Physiological responses to extreme hydrological events in the Pantanal wetland: heterogeneity of a plant community containing super-dominant species

Higo J. Dalmagro, Michael J. Lathuillière, George L. Vourlitis, Roberto C. Campos, Osvaldo Borges Pinto Jr, Mark S. Johnson, Carmen E.R. Ortíz, Francisco de A. Lobo & Eduardo G. Couto

Dalmagro, H.J. (higojdalmagro@gmail.com)[1],
Lathuillière, M.J. (corresponding author, mlathuilliere@alumni.ubc.ca)[2],
Vourlitis, G.L. (georgev@csusm.edu)[3],
Campos, R.C. (rc8444@gmail.com)[1],
Pinto Jr, O.B.
(osvaldo.borges@kroton.com.br)[1],
Johnson, M.S. (mark.johnson@ubc.ca)[2,4],
Ortíz, C.E. (cerortiz@ufmt.br)[5],
Lobo, F. de A. (f_a_lobo@ufmt.br)[6],
Couto, E.G. (couto@ufmt.br)[6]

[1]Programa de Pós-Graduação em Ciências Ambiental, Universidade de Cuiabá (UNIC), Cuiabá, Mato Grosso 78065-900, Brazil;
[2]Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;
[3]Biological Sciences Department, California State University, San Marcos, CA 92078, USA;
[4]Department of Earth, Ocean and Atmospheric Sciences, Vancouver, BC V6T 1Z4, Canada;
[5]Departamento de Botânica e Ecologia, Instituto de Biociências, Universidade Federal de Mato Grosso (UFMT), Cuiabá, Mato Grosso 78060-900, Brazil;
[6]Departamento de Solos e Engenharia Rural, Faculdade de Agronomia, Medicina Veterinária e Zootecnia (FAMEVZ), Universidade Federal de Mato Grosso (UFMT), Cuiabá, Mato Grosso 78060-900, Brazil

Abstract

Aims: We tested two mechanisms of adaptation to extreme hydrological stresses (flooding and drought) of species making up a tropical wetland plant community by measuring leaf gas exchange and water potential. We hypothesized that anoxic conditions that occur during flooding will decrease leaf gas exchange when compared to the dry season, and that 'super-dominant' species will have a distinctive physiological advantage when compared to other plants within the community.

Location: Northern Pantanal wetland, Private Natural Heritage Reserve of the Brazilian Social Service of Commerce (RPPN-SESC Pantanal), Mato Grosso, Brazil.

Methods: Two periods representing typical extreme hydrological conditions in the Pantanal wetland were selected based on historical soil and meteorological measurements: (1) a drought period when plants experience stress due to soil moisture deficits during a dry season that persists for several months (May to Sept), and (2) a flooding period when oxidation-reduction potential is negative for 30 d or more (Mar or Apr), indicating anoxic stress. Measurements of gas exchange and leaf water potential were made on seven species in drought and flood stress conditions. The seven species represent the majority of the plant community.

Results: As a whole, the plant community showed significantly lower potential net photosynthesis (P_N) during flooding when soil oxidation-reduction potential reached close to -900 mV when compared to the dry season, but the magnitude of the decline in P_N was species specific. Not all super-dominant species showed higher P_N compared to non-dominant species, but they did demonstrate higher stomatal conductance and transpiration leading to lower water use efficiency. The combination of higher P_N despite low soil water content suggests that the plant community had access to deep water resources. This access was also confirmed by the midday leaf water potential, which was similar for the flood and dry seasons.

Conclusions: Results suggest that the plant community may have high physiological performance under a wide range of soil oxidation-reduction potentials. Higher P_N rates of super-dominant species indicate a physiological advantage of these species in the different hydrological conditions.

Introduction

Wetlands are important ecosystems that provide key benefits, including water purification, carbon storage, biodiversity maintenance, recreation, etc. (Millenium Ecosystem Assessment 2005) and are currently under threat from environmental pollution, agricultural expansion, development projects (dams, channels), invasion of exotic species and global climate change (Girard 2010; Girard et al. 2010; Alho 2011; Junk 2013; Junk et al. 2013). South America is the continent with the largest wetland surface area, with close to 20% of land occupied by wetlands (Junk et al. 2013). With 11 Ramsar sites representing over six million hectares, Brazil can play an important role in protecting wetlands despite the current lack of environmental policy (Junk 2013).

