RESEARCH ARTICLE

Effects of flooding and shading on growth and gas exchange of *Vochysia divergens* Pohl (Vochysiaceae) of invasive species in the Brazilian Pantanal

Ândrea Carla Dalmolin[1]*, Higo José Dalmagro[1], Francisco de Almeida Lobo[2], Mario Zortéa Antunes Junior[3], Carmen Eugenia Rogríguez Ortíz[4], George Louis Vourlitis[5]

[1]Programa de Pós-Graduação em Física Ambiental, Instituto de Física, Universidade Federal de Mato Grosso, Cuiabá, MS, Brazil.

[2]Departamento de Solos e Engenharia Rural, Faculdade de Agronomia e Medicina Veterinária, Universidade Federal de Mato Grosso, Cuiabá, MS, Brazil.

[3]Programa de Pós-Graduação em Agricultura Tropical, Faculdade de Agronomia e Medicina Veterinária, Universidade Federal de Mato Grosso, Cuiabá, MS, Brazil.

[4]Departamento de Botânica e Ecologia, Instituto de Biociência, Universidade Federal de Mato Grosso, Cuiabá, MS, Brazil.

[5]Department of Biological Sciences, California State University, San Marcos, CA, USA.

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*Corresponding author: andreacarlad@gmail.com

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ABSTRACT

Vochysia divergens Pohl (commonly known as cambara) is a pioneer tree species that is native to the Amazon Basin but has been invading the seasonally flooded wetlands of the Brazilian Pantanal, forming monospecific communities. The physiological aspects associated with cambara invasion, including the effects of flooding and shading on growth and leaf gas exchange, are unknown but may shed light on why cambara is able to invade this novel habitat so rapidly. Thus, we conducted a manipulative experiment to quantify the effects of shading and flooding on the growth, gas exchange and leaf nutrient content of *V. divergens* saplings. Based on previous research we hypothesized that (1) experimental flooding would have no effect on the growth and gas exchange of *V. divergens,* and (2) experimental shading would reduce the growth and gas exchange of *V. divergens* regardless of the water treatment plants are subjected. Our data indicate that shading significantly increased the height, stomatal conductance (g_s), and transpiration (T) of *V. divergens* saplings, especially for plants exposed to normal irrigation. Experimental flooding significantly reduced rates of leaf production, plant height, and gas exchange; however, shaded plants exposed to flooding had a higher water use efficiency than plants exposed to full sun and flooding, because T was more depressed than net photosynthesis (A) in flooded plants exposed to full sun. Despite the inhibitory effects of flooding and shading, *V. divergens* saplings exhibited positive growth and C gain, regardless of the growth light environment or water level, indicating that the growth and leaf gas exchange of species is tolerant to both flooding and shading. Such tolerance to a wide variety of hydrological and growth light conditions presumably explains the ability of cambara to invade, and ultimately form dense, monospecific stands in the Brazilian Pantanal.

Keywords: cambara; physiological stress, photosynthesis, plant ecophysiology, stomatal conductance, tropical wetlands.

INTRODUCTION

Invasive species colonize a new area via accidental or intentional introduction and thrive, fundamentally altering native plant and animal species abundance, biodiversity, and ecosystem processes, such as carbon (C) and nutrient cycling and storage (Bossard et al., 2000; Vourlitis et al., 2011). Invasion into these novel habitats is often influenced by disturbances such as fire and/or grazing (Lake and Lieshman, 2004) or by events such as interannual variation in seasonal flooding (Nunes da Cunha and Junk, 2004). While it is difficult to determine which species will become invasive, species with invasive potential often share a wide range of traits including high reproductive output, vegetative reproduction, high relative and population growth rates, early reproductive age, and high resource use efficiency (Rejmanek and Richardson, 1996; Funk, 2008; Osunkoya et al., 2010). In particular, traits associated with maximizing C gain, such as high leaf area production, maximum photosynthesis, and specific leaf area (projected leaf area/leaf dry mass), appear to be positively correlated with invasive performance (Funk, 2008). Expression of these traits may be highly dependent on resource availability (Sala et al., 1996; Siemann and Rogers, 2007) and/or developmental stage (Ward et al., 2006); however, invasive species often exhibit high phenotypic and physiological plasticity (Funk, 2008), which allows them to expand their distribution across spatially heterogenous landscapes.

Physiological and/or phenotypic plasticity is of crucial importance for the survival of plant species that invade areas with substantially different resource availability. For example, plants invading areas subject to periodic flooding are exposed to extended periods of hypoxia and/or anoxia (Armstrong et al., 1994; Maurenza et al., 2009) and high concentrations of toxic products (McKee and McKevlin, 1993; Jackson and Colmer, 2005), and successful invaders must be able to tolerate widely fluctuating hydrological conditions. In contrast, riparian species invading drier upland areas must be able to tolerate periodic drought, and many successful invaders exhibit flexibility in root system morphology, which is critical for exploiting ephemeral and/or deep water reserves (Sala et al., 1996; Lite and Stromberg, 2005).

