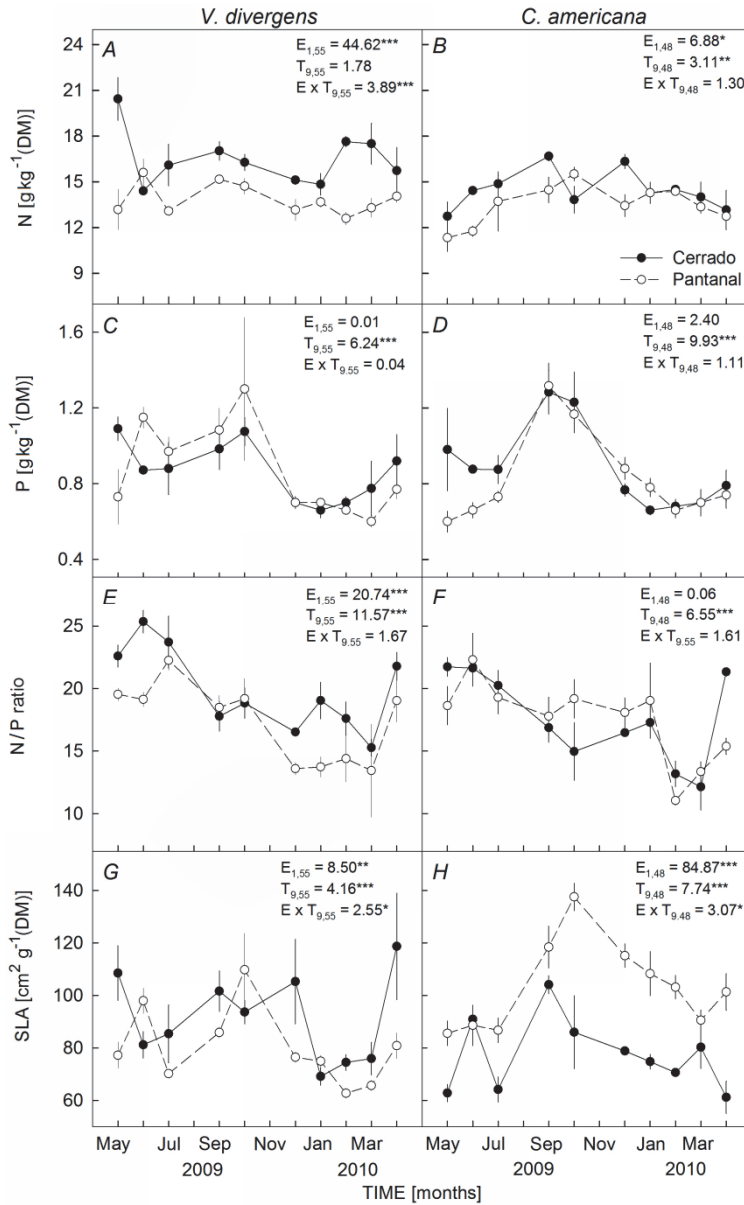g_{smax} varied significantly as a function of space and time in *V. divergens* (Fig. 4*E*), but not in *C. americana*

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Fig. 2. Mean (± 1 SE) mass-based (*A,B*) leaf nitrogen concentration, (*C,D*) leaf phosphorus concentration, (*E,F*) the leaf N/P ratio, and (*G,H*) specific leaf area in the Cerrado (*solid circles, solid lines*) and the Pantanal (*open circles, dotted lines*) in *Vochysia divergens* (*left panels*) and *Curatella americana* (*right panels*) during the May 2009– April 2010 study period. The results of a two-way *ANOVA* (*F*-statistics and degrees of freedom) for the main effects of ecosystem (E), time (T), and the E *vs.*T interaction are also shown. * – $p<0.05$; ** – $p<0.01$; *** – $p<0.001$.

(Fig. 4*F*). The spatial and temporal variations in g_{smax} in *V. divergens* were due to substantially higher [*ca.* 0.15 mol(H_2O) m^{-2} s^{-1}] rates during the June–July 2009 dry season, because during other times, g_{smax} was similar in *V. divergens* growing in the Pantanal and the Cerrado (Fig. 4*E*). As a result, C_i values were consistently higher in *V. divergens* in the Pantanal, especially during the dry season (Fig. 4*G*). The mean (± SE) ratio of the C_i to the chamber CO_2 concentration (C_i:C_a) in *V. divergens* was 0.60 ± 0.01 in the Cerrado and 0.68 ± 0.01 in the Pantanal, which is slightly below the optimum of 0.70 for C_3 plants (Wong *et al.* 1979). C_i was generally higher in *C. americana* than in *V. divergens*, and there was a significant temporal variation with higher C_i during the early–mid dry season (May–July) and a decline during the dry season (Fig. 4*H*). In the Pantanal, the lowest C_i was observed during the dry–wet season transition in

September, while in the Cerrado, C_i was generally the lowest during the wet season (Fig. 8*D*). On average, the C_i:C_a in *C. americana* was 0.76 in the Cerrado and 0.70 in the Pantanal, which is equal to, or slightly higher than the optimum for C_3 plants.