The Pantanal (Fig. S1) is one of the largest wetlands in the world, with an area of 160 000 km^2, over 80% of which is located in Brazil. It is characterized as a monomodal temporary wetland with a predictable annual flood pulse resulting from an intense wet season (Oct to Apr) followed by an intense dry season where there may be no measureable rainfall for 4 to 5 mo (Junk et al. 2006). Because of the large seasonal fluctuation in hydrology, the Pantanal is considered as a 'hyperseasonal savanna' (Nunes da Cunha & Junk 1999; Junk et al. 2006), or a savanna that is subjected to both wet season flooding and dry season drought (sensu Eiten 1972). In the northern Pantanal of Mato Grosso, Brazil, species must physiologically adapt to seasonal stresses when soils are either completely dry or fully saturated (Dalmagro et al. 2013, 2014). Flooding occurs in phase with the wet season when rivers overbank and inundate the surrounding floodplains. During that period, physical, chemical and biological processes severely deplete oxygen content in the soil through reduced oxygen diffusion, oxidation-reduction reactions and microorganism activity (Pezeshki & DeLaune 2012). The drop in soil oxygen content is accompanied by a reduction in soil oxidation-reduction potential (E_h) with several alterations in soil ionic content. For a soil pH of 4.5, reactions include denitrification and reduction of manganese (E_h of about 850 mV), reduction of iron (E_h about 200 mV) and sulfate ions (E_h about 0 mV) (Vepraskas & Faulkner 2000). This sequence of chemical reactions can further result in $E_h < -300$ mV (Turner & Patrick 1968; Pezeshki 2001) compared to well-drained soils, which typically have $E_h > 400$ mV (Patrick & DeLaune 1977; Gambrell & Patrick 1978; Ponnamperuma 1984). At a soil pH of 4.5, negative E_h values are also indicative of the reduction of CO_2 into CH_4, which is also of great interest for wetland biogeochemistry (Vepraskas & Faulkner 2000).

The soil's reduced conditions and oxygen deprivation can greatly affect plant physiology, such as reducing the oxygen concentration in plant tissue (Delaune et al. 1990; Armstrong et al. 1996) or preventing uptake of essential nutrients (Pezeshki & DeLaune 2012). Anoxic environments can also alter plant function as a result of the availability of essential soil nutrients (Pezeshki & DeLaune 2012) and production of phytotoxic compounds (Gambrell et al. 1991). Pezeshki & DeLaune (2012) list ethanol, lactic acid, acetaldehyde, aliphatic acids and cyanogenic compounds, in addition to reduced forms of the ions listed above (Delaune et al. 1978; Ponnamperuma 1984). Such compounds can accumulate in inundated soils at levels that can harm plants (Gambrell & Patrick 1978; Drew & Lynch 1980). Pezeshki & DeLaune (2012) report possible stomatal closure as a result of anoxic soil conditions, which also impede transpiration processes and plant growth.

Thus far, about 355 flood-tolerant tree species and 248 herbaceous aquatic species have been reported in the Pantanal (Pott & Pott 1994; Junk et al. 2006), and of this total, few species tolerate a very broad spectrum of flood and dry conditions, a behaviour that is favoured by pluriannual extreme dry and wet periods (Nunes da Cunha & Junk 1999). Most wetland-adapted species have developed a variety of mechanisms, including morphological (emission of adventitious roots), anatomical (aerenchyma formation in roots) and physiological changes, which may be rapid or slow in response to flooding (Schlüter & Furch 1992; Kozlowski 1997; Ferreira 2006; Dalmolin et al. 2012; Dalmagro et al. 2013, 2014; Kissmann et al. 2014). A change in long-term metabolism may only be observed in species that are highly tolerant to flooding, while physiological adjustments are more transient for species that can withstand short-term flooding (Piedade et al. 2011).

Many of the flood-tolerant species in the Pantanal are native to the upland savanna (locally known as cerrado), some have broad distributions and are immigrants from Amazonian river floodplains, such as Licania parvifolia Huber. (Chrysobalanaceae), Pouteria glomerata (Miq.) Radlk. (Sapotaceae) and Vochysia divergens Pohl (Vochysiaceae). In fact, none of the over 500 tree species occurring within the Pantanal are endemic to the biome (Junk et al. 2006). Some of these species have the capacity to invade grass-dominated savanna, forming monospecific stands (Nunes da Cunha & Junk 2001, 2004; Santos et al. 2006) and alter ecosystem properties (Vourlitis et al. 2011). These species, while native, have invaded so aggressively that they have been referred as 'super-dominant', or native species that have the properties of invasive species that can alter environmental characteristics (Matos & Pivello 2009). Some of the most common super-dominant species in the Northern Pantanal include Combretum lanceolatum Pohl (Combretaceae), Combretum laxum Jacq. (Combretaceae), Byrsonima orbignyana A. Juss. (Malpighiaceae),