The invasion of *Vochysia divergens* Pohl (commonly known as cambara) in the wetlands of the Brazilian Pantanal is a well-documented example of a species that has rapidly colonized large areas, forming dense, monospecific stands known as cambarazais (Pott and Pott, 1994; Silva et al., 2000; Nunes da Cunha and Junk, 2004; Ariera and Nunes da Cunha, 2006; Junk et al., 2006). *V. divergens* is a woody, evergreen, and light-demanding pioneer species that is native to the Amazon Basin (Pott and Pott, 1994; Lorenzi, 1998). *V. divergens* first arrived in the Pantanal in the 1970s (Nunes da Cunha and Junk, 2004), and aerial surveys conducted in 2000 revealed that over 3% of the Pantanal is now covered by monospecific *V. divergens* forests (Silva et al., 2000). The reason for the invasion is still poorly understood; however, interactions between inundation, soil physical properties, and fire appear to be critical for invasion success (Nunes da Cunha and Junk, 2004). Once established, *V. divergens* has been shown to significantly alter soil chemical properties such as nutrient concentration, cation exchange capacity, and soil organic matter content (Vourlitis et al., 2011).

Some researchers attribute the expansion of *V. divergens* in the Pantanal to rapid growth under intense light, tolerance to flooding, and the production of numerous water-dispersed seeds (Nunes da Cunha and Junk, 2004; Ariera and Nunes da Cunha, 2006). However, most studies on *V. divergens* deal with population and community dynamics (Junk and Nunes da Cunha, 2005; Ariera and Nunes da Cunha, 2006; Junk et al., 2006; Santos et al., 2006; Nunes da Cunha et al., 2007), and the physiological aspects of *V. divergens* invasion are largely unknown. For example, the expansion of *V. divergens* is most rapid in highlight, grassland-dominated areas (Nunes da Cunha and Junk, 2004), but seedlings and saplings are often subjected to shading by canopy trees and/or bunch grasses during recruitment. Coupled with prolonged seasonal flooding, which can cause mortality in flood-sensitive tree species (Larcher, 1995) and a decline in the growth and gas exchange of flood-adapted tree species (Fernández et al., 1999; Mielke et al., 2003; Maurenza et al., 2009; Herrera et al., 2010; Oliveira and Joly, 2010), *V. divergens* seedlings and saplings are likely subjected to physiological stress as they invade these novel habitats.

Based on the fact that *V. divergens* is considered a light-demanding pioneer species (Lorenzi, 1998), and the fact that this species is adapted to seasonal flooding in its native (Amazonian forest), we hypothesized that (1) flooding would have no effect on the growth and gas exchange of *V. divergens*, and (2) experimental shading would reduce the growth and gas exchange of *V. divergens* regardless of the water treatment plants are subjected. To quantify the effects of shading and flooding on the growth, gas exchange and leaf nutrient content of young *V. divergens* plants we conducted a manipulative experiment in wich we simulated canopy shading and the seasonal flood regime.

MATERIAL AND METHODS

Plant material and experimental setup: One year old *V. divergens* trees (saplings) that were approximately 0.5 m tall and a ≤0.3 m trunk diameter were harvested from the Pantanal in an area that *V. divergens* was invading (n=60 trees). Harvested saplings were returned to a shade house and transferred into 8 L plastic pots containing nutrient-rich native soil. Plants were allowed to recover for 3 months under natural understory shade, which was similar to the environmental that they were growing in prior to harvest, until they showed good health (production of new green leaves).

After the recovery phase, surviving plants (28 out of the initial 60) were randomly allocated to one of four treatment groups (n=7 plants per treatment group):

1. flooded plants exposed to full-sunlight (flooded-unshaded);
2. flooded plants exposed to simulated understory shade (flooded-shaded);
3. non-flooded plants exposed to full-sunlight (unflooded-unshaded);
4. non-flooded plants exposed to simulated understory shade (unflooded-shaded).

Simulated flooding was accomplished by placing each 8 L pot into a larger 10 L pot that was filled with water so that the water level was maintained 0.04 m above the soil. The non-flooded plants were manually irrigated every two days with approximately two liters of water, which was enough water to keep the soil moist but not saturated. Water was added to both treatments every two days to avoid large variations in water level (flooded) or soil moisture (unflooded). To simulate understory shade, pots were placed in a shade house covered with shade cloth, which attenuated approximately 78% of the ambient light. Spectrophotometric analysis indicated that the shade cloth transmitted wavelengths >600 nm, which are similar to those transmitted by a typical plant canopy (Holmes and Smith, 1977). Plants exposed to full sun were placed outside the shade house. Treatments were initiated on day of the year (DOY) 246 and continued until DOY 311, corresponding to a 65 day experimental period.