Φ of *V. divergens* did not vary significantly as a function of ecosystem or time (Fig. 5*A*); however, Φ in *C. americana* varied significantly between the Pantanal and Cerrado and in the course of time (Fig. 5*B*). On average, Φ in *C. americana* was higher in the Cerrado during the dry (June–July) and the wet (February–March) season, but for other times, spatial differences were negligible. Over time, Φ in *C. americana* increased during the dry–wet season transition and reached a peak in September, and declined into the wet season.

R_D was significantly higher in the Pantanal in *V. divergens* (Fig. 5*C*) and higher in the Cerrado in
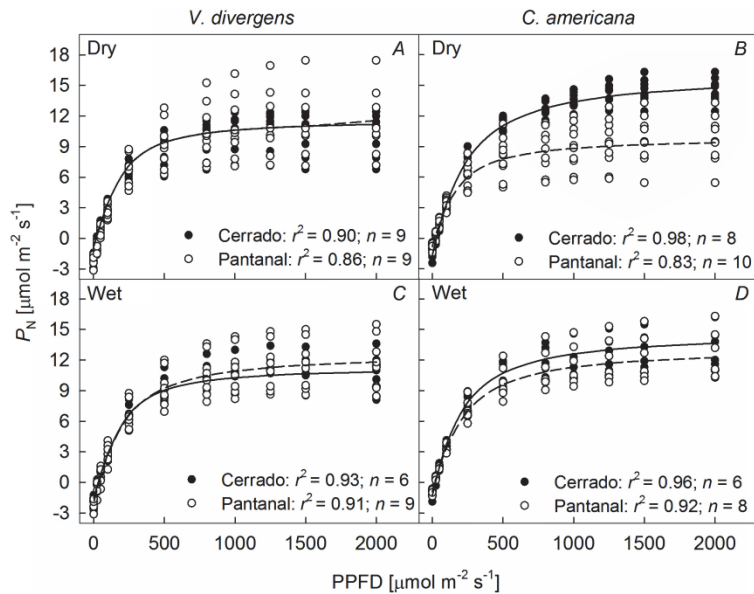
Fig. 3. Leaf net photosynthetic rate (P_N) *vs.* photosynthetic photon flux density (PPFD) in leaves of *Vochysia divergens* (*A,C*) and *Curatella americana* (*B,D*) during dry (*A,B*) and wet (*C,D*) periods in Pantanal (*open circles*) and in the Cerrado (*solid circles*) and the modeled photosynthetic light response curves calculated using Eq. 1 for the Pantanal (*dotted lines*) and the Cerrado (*solid lines*) during the May 2009–April 2010 study period. The coefficient of determination (r^2) of the model and the number of dates sampled per season (*n*) are also shown.

C. americana (Fig. 5*D*), especially during the June–August 2009 dry season. Temporal variations in R_D were not statistically significant in *V. divergens*, but in *C. americana*, R_D was significantly higher during the dry season (Fig. 5*D*), reached a peak during the dry–wet season transition in September, and exhibited the lowest value in the wet season.

The spatial and temporal patterns in the light compensation point (LCP; Fig. 5*E* and *F*) were nearly identical to that observed for R_D. In general, LCP was significantly higher in the Pantanal in *V. divergens* and higher in the Cerrado in *C. americana*, especially during the dry season. Temporal variations in LCP were not statistically significant in *V. divergens*, but in *C. americana*, LCP reached a peak during the dry–wet season transition in September and declined during the wet season (Fig. 5*F*).

Resource-use efficiency: Intrinsic water-use efficiency (WUE$_i$) of *V. divergens* was significantly higher in the Cerrado than the Pantanal (Fig. 6 *A*), but in *C. americana*, WUE$_i$ was not significantly different between ecosystems (Fig. 6*B*). Both species exhibited significant variations in WUE$_i$ over time, and in general, WUE$_i$ was the lowest in the dry season, increased during the dry–wet season transition, and declined during the wet season, except in *C. americana* in the Cerrado, which had the highest WUE$_i$ at end of the wet season in March.

PUE of *V. divergens* did not vary significantly between ecosystems or over time (Fig. 6*C*); however, PUE of *C. americana* was consistently higher in the Pantanal and varied significantly over time (Fig. 6*D*). PUE of *C. americana* increased substantially during the dry–wet season transition in September–October and reached a peak during the wet season in February. PUE declined during the wet–dry season transition (March–April); however, *C. americana* exhibited a secondary

peak of PUE in May 2009 (Fig. 6*D*).

NUE of *V. divergens* did not vary significantly between ecosystems but exhibited consistent variations over time, with individuals in both ecosystems exhibiting stable values [6–8 µmol(CO$_2$) g^{-1}(N) s^{-1}] during the dry season and the dry–wet season transition, declining to <6 µmol(CO$_2$) g^{-1}(N) s^{-1} during the wet season, and increasing again during the wet–dry season transition (Fig. 6*E*). In *C. americana*, NUE did not vary consistently over time but it was significantly higher in the Pantanal, especially during dry–wet season transition in October (Fig. 6*F*).