L. parvifolia, *Curatella americana* L. (Dilleniaceae) and *V. divergens* (Junk et al. 2006; Santos et al. 2006).

Such super-dominant species represent an important threat to the current status of wetlands in South America (Nunes da Cunha & Junk 2001, 2004; Santos et al. 2006; Dalmagro et al. 2013; Junk 2013), therefore, it is important to understand their colonization mechanisms. This study aims to further understanding of the mechanisms of invasion of a plant community in the northern Pantanal of Mato Grosso. Following from previous work (Johnson et al. 2013; Messias et al. 2013; Dalmagro et al. 2014), we combine soil parameter measurements with leaf measurements to further understand species' adaptability to flooding. We hypothesize that anoxic conditions during seasonal flooding will cause a decline in the physiological performance of tree species such that potential net photosynthesis rates (P_N) and stomatal conductance (g_s) will be significantly lower than in the dry season. We further hypothesize that super-dominant tree species will have higher rates of leaf gas exchange and will show less seasonal variation in their physiological performance compared to other tree species within the plant community that are not super-dominant. To test these hypotheses we studied P_N of a plant community composed of seven tree species occurring on hyperseasonal savanna, four that are considered to be super-dominant (Junk & Nunes da Cunha 2012) and three that are native species of the cerrado and Pantanal (Arieira & Nunes da Cunha 2006). Such information will further the understanding of how drought and flooding cycles affect tree gas exchange and whether variations in physiological performance help certain species become dominant in tree island communities of the northern Pantanal.

Methods

Site description

The study site is located in the northern Pantanal of Mato Grosso, Brazil (16°34.44′ S, 56°16.94′ W, 120 m a.s.l.), about 160 km south of Cuiabá and 60 km southeast of Poconé (Fig. S1). The site is part of the Private Natural Heritage Reserve of the Brazilian Social Service of Commerce (RPPN-SESC), which is included in the Ramsar Convention list of Wetlands of International Importance. The site is characterized as a tree island (locally known as *cordilheira*) located in a transition zone between a monodominant forest of *V. divergens* (locally known as *cambará*) and scrub-forest savanna (locally known as *campo cerrado*) containing *C. americana*, with an understorey of grasses, *Gymnopogon spicatus* (Spreng.) Kuntze (Poaceae), and perennial herbs, *Mimosa pellita* Humb. et Bonpl. (Mimosaceae) (Vourlitis et al. 2011).

The climate is seasonal, with a rainy season (Oct to Apr) and a dry season (May to Sept). The average annual temperature is 25 °C and precipitation over the last 3 yrs has averaged 1345 mm·yr^{-1} (Fig. S2a), which is approximately 50 mm below the long-term (30-yr) average for the region (Vourlitis & da Rocha 2011). During the study period, the vapour pressure deficit (*VPD*) increased from a minimum of 0.15 kPa during the flooded season to as high as 1.3 kPa during the dry season (Fig. S2a).

Flooding in the reserve typically occurs between December and May, with water levels that can reach 2 m because of flooding from the Cuiabá River located 12 km north (Girard et al. 2010). In 2014, parts of the RPPN-SESC Pantanal recorded >160 d of flooding based on the Cuiabá River stage being above 3 m, which is the level at which the river connects to channels located in the reserve (Girard et al. 2010). The Cuiabá River reached a maximum height of 5 m on 29 Mar 2014, higher than any other level recorded in the preceding 5 yrs. A water gauge located inside the reserve, about 2 km from the research site, registered 140 d of flooding. The large flooding during the 2014 season resulted in a longer period of soil saturation (e.g. volumetric water content above 0.30 m^3·m^{-3}; Fig. S2b, more negative values of E_h (Fig. S2c) and lower concentrations of soil oxygen (Fig. S2d) when compared to the three preceding years.

Tree islands in the northern Pantanal are zones immune to complete flooding in most years and act as important areas of refuge for fauna. These landscape features present unique biogeochemical characteristics, especially with respect to soil oxidation-reduction (Messias et al. 2013) and soil respiration (Johnson et al. 2013). Soil at the tree island site was classified as Haplic Planosol (Johnson et al. 2013) with a sandy loam texture, a low concentration of organic matter (10–15 kg·dry soil^{-1}) and an average pH of 4.7 (Vourlitis et al. 2011). The total litter production is 2.05 t·ha^{-1}·yr^{-1}, consisting largely of leaves (85%), and litter production is highest at the end of the flood season and lowest at the beginning of the flood season (Brandão 2012).