Measurements of photosynthetic active radiation (PAR) were performed inside and outside the shadehouse using quantum sensors (LI-190SB, LI-COR, Lincoln, NE, USA). Air temperature was also measured within and outside the shadehouse using type-T (copper-constantan) thermocouples, while relative humidity was measured outside the shadehouse using a shielded thermistor and relative humidity sensor (HMP-35, Vaisala, Inc., Helsinki, Finland). Data were stored as hourly averages on a datalogger (CR 1000, Campbell Scientific, Inc., Logan, UT, USA).

Growth analysis and gas exchange: To evaluate tree growth, height and leaf number were recorded twice before (DOY 217 and 230) and three times after the initiation of the treatments (DOY 277, 294 and 311). During each measurement, all leaves on each plant were counted and the height of the main trunk was measured from the soil surface to the apex of the plant.

Gas exchange measurements were initiated the day after the treatments started (DOY 247) and 19 measurements were carried out over the 65 day experiment. Rates of stomatal conductance to water vapour (g_s), net photosynthesis (A), and transpiration (E), and intercellular concentration of CO_2 (C_i) were measured using a portable photosynthesis system (LI-6400, LI-COR Bioscience, Lincoln, NE, USA). The system was adjusted to provide a photosynthetically active radiation (PAR) of 1,000 µmol m^{-2} s^{-1}, block temperature of 28°C, relative humidity of 50–60%, and an ambient concentration of CO_2 (C_a) of 400 µmol mol^{-1}. These temperature, humidity, and C_a values were chosen to provide optimal conditions for leaf gas exchange, while the PAR of 1,000 µmol m^{-2} s^{-1} ensures light saturating PAR for both shaded and unshaded leaves (Miranda et al. 2005). Measurements were started after a period of approximately seven min, to allow the control system of the photosynthesis system and the leaf to adjust to the measurement conditions. Gas exchange was measured using the fourth or fifth leaf from the apex that was fully expanded and had no obvious disease symptoms such as chlorosis (n=1 leaf per plant). All measurements were performed between 0700 h to 1200 h, local time, and plants within all treatments were measured each hour to ensure that diurnal variations in temperature and/or humidity would affect each treatment combination equally. Leaf gas exchange and the C_i were calculated using the LI-6400 system software and the instantaneous water use efficiency (WUE) was calculated as the ratio between A and E.

Foliar macronutrients: Analysis of leaf macronutrients was done on DOY 307 when plants had many leaves and harvesting leaves would presumably not detrimentally affect plant physiological performance. Four leaves per plant were harvested, washed in distilled water, placed in an oven at 60°C for 72 hours, and ground in Willey type mill (Miyazawa et al., 2009). Ca^{2+} and Mg^{2+} concentration was determined by atomic absorption spectrophotometry (AA-1475, Varian, Inc., Palo Alto, CA USA) after nitropercloric digestion (Borges et al., 2005). P was determined by colorimetric analysis using the vitamin C method (Braga and DeFelipe, 1974). K^+ concentration was determined by flame atomic emission spectrometry (DM-61, Digimed, São Paulo, Brazil) following Isaac and Kerber (1971). Total N was determined using the micro-Kjedahl method (Golterman et al., 1978).

Statistical analysis: The rate of leaf production and plant growth (height) was estimated using linear regression, and while non-linear models may be more appropriate for assessing plant growth characteristics (Hunt and Parsons, 1974), linear models performed as well or better than non-linear models to characterize the change in leaf production and plant height over time. Differences in growth rate, calculated as the slope of the linear trend, were assessed using two-way ANOVA with water level and growth light condition as fixed effects. A repeated-measures ANOVA was used to assess treatment effects on leaf gas exchange with water level and growth light condition as fixed effects, and a two-way ANOVA was used to assess the effects of water level and light on leaf macronutrient concentration.