Relationships between mass-based R_D, P_{max}, SLA, and leaf N and P concentrations: P$_{mass}$ was significantly positively correlated with SLA in *V. divergens;* the slope of the regression was significantly higher for the Pantanal (Fig. 7*A*). N$_{mass}$ also increased significantly with SLA, with no differences in regression statistics (*i.e.*, slope and intercept) between the Pantanal and the Cerrado (Fig. 7*B*). R_{Dmass} (Fig. 7*C*) and $P_{max,m}$ (Fig. 7*D*), but not area-based P_{max} (data not shown), also increased as a function of SLA and there were no differences in the regression statistics between the Pantanal and the Cerrado. N$_{mass}$ increased as a function of P$_{mass}$ in *V. divergens* in the Pantanal and the Cerrado (Fig. 7*E*); however, R_{Dmass} (Fig. 7*F*) and $P_{max,m}$ (Fig. 7*G*) increased as a function of P$_{mass}$ for trees in the Cerrado but not in the Pantanal. Similarly, R_{Dmass} (Fig. 7*H*) and $P_{max,m}$ (Fig. 7*I*) increased as a function of N$_{mass}$ in trees in the Cerrado only, while rates of $P_{max,m}$ increased similarly as a function of R_{Dmass} for both ecosystems (Fig. 7*J*).

In *C. americana*, P$_{mass}$, N$_{mass}$, R_{Dmass}, and $P_{max,m}$ (but not area-based P_{max}, data not shown) were all positively correlated with SLA (Fig. 8*A–D*), and the slope of the regression for N$_{mass}$ (Fig. 8*B*) and R_{Dmass} (Fig. 8*C*) was

Table 2. Multivariate analysis of variance (*MANOVA*) results for the area-based maximum rate of net photosynthesis (P_{max}), dark respiration rate (R_D), maximum quantum yield (Φ), maximum stomatal conductance (g_{smax}), internal CO_2 concentration (C_i), light-compensation point (LCP), intrinsic water-use efficiency (WUE_i), N-use efficiency (NUE) and P-use efficiency (PUE) of *V. divergens* and *C. americana* as a function of ecosystem and time (months). The probability of type-I error (*p*-value), the *F*-statistic calculated using Wilks' criterion, and the associated effect and error degrees of freedom (effect, error *df*) are shown.

Source	*Vochysia divergens*			*Curratella americana*		
	F-statistic	*df*	*p*	*F*-statistic	*df*	*p*
Ecosystem	5.61	13, 43	<0.001	8.60	13, 36	<0.001
Time	2.36	117, 335	<0.001	2.33	117, 283	<0.001
Ecosystem × time	1.90	117, 335	<0.001	1.37	117, 283	<0.018

Fig. 4. Mean (± 1 SE) maximum light-saturated (*A,B*) area-based (P_{max}) and (*C,D*) mass-based ($P_{max,m}$) leaf photosynthetic rate, maximum light-saturated, area-based stomatal conductance (*E,F*) (g_{smax}), and the intercellular leaf CO_2 concentration (*G,H*) (C_i) in *Vochysia divergens* (*left panels*) and *Curatella americana* (*right panels*) growing in the Cerrado (*solid circles*, *solid lines*) and in the Pantanal (*open circles*, *dotted lines*) during the May 2009–April 2010 study period. The results of a one-way *ANOVA* (*F*-statistics and degrees of freedom) for the main effects of ecosystem (E) and time (T) are also shown. * – *p*<0.05; ** – *p*<0.01; *** – *p*<0.001.

significantly higher in the Cerrado. N_{mass} (Fig. 8*E*) and R_{Dmass} (Fig. 8*F*) were also positively correlated with P_{mass}, but in both cases there was no difference between the Pantanal and Cerrado regression statistics. However, $P_{max,m}$ increased significantly as a function of P_{mass} for the Pantanal only (Fig. 8*G*). R_{Dmass} (Fig. 8*H*), and $P_{max,m}$ (Fig. 8*I*) also increased as a function of N_{mass}, with both ecosystems having similar relationships. $P_{max,m}$ increased as a function of R_{Dmass} for both ecosystems with both ecosystems having similar relationships (Fig. 8*J*).