Tree species abundance was estimated in early 2014 by counting and identifying all trees over 1.5 m in height found within a 100-m radius demarcated from the centre of the tree island. Of the species identified, seven were selected for study, accounted for over 80% of the species with the highest density and frequency in the area, including *V. divergens*, *C. americana*, *Tocoyena formosa* (Cham. st Schldl.) K. Schum. (Rubiaceae), *Alchornea discolor* Poepp. (Euphorbiaceae), *L. parvifolia*, *B. orbignyana* and *Duroia duckei* Huber (Rubiaceae). Both *C. americana* and *T. formosa* are considered deciduous, while all others are considered evergreen (Pott & Pott 1994; Lorenzi 2009).

Soil parameter and micrometeorology measurements

Soil parameter measurements were carried out with two sets of soil sensors placed at 10-cm and 30-cm depths connected to a CR1000 datalogger (Campbell Scientific, Logan, UT, US) with readings taken half hourly. At each soil depth we measured volumetric water content (VWC, $m^3 \cdot m^{-3}$) and temperature (EC-5; Decagon Devices, Pullman, WA, US), water matric potential (MPS-2, Decagon Devices), oxidation-reduction potential (Cole Parmer, Vernon Hills, IL, US), CO_2 concentration in the soil through infrared gas analysers (GMM221; Vaisala Inc., Helsinki, FI) and oxygen concentration in the soil (SO-100; Apogee Instruments, Logan, UT, US). A meteorological station (WXT520; Vaisala Inc.) installed 2 m above the ground allowed for measurements of air temperature, atmospheric pressure, relative humidity, wind velocity, wind direction and precipitation. Sensors were operational between Nov 2008 and Aug 2014 on a near-continuous basis. Routine data collection and sensor installation are further described in Johnson et al. (2013).

Eight soil samples at 10-cm and 30-cm depths were taken near the automatic station on a monthly basis between Oct 2013 and Aug 2014 (except for Jun and Jul 2014) and mixed in deionized water in a 2:1 water:soil slurry in order to measure pH and E_h with a portable instrument (Hanna Instruments, Corrolton, TX, US). These samples were used for QA/QC of the *in situ* measurements prior to evaluating reduction reactions in relation to E_h and pH levels in soil following Vepraskas & Faulkner (2000). Direct readings from the oxidation-reduction potential sensors are internally referenced to a saturated K/KCl reference electrode, requiring an adjustment from raw millivolt output to obtain E_h, which includes a correction based on the soil temperature (Vepraskas & Faulkner 2000), as

$$E_h = ORP - 0.6743 T_s + 213.76 \qquad (1)$$

where T_s is the soil temperature (°C) and ORP (mV) is the field measurement of oxidation-reduction potential against the saturated K/KCl electrode.

Gas exchange and leaf water potential measurements

Two campaigns of gas exchange and leaf water potential measurements were undertaken in 2014 at the tree island: on 29 Apr 2014 during flooding when soil E_h was −947 mV at 30-cm depths (flooded), and on 8 Aug 2014 in the dry season when E_h was +924 mV (dry). Five individuals were selected and tagged per species (35 trees) to allow for repeated measurements on the same individuals during the campaigns. The distance between the selected species was about 10 m. On each individual, we selected

the second node containing fully expanded leaves from the apex to the base and chose three leaves from this node to carry out measurements of leaf gas exchange (one leaf), and leaf water potential (two leaves).

Gas exchange measurements were made with a portable photosynthesis system LI-6400XT (LI-COR Inc., Lincoln, NE, US). Each leaf was subjected to a photon flux of 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to guarantee light saturation of photosynthesis. We used a block temperature of 28 °C, a reference CO_2 air concentration fixed at 400 $\mu mol \cdot mol^{-1}$ and a reference relative humidity of 60% to minimize stomatal heterogeneity. The P_N ($\mu mol(CO_2) \cdot m^{-2} \cdot s^{-1}$), transpiration rate ($E$, $mmol(H_2O) \cdot m^{-2} \cdot s^{-1}$) and stomatal conductance (g_s, $mol(H_2O) \cdot m^{-2} \cdot s^{-1}$) were calculated by the LI-6400xt data analysis program. The intrinsic water use efficiency (WUE, $\mu mol(CO_2) \cdot mol^{-1}(H_2O)$) was calculated as the ratio of P_N and g_s, while C_i/C_a ratio was calculated between the CO_2 concentrations in the intercellular space (C_i, $\mu mol(CO_2) \cdot mol^{-1}$ (air)) and environment (C_a, $\mu mol(CO_2) \cdot mol^{-1}$(air)). Water use efficiency (WUE) has been used as a measure of the ability of plant species to establish in environments with different water availability, and links C and H_2O cycles of terrestrial vegetation (Cernusak et al. 2007; Ito & Inatomi 2011), while the C_i/C_a ratio is used to understand the balance between consumption and replacement of CO_2. According to Wong et al. (1979), the ratio C_i/C_a is normally 0.7 for C_3 trees such as those measured here.