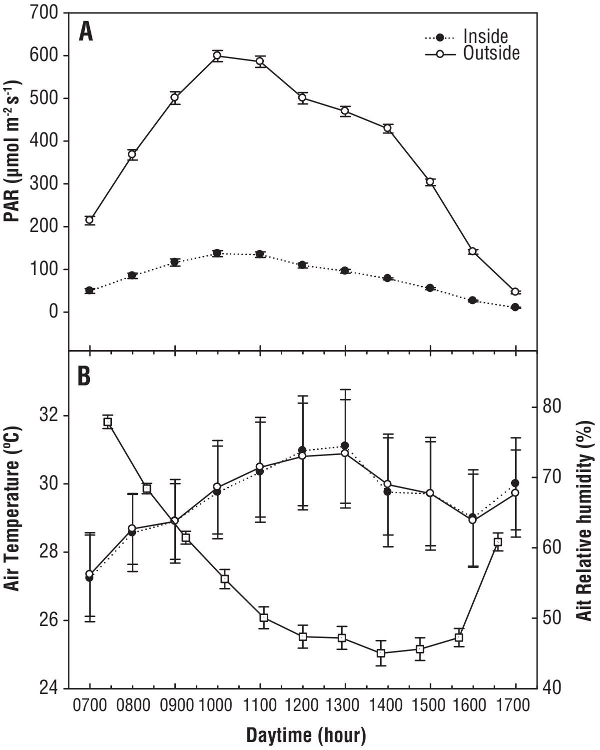

Figure 1. (A) Photosynthetic active radiation (PAR µmol m^{-2} s^{-1}) and (B) air temperature and relative humidity inside (closed symbols, dashed lines) and outside (open symbols, solid lines) the shadehouse. Mean (±SE; n=61 days).

RESULTS

Microclimate: There as a significant difference in mean (±SD) PAR inside (570±14 µmol m^{-2} s^{-1}) and outside (125±7 µmol m^{-2} s^{-1}) the shadehouse (Figure 1A). The average (±SD) temperature inside the shadehouse (35.8±0.8°C) was not statistically different from the mean temperature outside the shadehouse (36.1±0.76°C), and the highest average temperature for both environments was observed at 1400 h, local time (Figure 1B). The mean (±SD) relative humidity outside the shadehouse was 55.2±1.5%, and was highest in the early morning hours and lowest during the mid-afternoon hours when temperature was at a diurnal maximum (Figure 1B).

Plant growth and leaf production: All plants exposed to shading and flooding survived the 65th day of the experimental period, although many plants exhibited leaf chlorosis. We did not observe the development of hypertrophic lenticels or adventitious roots over the course of the experiment.

Leaf production declined significantly for plants exposed to flooding but not shading (Figure 2A). The mean (±95% confidence interval – CI) rate of leaf production of non-flooded plants exposed to full-sun and shade was 0.36±0.14 leaves day^{-1} and 0.47±0.15 leaves day, respectively. In contrast, plants exposed to flooded conditions produced on average 0.03 (full-sunlight) and 0.06 (shaded) leaves day^{-1}, indicating that flooded plants produced few leaves over the 61st day of experiment (Figure 2A).

Variations in water table and shading significantly affected plant height and there was a significant water table (W) and light (L) interaction (Figure 2B). Plants exposed to the shade and normal irrigation treatment had the highest mean (±95%CI) growth rate (0.040±0.007 m day^{-1}) followed by plants exposed to full sun and normal irrigation (0.017±0.005 m day^{-1}). In general, plants exposed to shading had a higher growth rate than plants exposed to full-sunlight in their respective water table treatments (Figure 2B).

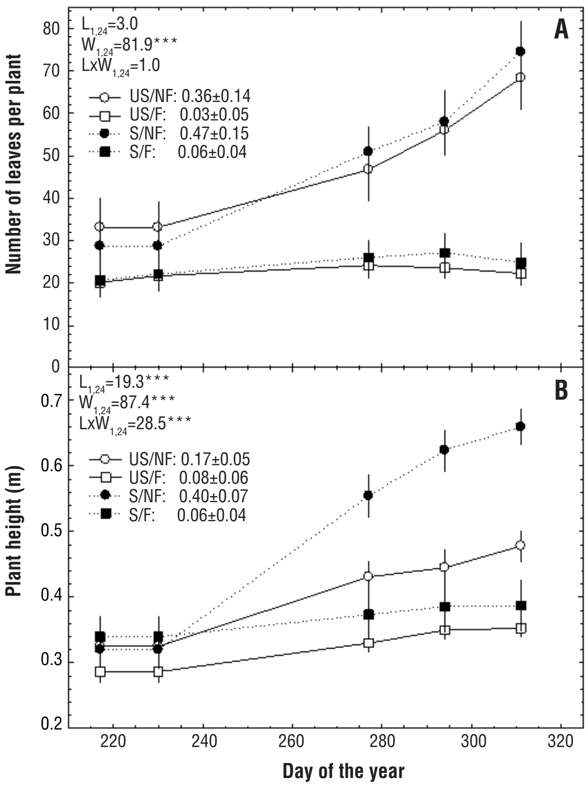

Figure 2. The mean (±SE; n=7 plants per treatment combination) number of leaves per plant (A) and plant height (B) for *Vochysia divergens* saplings exposed to unshaded (open symbols, solid lines) or shaded (closed symbols, dashed lines) and flooded (squares) or non-flooded (circles) conditions. The mean (±95% confidence interval) rates of leaf production (A) and plant growth (B) for each light (shaded (S) and unshaded (US)) and water table (flooded (F) and non-flooded (NF)) treatment combination are shown with the figure legends. The results of a 2-way ANOVA (F-statistics, degrees of freedom) for the rate of leaf production (A) and plant growth (B) as a function of water table depth (W), light (L) and the LxW interaction are also shown. ***(p<0.001).