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Fig. 5. Mean (± 1 SE) area-based (*A,B*) maximum quantum yield (Φ), (*C,D*) leaf dark respiration (R_D), and (*E,F*) the light compensation point (LCP) in *Vochysia divergens* (*left panels*) and *Curatella americana* (*r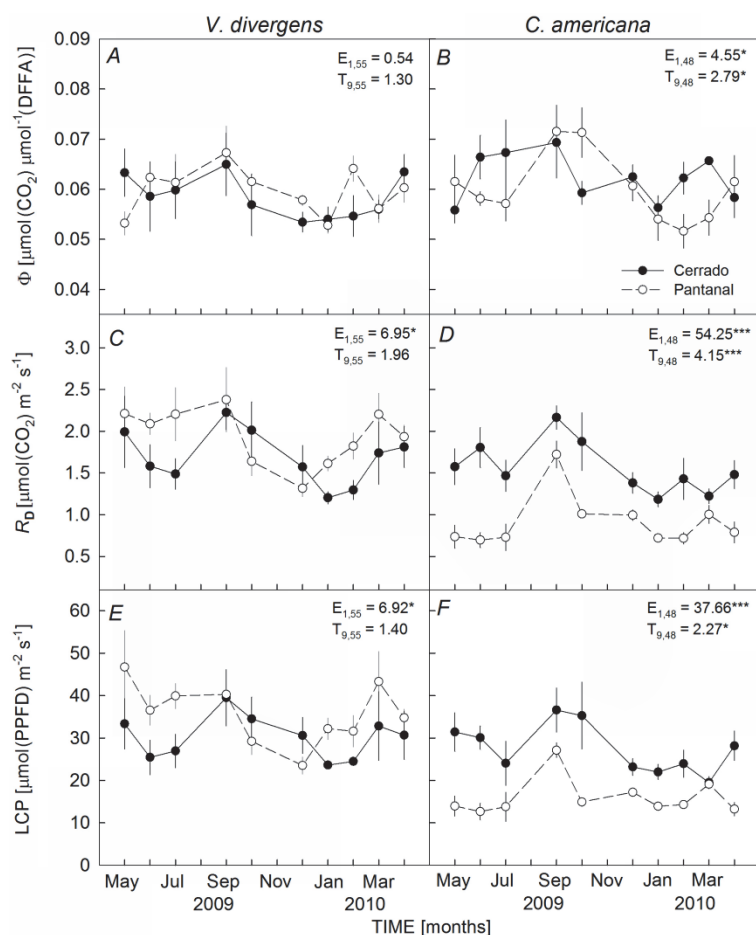ight panels*) growing in the Cerrado (*solid circles, solid lines*) and in the Pantanal (*open circles, dotted lines*) during the May 2009–April 2010 study period. The results of a one-way *ANOVA* (*F*-statistics and degrees of freedom) for the main effects of ecosystem (E) and time (T) are also shown. * – $p<0.05$; ** – $p<0.01$; *** – $p<0.001$.

Discussion

Ecosystem differences: In Mato Grosso, the main factor, which differentiates the Cerrado from the Pantanal, is hydrology because the climate and soils are very similar (Fig. 1; da Cunha and Junk 2004, Biudes *et al.* 2008, Vourlitis and da Rocha 2011, Vourlitis *et al.* 2011). While both species are found in well-drained Cerrado and the seasonally flooded Pantanal, *V. divergens* is a flood-adapted, pioneer tree species native to the Amazon (Pott and Pott 1994), while *C. americana* is native to upland Cerrado (Medina and Francisco 1994, Lorenzi 2002). Given their ability to expand outside of their native range and to withstand both seasonal drought (Cerrado) and flooding (Pantanal), we hypothesized that neither *V. divergens* or *C. americana* would experience a signifi-cant decline in physiological potential, such as the maximum, light-saturated photosynthesis (P_{max}) in their naturalized habitat. When assessing all gas-exchange variables combined, *V. divergens* had higher rates of R_D (Fig. 5*C*) and g_{max} (Fig. 4*E*) in the seasonally flooded Pantanal, which is more closely associated with lowland Amazonian forest, while *C. americana* had a higher rate

of P_{max}, R_D, (Figs. 4*B*, 5*D*), and Φ (Fig. 5*B*) in the Cerrado, suggesting that each species performed better in the habitat that it was adapted to. Even so, our data indicate that both species have broad tolerance for seasonal variations in hydrology, allowing them to tolerate seasonal drought, which develops during the dry season in the Cerrado, and seasonal flooding, which develops during the wet season in the Pantanal. We described some of the traits, which might allow each species to cope physiologically with the different hydrology of their naturalized habitat.