Water potential in the leaf (Ψω, MPa) was determined in leaves that were next to those measured for gas exchange. The predawn Ψω (Ψω_{pd}, MPa) was measured between 03:30 and 05:30 h local time, and again at midday (Ψω_{md}, MPa) between 12:00 and 14:00 h local time. Measurements of Ψω were made using a pressure chamber (Scholander et al. 1965), which determines the negative hydrostatic pressure (tension) that exists in the xylem of the stem leaves.

Data analysis

The parameters of gas exchange and water potential were tested for normality and homogeneity of variance using the Kolmogorov-Smirnov and Levene median tests, respectively. Since our data did not meet the requirements for a parametric test, we used the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Scheirer et al. 1976), followed by Dunn's paired comparisons test to test for differences among species (S) and the hydrology periods (H) (Sokal & Rohlf 1995). Data are presented as means ±95% confidence intervals to illustrate significant differences between means, which is appropriate because the results of the Dunn's test were consistent with the degree of over-

lap between confidence intervals. All analyses were performed using SPPS 17.0 (SPSS Inc., Chicago, IL, US).

Results

Variations in gas exchange among species and different soil hydrological conditions

There were significant interactions among species and hydrology for P_N (SxH$_{6,136}$ = 11.90, $P < 0.05$; Fig. 1a), with three different groups emerging. The highest rates of P_N were observed for *V. divergens* and *B. orbignyana*, intermediate rates were observed for *C. americana*, *D. duckei*, *A. discolor* and *L. parvifolia,* and the lowest P_N was observed for *T. formosa*. In general, *V. digergens*, *B. orbignyana*, *D. duckei* and *L. parvifolia* had higher rates of P_N during the dry season, while *C. americana*, *A. discolor* and *T. formosa* had similar rates of P_N during the dry and flooded periods, accounting for the significant SxH interaction (Fig. 1a).

Differences in g_s were observed among species ($S_{6,136}$ = 139.48, $P < 0.001$), and *V. digervens* and *B. orbignyana* had significantly higher g_s than *D. duckei*,

A. discolor and *T. formosa*, while *T. formosa* had the lowest g_s of all of the species (Fig. 1b). There were also differences in g_s between seasons ($H_{1,136}$ = 26.32, $P < 0.001$), with six out of the seven species (except *C. americana*) having higher g_s during the dry season (Fig. 1b), but this difference was not statistically significant.

There was a significant SxH interaction for the C_i/C_a ratio ($H_{6,136}$ = 19.97, $P < 0.01$), and the highest C_i/C_a ratio was observed for *L. parvifolia* and *T. formosa*, while the lowest was observed for *A. discolor* (Fig. S3a). Only *V. divergens* had a significantly lower C_i/C_a ratio during the dry season ($\pm$95% CI), which likely accounts of the significant SxH interaction (Fig. S3a).

Variations in leaf water potential among species and different soil hydrological conditions