Gas exchange and leaf macronutrient concentration: Shading did not affect rates of net photosynthesis (*A*) but flooding rapidly and significantly reduced *A* after the treatment was initiated (Figure 3A). Day-to-day variations in *A* were large regardless of treatment group and there did not appear to be a discernable temporal trend in *A*. When averaged over the experimental period, mean (±95%CI) *A* was 3.0±0.5 and 3.5±0.4 µmol m^{-2} s^{-1} for flooded trees exposed to shading and full-sun, respectively, which was 30% of the *A* of plants exposed to normal irrigation (Figure 3A).

Rates of transpiration (*T*) and stomatal conductance (g_s) were significantly affected by flooding and shading, with the highest *T* and g_s observed for plants exposed to shading and normal irrigation (Figure 3B). When averaged over the study period, significant shading and flooding effects on g_s were apparent and there was a significant LxW interaction (Figure 4B). This interaction was caused by a significantly higher g_s for plants exposed to shading and normal irrigation (0.27±0.07 mol m^{-2} s^{-1}) compared to plants exposed to full-sunlight and normal irrigation (0.15±0.04 mol m^{-2} s^{-1}).

The ratio of internal to external CO_2 concentration (C_i:C_a) was significantly affected by flooding but not shading; however, there was a significant LxW interaction (Figure 3C). Temporal variations in the C_i:C_a were relatively larger for shaded plants; however, the significant LxW interaction occurred because plants exposed to shading and normal irrigation had the highest C_i:C_a (0.65–0.8) while plants exposed to shading and flooding had the lowest (0.45–0.6; Figure 3C). When averaged over the experimental period, the effect of flooding on the C_i:C_a was again dependent on light level (Figure 4C), but only plants exposed to shade and normal irrigation had a C_i:C_a that was close to the theoretical optimum ratio of 0.70 for C_3 plants (Wong et al., 1979).

Time series for the instantaneous WUE were similar to those observed for C_i:C_a (data not shown), and there was a significant effect of water table depth and a significant LxW interaction for WUE values averaged over the experimental period (Figure 4D). Shaded plants exposed to flooding had the highest WUE followed by unshaded plants exposed to normal irrigation.

Leaf macronutrient concentrations were significantly lower in flooded plants for all macronutrients except N (Table 1). Differences in leaf macronutrient concentration between flooded and normally irrigated plants appeared to be slightly larger in plants exposed to shaded conditions; however, the direct effects of light were not statistically significantly and there was no LxW interaction (Table 1).

DISCUSSION

Effects of flooding and shading on *V. divergens* physiological performance: We originally hypothesized that flooding would have no effect on the growth and gas exchange of *V. divergens*, but experimental shading would reduce the growth and gas exchange of *V. divergens* based on the fact that *V. divergens* is considered a light-demanding pioneer species that this species is considered to be light