In *V. divergens*, flexible WUE_i might be a key trait for withstanding prolonged drought in the Cerrado. Rates of g_{smax} were lower in *V. divergens* in the Cerrado, especially during the dry season, while P_{max} was similar between the Cerrado and the Pantanal, resulting in an increase in WUE_i. The ability to use water more efficiently in seasonally dry habitats would be a signifi-cant advantage during the long dry season (Wright *et al.* 2001). In contrast, *C. americana* exhibited similar rates of g_{smax} (Fig. 4*F*) and WUE_i (Fig. 6*B*) in the Cerrado and the
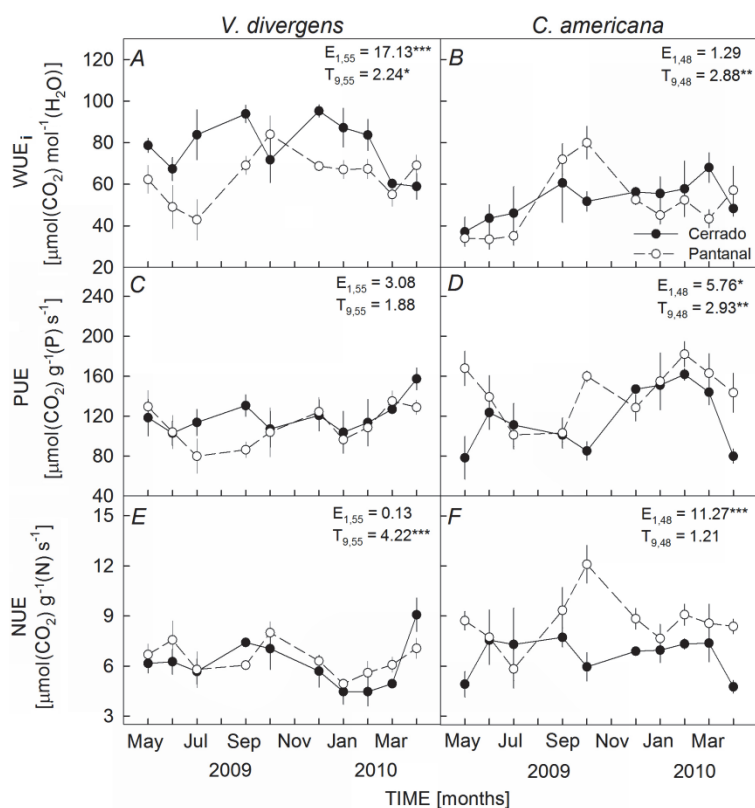
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Fig. 6. Mean ($\pm$ 1 SE) intrinsic water-use efficiency (WUEi) (*A,B*), nitrogen-use efficiency (NUE) (*C,D*), and phosphorus-use efficiency (PUE) (*E,F*) in *Vochysia divergens* (*left panels*) and *Curatella americana* (*right panels*) growing in the Cerrado (*solid circles*, *solid lines*) and the Pantanal (*open circles*, *dotted lines*) during the May 2009–April 2010 study period. The results of a one-way *ANOVA* (*F*-statistics and degrees of freedom) for the main effects of ecosystem (E) and time (T) are also shown. * – $p<0.05$; ** – $p<0.01$; *** – $p<0.001$.

Pantanal, indicating a relatively smaller capacity for physiological adjustment and a strategy of water conservation, which is presumably indicative of its origin in a dry environment (Wright *et al.* 2001). Moreover, the low concentration of N observed in the Pantanal (Fig. 2*B*) may have been the cause of reduction in P_{max} in this ecosystem (Fig. 4*B*). Since most of N in the leaf is found in the photosynthetic complexes (Field and Mooney 1986), a reduction at the level and/or activity of Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) may have caused the reduction in P_{max} observed here. The fact that C_i and g_{smax} did not change reinforces the idea that a nonstomatal factor was responsible for this reduction in P_{max} (Gulías *et al.* 2003), thus making the analysis of CO_2 curves an object for future studies of these species in this ecosystem.

Both species had significantly higher SLA in their naturalized habitats (Fig. 2*G,H*). High SLA is correlated with a reduction in the allocation to leaf structure, an increase in tissue N concentration, and a higher photo-synthetic capacity (Reich *et al.* 1999); such trends were supported by our data for both species (Figs. 7, 8). Thus, the increase in SLA in *V. divergens* in the Cerrado was presumably in response to a higher leaf N concentration in the Cerrado (Fig. 2*A,B*) as SLA was shown to be positively related to N availability (Knops and Reinhart 2000). In *C. americana*, SLA was almost always higher in the Pantanal than in the Cerrado, which is likely due to higher water availability in the Pantanal (Pierce *et al.* 1994), especially during the dry–wet season transition,

when leaf expansion occurs (Dalmagro *et al.* 2013). Given that photosynthetic capacity is highly correlated with SLA (Reich *et al.* 1999, Wright *et al.* 2001), the increase in SLA should lead to a higher $P_{max,m}$ in their naturalized habitats. In *V. divergens*, the increase in SLA in the Cerrado caused $P_{max,m}$ to be significantly higher in the Cerrado, while in *C. americana*, the increase in SLA caused ecosystem differences in $P_{max,m}$ in the Pantanal to be negligible.