There was a significant SxH interaction for $\Psi\omega_{pd}$ (SxH$_{6,63}$ = 13.87, $P < 0.05$) because while most species had lower $\Psi\omega_{pd}$ during the dry season, only *B. orbignyana*, *A. discolor* and *T. formosa* had significantly lower dry season
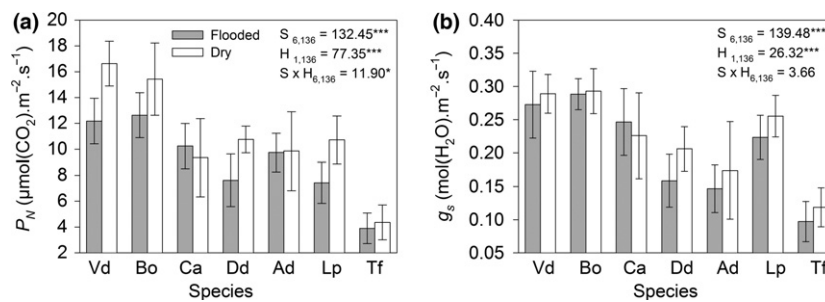
Fig. 1. Mean ($\pm$95% CI; n = 5) (**a**) potential net photosynthetic rate (P_N), and (**b**) stomatal conductance (g_s) of seven dominant species *V. divergens* (Vd), *B. orbignyana* (Bo), *C. americana* (Ca), *D. duckei* (Dd), *A. discolor* (Ad), *L. parvifolia* (Lp) and *T. formosa* (Tf) at the northern Pantanal tree island measured on 29 Apr 2014 (flooded) and 8 Aug 2014 (dry). Statistical results are expressed as H-statistic and the probability the type I error (P) obtained from the Kruskal–Wallis ANOVA to test with species (S) and hydrological period (H) as fixed effects. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
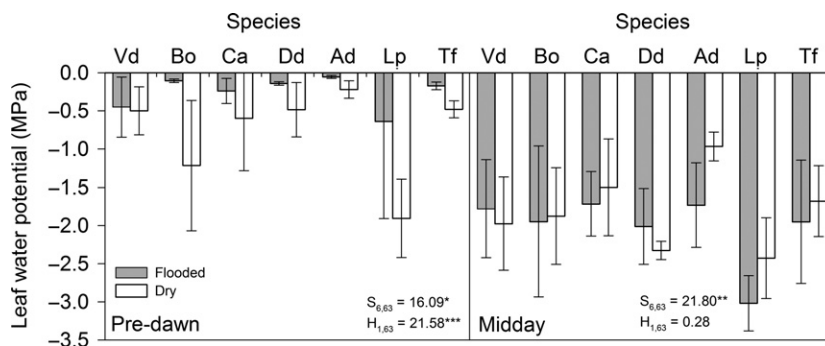
Fig. 2. Mean values ($\pm$95% CI; n = 5) of predawn ($\Psi\omega_{pd}$) and midday ($\Psi\omega_{md}$) leaf water potential of seven dominant species *V. divergens* (Vd), *B. orbignyana* (Bo), *C. americana* (Ca), *D. duckei* (Dd), *A. discolor* (Ad), *L. parvifolia* (Lp) and *T. formosa* (Tf) at the northern Pantanal tree island measured on 29 Apr 2014 (flooded) and 8 Aug 2014 (dry). Statistical results are expressed as H-statistic and the probability the type I error (P) obtained from the Kruskal-Wallis ANOVA to test with species (S) and hydrological period (H) as fixed effects. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

$\Psi\omega_{pd}$ (Fig. 2). The value of $\Psi\omega_{pd}$ was between -0.1 and -0.2 MPa for *B. orbignyana*, *A. discolor* and *T. formosa* during the flooded period and between -0.25 and -1.25 MPa during the dry season, while *L. parvifolia* had the lowest $\Psi\omega_{pd}$ of all species at -1.9 MPa (Fig. 2). Midday rates of water potential ($\Psi\omega_{md}$) were on average lower than $\Psi\omega_{pd}$, and there was a statistically significant difference between species ($S_{6,63} = 19.40$, $P < 0.01$), with *A. discolor* having the highest $\Psi\omega_{md}$ and *L. parvifolia* the lowest (Fig. 2).

The E also varied significantly among species ($S_{6,136} = 138.20$, $P < 0.001$) and between hydrologic periods ($H_{1,136} = 18.57$, $P < 0.001$). As with g_s, *V. divergens* and *B. orbignyana* had significantly higher E than *D. duckei*, *A. discolor* and *T. formosa*, and once again *T. formosa* had the lowest E (Fig. S3b). In contrast to g_s, however, five of seven species had on average lower rates of E during the dry season, with only *D. duckei* and *T. formosa* exhibiting the opposite seasonal trend (Fig. S3b).

There was a significant SxH interaction with *WUE* ($H_{6,136} = 20.29$, $P < 0.01$) that was apparently due to the divergent seasonal response of *A. discolor*, which had the highest *WUE* compared the other six species, especially during the flooded season (Fig. S3c). There was, however, a broad overlap in *WUE* for all species except *A. discolor* (Fig. S3c). *V. divergens*, *B. orbignyana*, *D. duckei* and *L. parvifolia* had higher average *WUE* during the dry season, but this difference was only statistically significant for *V. divergens*, while *A. discolor* and *T. formosa* had higher average *WUE* during the flooded season (Fig. S3c).