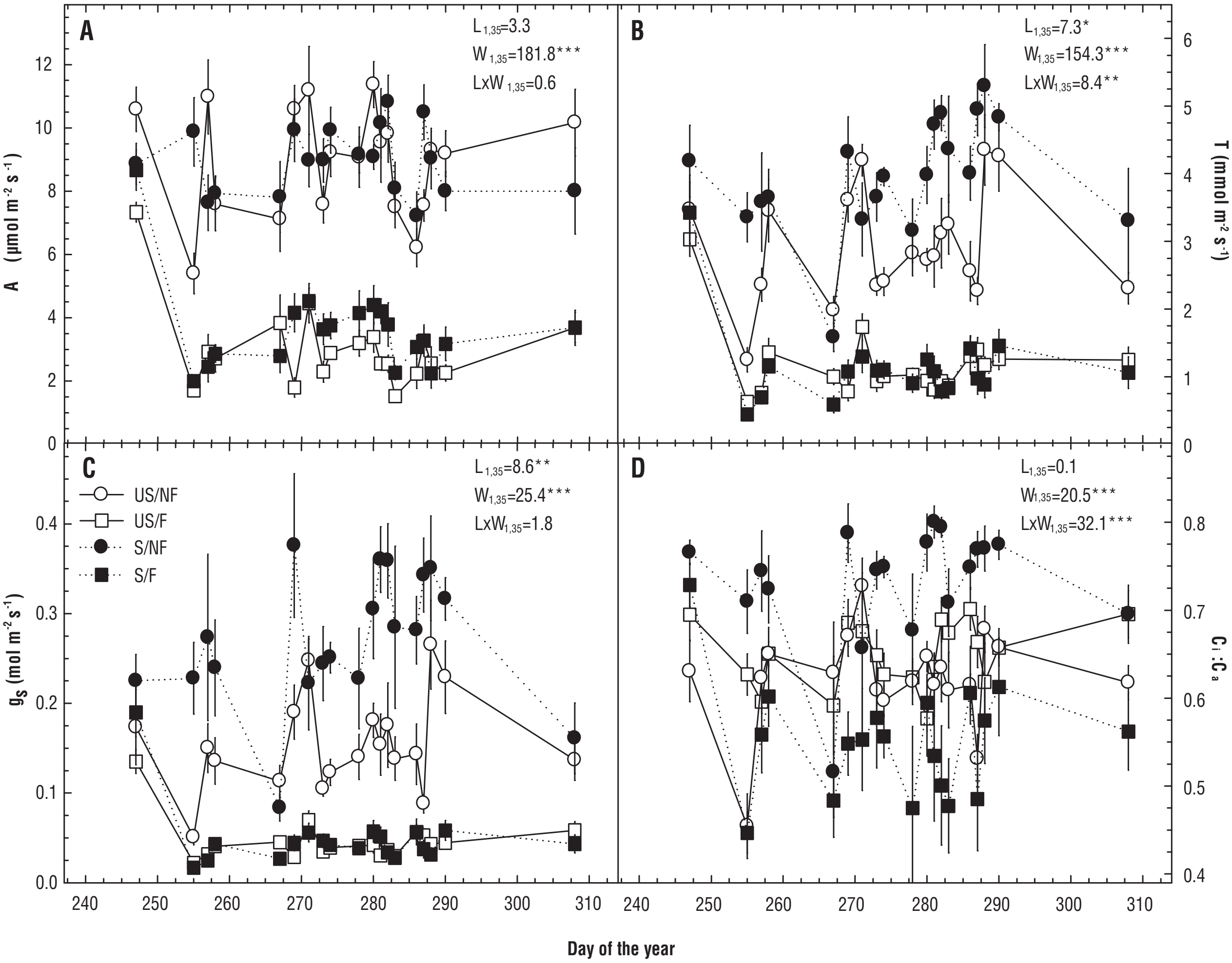

Figure 3. Time series for the rate of (A) net photosynthesis, (B) transpiration, (C) stomatal conductance, and (D) the C_i:C_a ratio for *Vochysia divergens* saplings exposed to unshaded (open symbols, solid lines) or shaded (closed symbols, dashed lines) and flooded (squares) or non-flooded (circles) conditions. The results of repeated-measures ANOVA for water table depth (W), light (L) and the LxW interaction are also shown. Mean (±SE; n=7 plants per treatment combination). **(p<0.01) ***(p<0.001).

demanding and adapted to seasonal flooding in its native Amazonian forest (Lorenzi, 1998). However, our data suggest that flooding was more important for determining growth and leaf gas exchange, while shading was either less important or dependent on the water level the saplings were exposed to.

While flooding resulted in a decline in growth, some of the anatomical and morphological features commonly found in plants adapted to flooding, like hypertrophy of lenticels and the presence of adventitious roots (Colmer and Greenway, 2010; Shimamura et al., 2010), were not observed in *V. divergens* saplings. However, flooded *V. divergens* saplings showed reduced growth and chlorotic leaves, which is a common response to flooding (Ishida et al., 2002; Mielke et al., 2003). Plants subjected to hypoxia or anoxia exhibit a reduction in chlorophyll synthesis because of an accumulation of ethylene (Sena and Kozlowski, 1988) and/or a reduction in cytokinin synthesis (Zhang et al., 2000). Moreover, the microbial production of ethylene in anoxic soils provides an additional exogenous source to plants (Hunt et al., 1981). In turn, ethylene promotes an increase in the activity of chlorophyllase and oxidase enzymes, which are responsible for the degradation of chlorophyll (Jacomino et al., 2003). Furthermore, the reduction in foliar nutrient concentrations in flooded *V. divergens* plants implies a decline in nutrient uptake, and under anaerobic conditions ATP levels are reduced, which