Both species also appeared to have more flexibility in nutrient use in their naturalized habitats. *V. divergens* had a significantly higher increase in the rate of $P_{max,m}$ per unit P in the Cerrado (Fig. 7), while the opposite was true for *C. americana* (Fig. 8), suggesting that each species had greater ability to adjust $P_{max,m}$ as P availability increased in their naturalized habitat. Both species exhibited and N/P ratio > 15 for the majority of the study period, suggesting greater limitation by P than N (Koerselman and Mueleman 1996). An ability to adjust rapidly $P_{max,m}$ as a function of P availability might be a key trait for maximizing leaf C gain in P-limiting habitats. However, *V. divergens* also had a greater increase in $P_{max,m}$ per unit N (Fig. 7), while *C. americana* had higher NUE and PUE in the Pantanal (Fig. 6*D,F*). High NUE and/or flexibility resource use are key traits for plants in novel environments (Funk and Vitousek 2007, Funk 2008). This is likely true in the nutrient-poor soils of the Cerrado and the Pantanal (Lopes and Cox 1977, Vourlitis *et al.* 2011).
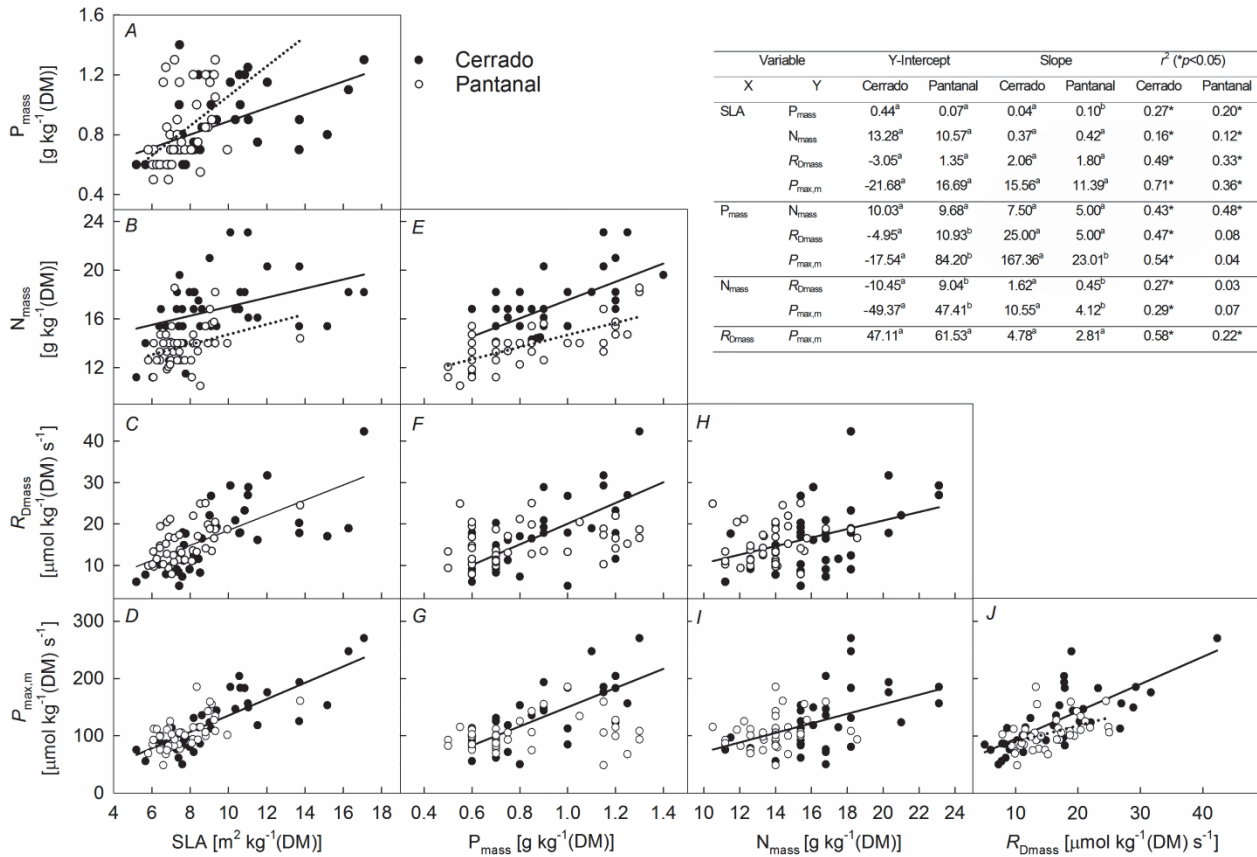
Variable		Y-Intercept		Slope		r^2 (*$p<0.05$)	
X	Y	Cerrado	Pantanal	Cerrado	Pantanal	Cerrado	Pantanal
SLA	P_{mass}	0.44[a]	0.07[a]	0.04[a]	0.10[b]	0.27*	0.20*
	N_{mass}	13.28[a]	10.57[a]	0.37[a]	0.42[a]	0.16*	0.12*
	R_{Dmass}	-3.05[a]	1.35[a]	2.06[a]	1.80[a]	0.49*	0.33*
	$P_{max,m}$	-21.68[a]	16.69[a]	15.56[a]	11.39[a]	0.71*	0.36*
P_{mass}	N_{mass}	10.03[a]	9.68[a]	7.50[a]	5.00[a]	0.43*	0.48*
	R_{Dmass}	-4.95[a]	10.93[a]	25.00[a]	5.00[a]	0.47*	0.08
	$P_{max,m}$	-17.54[a]	84.20[b]	167.36[a]	23.01[b]	0.54*	0.04
N_{mass}	R_{Dmass}	-10.45[a]	9.04[b]	1.62[a]	0.45[b]	0.27*	0.03
	$P_{max,m}$	-49.37[a]	47.41[b]	10.55[a]	4.12[b]	0.29*	0.07
R_{Dmass}	$P_{max,m}$	47.11[a]	61.53[a]	4.78[a]	2.81[a]	0.58*	0.22*

Fig. 7. Pair-wise scatter plots of mass-based maximum rate of photosynthesis ($P_{max,m}$), dark respiration rate (R_{Dmass}), specific leaf area (SLA), P concentration (P_{mass}), and leaf N concentration (N_{mass}) in *V. divergens* growing in the Cerrado (*closed symbols and continuous lines*) and in the Pantanal (*open symbols and dotted lines*) during the May 2009–April 2010 study period. Regression lines indicate significant linear trends. The table inset displays the linear regression coefficients (y-intercept, slope, and r^2 value) for each pair-wise comparison. Significant linear trends ($p<0.05$) are identified by an asterisk adjacent to each r^2 value. For each comparison, coefficients with a different lowercase letter are significantly different between the Cerrado and the Pantanal using a parameter-inequality randomization test with 1,000 iterations.