Discussion

Apparent decrease in net potential photosynthesis during flooding

We hypothesized that the anoxia that develops in response to seasonal flooding would cause a decline in the physiological performance, such that P_N and g_s would be significantly lower under flood conditions. Soil O_2 levels were near zero during the flooded period when E_h dropped to -947 mV, indicating hypoxic soil conditions, which persisted in the plant rooting zone during the flooded period of 2014. The decrease in E_h associated with flooding leads to an increase in O_2 demand within the soil profile and the production of phytotoxins that are by-products of the chemical reductions in the soil (Pezeshki & DeLaune 2012). These conditions impose severe stress on the roots of plants, affecting gas exchange rates (Pezeshki & DeLaune 2012). Flooding can cause a decline in P_N because of internal CO_2 limitations that occur in response to stomatal closure, or through biochemical limitations such as reductions in the rate of carboxylation (V_{cmax}) and electron transport (J_{max}) resulting from anoxia that causes nutrient deficiency and a concomitant decline in Rubisco content

and/or activity, carboxylation efficiency and the maximum quantum yield (Barrios & Herrera 1994; Lawlor 2002; Rengifo et al. 2005; Herrera et al. 2010). Species such as *V. divergens* and *B. orbignyana* appeared to suffer more from biochemical limitations because the decline in P_N was not accompanied by a decline in g_s or C_i. In contrast, species such as *D. duckei*, and *L. parvifolia* appeared to suffer from both metabolic and stomatal limitations as g_s declined in response to seasonal flooding. Regardless of the mechanism, seasonal flooding led to a decline in *WUE*, especially for *V. divergens* and *B. orbignyana*, because of the decline in P_N. Reductions in P_N of some species in response to seasonal flooding is an effective strategy to reduce metabolic demand during times of hydrological stress. Other species, such as *A. discolor* and *T. formosa*, had a P_N that was broadly tolerant to seasonal flooding even with declines in g_s and C_i. Thus, flooding caused a slight increase in *WUE* for these species.

In general, most species had higher P_N values during the dry season when surface soil *VWC* was low and rainfall was sporadic, suggesting that most of the tree species studied here were not water-limited. Maximizing carbon balance during favourable conditions is crucial for plant survival in areas with potentially unfavourable conditions, such as the Pantanal.

For some species (*V. divergens*, *C. americana*, *D. duckei* and *L. parvifolia*), there was no statistically different $\Psi\omega_{pd}$ between the dry and flooded periods. This similarity suggests that during the dry period these species were probably able to extract water from deep reserves with similar soil water status during flooding (Medina 1982; Sarmiento 1984; Goldstein et al. 1989; Medina & Francisco 1994; Haase 1999; Bucci et al. 2005; Franco et al. 2005; Guerfel et al. 2009; Sanches et al. 2011; Vourlitis et al. 2011; Dalmagro et al. 2013), further reinforced by $\Psi\omega_{md}$, whose values were also similar between dry and flooded periods. For *B. orbinyana*, *A. discolor* and *T. formosa*, however, the higher *VPD*, lower *VWC* and lower rate of hydraulic conductivity caused $\Psi\omega_{pd}$ to be significantly lower in the dry season. Lower *VWC* and/or higher evaporative demand would have also caused $\Psi\omega_{md}$ to decline. In contrast, during the flooded period there is plenty of available water, but water uptake may be restricted by low soil O_2 content, which, coupled with higher average rates of E, may have caused $\Psi\omega_{md}$ to decline compared to $\Psi\omega_{pd}$.

Physiological performance of super-dominant species

We hypothesized that super-dominant tree species would have higher rates of leaf gas exchange and would show less seasonal variation in their physiological performance compared to other tree species that are not considered to be super-dominant. However, not all of the super-dominant

species observed here exhibited higher physiological performance and/or lower seasonal variation than other species. For example, *B. orbignyana* and *V. divergens,* which are considered to be super-dominant, had the highest rates of P_N, especially during the dry season, while *L. parvifolia* and *C. americana*, which are also considered to be super-dominant, had rates of P_N that were similar to the non-super-dominant species *D. duckei* and *A. discolor*. Furthermore, *V. divergens* and *D. duckei* had significantly lower P_N during the flooded period, while *B. orbignyana, L. parvifolia, C. americana* and *T. formosa* displayed no statistically significant seasonal variation in P_N. Thus, super-dominant tree species did not consistently show less seasonal variation in their physiological performance compared to other tree species, as hypothesized. While there is debate about the relationship between photosynthesis and plant growth (Rhodenbaugh & Pallardy 1993; Sinclair et al. 2004), there is considerable evidence that changes in photosynthetic capacity can directly affect the production of biomass (Long et al. 2006; von Caemmerer & Evans 2010). Thus, the higher P_N observed in *V. divergens* and *B. orbignyana*, even at reduced levels during flooding, can help explain their expansion in the northern Pantanal.