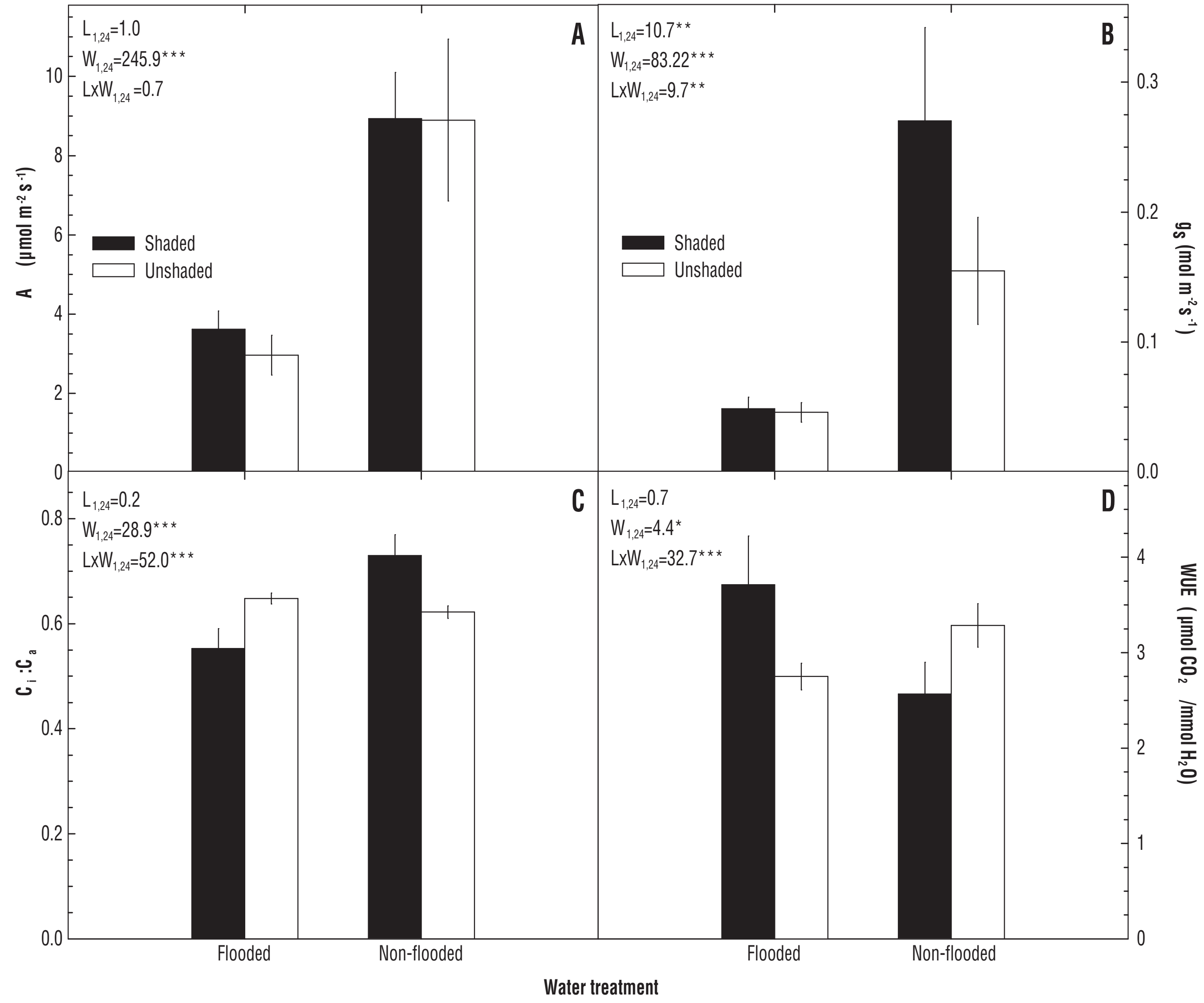

Figure 4. Net photosynthesis rate (A), stomatal conductance (B), the C_i:C_a ratio (C), and the instantaneous water use efficiency (D) for *Vochysia divergens* saplings exposed to unshaded (open bars) or shaded (closed bars) and flooded or non-flooded conditions. The results of a 2-way ANOVA (F-statistics, degrees of freedom) for water table depth (W), light (L) and the LxW interaction are also shown. Data were averaged over the 65th day of experimental period. Mean (±95% confidence interval; n=7 plants per treatment combination). **(p<0.01) ***(p<0.001).

Table 1. Mean leaf (±SE) tissue nitrogen, phosphorus, potassium, calcium, and magnesium concentration (g kg^{-1}) of *Vochysia divergens* saplings exposed to different water table (flooded vs. non-flooded) and light (shaded vs. full-sun) treatment combinations (n=7 plants per treatment combination). The results of a 2-way ANOVA (F-statistic, degrees of freedom) with light and water treatment as fixed effects are also shown.