Temporal trends: In general, many of the leaf morphological (SLA), physiological (R_D, LCP, Φ) and N and P dynamics exhibited a transient increase during the dry–wet season transition, which was a critical period in the phenology of both species. For many tropical trees, the dry season serves as a trigger for flowering, fruiting, and the initiation of stem and new leaf production (Baker *et al.* 2002, Borchert 1994, da Silva *et al.* 2002). This is true for both *V. divergens* and *C. americana*, which were observed to initiate the production of new leaves, flowers, and fruits during the dry season (Dalmagro *et al.* 2013). Leaf nutrient concentrations were relatively higher in the dry season and during the dry–wet season transition to support these growth sinks, a trend that is consistent with other research in the Cerrado (Leitão and Silva 2004). P levels in soil are low in the Cerrado and the Pantanal (Franco *et al.* 2005, Vourlitis *et al.* 2011, 2013), and most of available P is provided by the organic matter enriched by the decomposition of plant material from fallen leaves during the months before the rainy season (Mendes

1996). An increase in the production of new leaves and reproductive organs may also lead to higher R_D (Fig. 5), as assimilates and nutrients are translocated to growth sinks (Penning de Vries 1975), and a concomitant increase in LCP (Lewis *et al.* 2000).

There was no significant seasonal variation in P_{max} in either species. In *V. divergens*, the consistency in P_{max} occurred despite a significant seasonal variation in g_{smax}, which tended to be higher in June–July during the dry season, resulting in higher C_i values (Fig. 4*E,G*). In *C. americana*, g_{smax} showed no difference between the seasons (Fig. 4*F*), following the trend in P_{max}, but higher C_i values tended to be the highest in the dry–wet season transition (Fig. 4*H*). Little seasonal variation in gas-exchange parameters, regardless of ecosystem, can be attributed to the ability of roots to access a source of groundwater (Nepstad *et al.* 1994), even during the dry season (Haase 1999, Biudes *et al.* 2008, Sanchez *et al.* 2011, Vourlitis *et al.* 2011). In particular, several lines of evidence, such as little seasonal variation in canopy
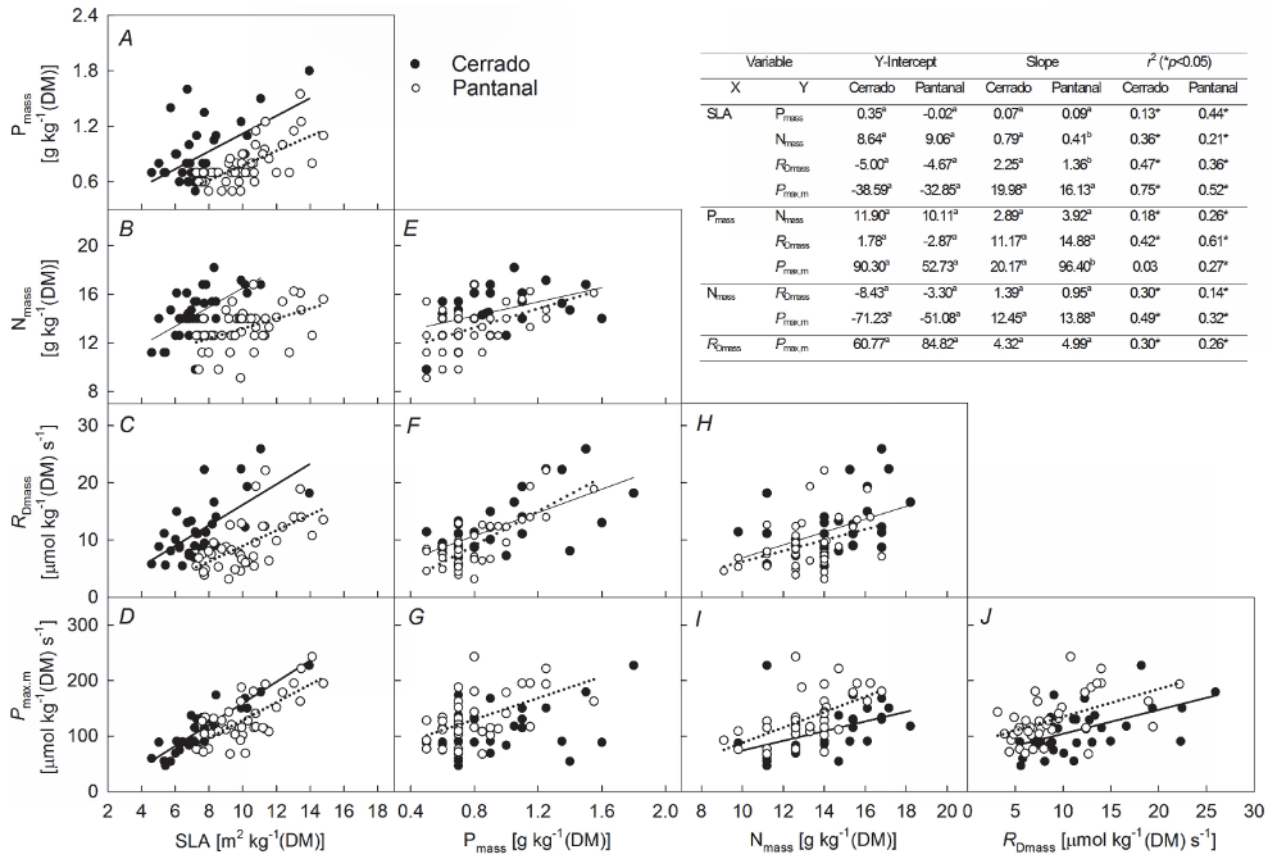
Variable		Y-Intercept		Slope		r^2 (*$p<0.05$)	
X	Y	Cerrado	Pantanal	Cerrado	Pantanal	Cerrado	Pantanal
SLA	P_{mass}	0.35[a]	-0.02[a]	0.07[a]	0.09[a]	0.13*	0.44*
	N_{mass}	8.64[a]	9.06[a]	0.79[a]	0.41[a]	0.36*	0.21*
	R_{Dmass}	-5.00[a]	-4.67[a]	2.25[a]	1.36[b]	0.47*	0.36*
	$P_{max,m}$	-38.59[a]	-32.85[a]	19.98[a]	16.13[a]	0.75*	0.52*
P_{mass}	N_{mass}	11.90[a]	10.11[a]	2.89[a]	3.92[a]	0.18*	0.26*
	R_{Dmass}	1.78[a]	-2.87[a]	11.17[a]	14.88[a]	0.42*	0.61*
	$P_{max,m}$	90.30[a]	52.73[a]	20.17[a]	96.40[b]	0.03	0.27*
N_{mass}	R_{Dmass}	-8.43[a]	-3.30[a]	1.39[a]	0.95[a]	0.30*	0.14*
	$P_{max,m}$	-71.23[a]	-51.08[a]	12.45[a]	13.88[a]	0.49*	0.32*
R_{Dmass}	$P_{max,m}$	60.77[a]	84.82[a]	4.32[a]	4.99[a]	0.30*	0.26*