While the propensity for invasion success of these super-dominant species could not be solely explained by their physiological performance, their ability to thrive in both flooded and upland habitats may interact with other phenological and/or life-history characteristics that may explain their ability to expand and persist in novel habitats. First, all of the super-dominant species studied here are pioneer species that have large reproductive output and rapid growth rates in disturbed environments (Pott & Pott 1994; Lorenzi 2009), and in turn, many invasive species tend to be pioneer species (Lambdon et al. 2008; Raphael et al. 2015). In particular, *C. americana, L. parvifolia* and *V. divergens* produce copious amounts of seed that ripen between Oct and Jan (Lorenzi 2009), which is before seasonal flooding but after the beginning of the rainy season when soil moisture is adequate for germination. This hydrological window of opportunity is critical for the germination, recruitment and expansion of super-dominant species like *V. divergens* in the Pantanal (Nunes da Cunha & Junk 2004), and the physiological tolerance to large fluctuations in hydrology presumably allows these species to persist once established.

In contrast, super-dominant species did appear to have higher rates of g_s and E than non-super-dominant species, leading to generally lower *WUE*. For example, *L. parvifolia* and *A. discolor* showed the same rate of P_N, but with very different strategies of water conservation. *L. parvifolia* had high values of g_s, E and C_i/C_a, and low values of $\Psi\omega$ and *WUE*, while *A. discolor* had low values of g_s, E and C_i/C_a and high values of $\Psi\omega$ and *WUE*. The strategy of *A. discolor* to

maintain reduced g_s can prevent excessive transpiration under conditions when water absorption capacity may be impaired. These impairments occur during drought when water availability is limiting, or during flooding when root activity is limited by negative E_h. Low levels of g_s are not necessarily associated with leaf dehydration, and for many species low values of g_s can occur without a reduction in leaf water potential (Kozlowski 1997). In the case of *A. discolor*, we observed higher $\Psi\omega_{pd}$ and $\Psi\omega_{md}$ regardless of hydrological periods, demonstrating that a reduction in g_s leads to higher water conservation. In contrast, *L. parvifolia* showed higher values of g_s and E, which led to lower leaf water potential, to the point that during the flood $\Psi\omega_{md}$ reached the critical value of -3.0 MPa for woody plants (Franco et al. 2005).

Conclusions

The physiological performance of tree species occurring within a tree island community in the northern Pantanal is strongly influenced by low E_h and soil O_2 concentration that occur in response to seasonal flooding. Most of the tree species have higher rates of P_N during the dry season, when soil E_h is positive but water availability is adequate. While some of the super-dominant species have higher rates of P_N there is not a consistent physiological advantage for these species under the varying hydrological conditions observed here. For some species, such as *V. divergens* and *B. orbignyana*, higher rates of P_N relative to other species during both dry and flooded periods may help explain their super-dominance in tree island communities in the northern Pantanal. In particular, *V. divergens* is a species that has been shown to be able to persist and expand to different habitats, colonizing large areas of the northern Pantanal and forming extensive single-species forests. This expansion of *V. divergens* is changing the dynamics of competition, affecting the community composition, structure and resource availability in the northern Pantanal (Junk et al. 2006; Santos et al. 2006; Sanches et al. 2011; Vourlitis et al. 2011). While there is still much uncertainty about the physiological processes and mechanisms that influence species distributions in tropical wetlands, our results suggest that some species may have high physiological performance under a wide range of soil E_h conditions. This high physiological performance may help explain their super-dominance in tree islands in the northern Pantanal, and presumably, other tree islands with wide seasonal variations in hydrology.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 (Figure S1). Location of the Pantanal in southwestern Brazil and the location of the tree island research site within the Private Natural Heritage Reserve of the Brazilian Social Service of Commerce in the northern Pantanal of Mato Grosso.

Appendix S2 (Figure S2). Daily accumulated precipitation, average vapour pressure deficit soil volumetric water content (VWC, m$^3 \cdot$m^{-3}) (b), soil oxidation-reduction potential and soil oxygen concentration for 2014 and series average (2010–2013).

Appendix S3 (Figure S3). Mean transpiration intrinsic water use efficiency and the ratio of internal to external CO_2 concentration of seven dominant species .