Element	Shaded		Unshaded		F-statistics		
	Flooded	Non-flooded	Flooded	Non-flooded	Light	Water	Light x water
N	8.10±0.43	11.90±1.37	11.20±1.06	11.67±1.04	1.9	4.1	2.5
P	0.46±0.03	0.75±0.05	0.51±0.03	0.67±0.02	0.1	40.5*	4.0
K	3.49±0.38	7.03±1.00	4.69±0.23	6.53±0.36	0.4	21.5*	2.1
Ca	1.89±0.21	2.68±0.22	2.17±0.10	2.88±0.26	1.3	12.4**	0.1
Mg	0.81±0.09	1.62±0.14	1.20±0.05	1.63±0.15	2.9	27.0*	2.4

*p<0.01; **p<0.001.

impairs the active absorption of nutrients (Ishida and Carvalho, 2002; Rehen et al., 2009). While speculative, a decline in tissue nutrient concentration may have in part explained the flood-induced decline in growth and gas exchange for the *V. divergens* saplings studied here.

While biochemical limitations to *V. divergens* physiological performance were likely important, only plants exposed to the normal irrigation and shade treatment had a C_i:C_a similar to the optimum value of 0.7 for C_3 plants (Wong et al., 1979), indicating that stomatal limitations to *A* and plant growth were important as well. Interestingly plants exposed to normal irrigation and full-sunlight exhibited a decline in g_s and C_i:C_a compared to shaded plants, presumably because shading reduced leaf temperature and the leaf-air vapor pressure deficit, alleviating a decline in leaf water potential that would ultimately limit g_s.

Plants exposed to flooding have increased levels of abscisic acid (ABA) (Wilkinson and Davies, 2002), which causes a decline in g_s (Holbrook et al., 2002) even without any apparent loss of turgor (Maurenza et al., 2009). Anaerobic production of ethanol and lactic acid (Crawford, 1992; Drew, 1997; Oliveira and Joly, 2010) can also lead to a reduction in xylem water potential and g_s (Pezeshki et al., 1993; Herrera et al., 2010).

The reduction in g_s can be considered a survival mechanism for plants in flood conditions (Mielke et al., 2003). Flooding reduces the hydraulic conductivity of the root because hypoxia induces root suberisation or lignification (Clark and Harris, 1981) and/or a decrease in the synthesis of aquaporins of root cell membranes (Tournaire-Roux et al., 2003). Under these conditions, regulation in the gas exchange by the stomata becomes critical for survival because water loss from transpiration cannot be balanced by water uptake. The immediate consequence of the reduction in g_s is a reduction in the availability of photoassimilates leading to a decline in growth (Bradford, 1983; Kozlowski, 1997; Kozlowski and Pallardy, 2002). For *V. divergens* saplings the growth rate was significantly positive correlated with g_s ($r=0.86$; $p<0.001$). For many flood-sensitive species the decline in g_s to an immediate decline in C uptake and eventual death (Larcher, 1995); while for more flood tolerant species, declines in conductance may limit C uptake but positive C gain may protect individuals from mortality until flooding subsides (Joly and Crawford, 1982; Mielke et al., 2003).

Links between *V. divergens* physiological performance and invasion success: Our data indicate that *V. divergens* was tolerant of shading, and in some cases shading helped increase gas exchange (g_s) that maximized growth. This result is consistent with Dalmolin et al. (*in press*), who measured *A* x PAR curves and found no significant differences in the PAR response for shaded and unshaded plants. In retrospect, this result is really not too surprising, regardless of whether *V. divergens* is considered pioneer species, because in the field one can observe that saplings that are below dense tree and/or grass canopies. According to Joly and Crawford (1982), *V. divergens* also appears to be flood-tolerant because it is able to accumulate biomass during flood exposure. Clearly flooding reduced growth and physiological performance in *V. divergens* saplings; however, plants exhibited rapid, highly flexible changes in growth and gas exchange in response to flooding. Such flooding and shade tolerance presumably promotes the establishment and recruitment of *V. divergens* in seasonally-flooded areas that exhibit significant variations in hydrology over a short period of time (Funk, 2008). One could envision a scenario where seeds carried by seasonal floodwaters are dispersed to new habitat, and provided germination conditions are favorable, seedlings and saplings survive, grow, and gain C in flooded areas regardless of the growth light environment. As the seasonal flood waters recede, gas exchange and growth can increase rapidly, thus promoting the establishment of *V. divergens* in grass-dominated areas of the Pantanal. Clearly, this scenario is speculative and more research is needed to determine if similar patterns hold in their naturalized setting and to better explain the mechanisms of flood and shade tolerance for this species.

In conclusion, saplings of *V. divergens* showed little change in growth and gas exchange in response to experimental shading, but experimental flooding significantly reduced rates of physiological performance. However, *V. divergens* saplings exhibited positive growth and C gain in the flooded and shaded treatment, indicating that this species is tolerant to both flooding and shading. Such tolerance, and the physiological flexibility to gain C in a wide variety of hydrological and growth light conditions, presumably explains the ability of *V. divergens* to invade, and ultimately form dense, monospecific stands, in the Brazilian Pantanal.

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