Fig. 8. Pair-wise scatter plots of mass-based maximum rate of photosynthesis ($P_{max,m}$), dark respiration rate (R_{Dmass}), specific leaf area (SLA), P concentration (P_{mass}), and leaf N concentration (N_{mass}) in *C. americana* growing in the Cerrado (*closed symbols and continuous lines*) and the Pantanal (*open symbols and dotted lines*) for during the May 2009–April 2010 study period. Regression lines indicate significant linear trends. The table inset displays the linear regression coefficients (y-intercept, slope, and r^2 value) for each pair-wise comparison. Significant linear trends ($p<0.05$) are identified by an asterisk adjacent to each r^2 value. For each comparison, coefficients with a different lowercase letter are significantly different between the Cerrado and the Pantanal using a parameter-inequality randomization test with 1,000 iterations.

conductance and evapotranspiration (Biudes *et al.* 2008, Sanches *et al.* 2011, Vourlitis and da Rocha 2011) and the ability to redistribute leached nutrients from hydraulic redistribution (Vourlitis *et al.* 2011), indicate that *V. divergens* has a root system that can access deep water reserves during the dry season; however, little is known about the root morphology of *C. americana*. For plants subjected to seasonal drought, such as in the Cerrado, the ability to develop an extensive root system before the dry season is a decisive factor for their survival (Hulbert 1955, Roché *et al.* 1994, Mokany *et al.* 2006), because it enables plants to maintain a more favourable water balance and higher rates of leaf gas exchange during periods of drought (Tschaplinski and Blake 1989a). Greater root development also allows greater supply of nutrients to the expanding tissues (Rhodenbaugh and Pallardy 1993).

In conclusion, we hypothesized that neither *V. divergens* or *C. americana* would experience a significant decline in P_{max} in their naturalized habitat. This hypothesis was supported in *V. divergens*, but not in

C. americana, which had significantly lower rates of P_{max} in the Pantanal. While physiological performance for each species was generally higher in the habitat that they were adapted to, our data indicate that both species have broad tolerance for seasonal variations in hydrology. For the flood-adapted *V. divergens*, flexible WUE_i, higher SLA, and a greater ability to adjust $P_{max,m}$ as N and P availability increased appeared to be key traits for withstanding prolonged drought in the Cerrado. For *C. americana*, increases in SLA and higher NUE appeared to be important in maintaining high rates of mass-based gas exchange in the seasonally flooded Pantanal. While there is considerable debate on a direct link between photosynthesis and plant growth and/or recruitment (*e.g.*, Rhodenbaugh and Pallardy 1993, Sinclair *et al.* 2004), there is considerable evidence that variations in photosynthetic capacity can directly affect biomass production and survival (Long *et al.* 2006, von Caemmerer and Evans 2010). Flexibility in physiology and resource use may allow these species to invade and persist in habitats with broadly differing hydrology.

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