Water Relations of *Chusquea ramosissima* and *Merostachys claussenii* in Iguazu National Park, Argentina[1]

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Bamboos are prominent components of many tropical ecosystems, yet little is known about the physiological mechanisms utilized by these gigantic forest grasses. Here, we present data on the water transport properties of *Chusquea ramosissima* and *Merostachys claussenii*, monocarpic bamboo grasses native to the subtropical Atlantic forests of Argentina. *C. ramosissima* and *M. claussenii* differed in their growth form and exhibited contrasting strategies of water transport. Maximum xylem hydraulic conductivity of *C. ramosissima* culms was 2-fold higher than that of *M. claussenii*. *C. ramosissima* cavitated at relatively high water potentials (50% loss of conductivity at ≥1 MPa), whereas *M. claussenii* was more drought tolerant (50% loss at ≤3 MPa). Both species exhibited significant loss of hydraulic conductivity during the day, which was reversed overnight due to the generation of root pressure. The photosynthetic capacities of both bamboo species, estimated based on electron transport rates, were moderate, reflecting both the large amount of leaf area supported by culms and diurnal loss of hydraulic conductivity due to cavitation. Leaf hydraulic conductance was also relatively low for both species, congruent with their modest photosynthetic capacities. Within its native range, *C. ramosissima* is highly invasive due to its ability to colonize and persist in both forest gaps and land cleared for agriculture. We propose that a highly vulnerable vasculature, coupled with diurnal root pressure and an allometry that allows substantial leaf area to be supported on relatively slender culms, are key traits contributing to the ecological success of *C. ramosissima*.

Bamboos are woody grasses that have dramatic effects on turnover rates, species composition, and biomass of forests (Judziewicz et al., 1999; Silveira, 1999; Saha and Howe, 2001; Griscom and Ashton, 2003). Like many invasive grasses, bamboos are aggressive competitors because they monopolize space by exhibiting clonal growth (Acosta et al., 2006), as well as alter light availability and quality in the forest understory (Coleman and Levine, 2007; Ito and Hino, 2007). Bamboos have a competitive advantage under a moderate disturbance regime due to a clonal growth form that combines underground storage organs with short-lived, fast-growing culms (Gagnon et al., 2007). The physiological mechanisms underlying their rapid spread and success in colonizing gaps, however, are not well understood.

Rapid plant growth has been related to high xylem-specific conductivity (Rosner et al., 2007) because an enhanced ability to transport water enables greater stomatal conductance and thus higher photosynthetic rates (Meinzer and Grantz, 1991; Sperry et al., 1993; Meinzer et al., 1995; Saliendra et al., 1995; Lambers et al., 1998; Hubbard et al., 1999). Studies on fast-growing pioneer species suggest that high growth rates are accompanied by a trade-off between hydraulic conductivity and vulnerability to cavitation (Barigah et al., 2006). Little is known, however, about the vulnerability of bamboo xylem to cavitation or their xylem- and leaf-specific conductivity. A study of *Rhipidocladum racemiflorum* (Cochard et al., 1994) shows that this climbing rainforest bamboo is relatively resistant to cavitation, but also able to generate root pressure to refill embolized vessels. Root pressure as a mechanism of cavitation repair has been reported in other grasses, such as *Chloris gayana* (Ogata et al., 1985), rice (*Oryza sativa*; Stiller et al., 2003), and maize (*Zea mays*; McCully et al., 1998). Rice is vulnerable to cavitation (Stiller et al., 2003), but refills embolized

vessels on a daily basis either by generating positive root pressure or by other, less well-understood, refilling mechanisms (Stiller et al., 2005). Similarly, drought-induced cavitation followed by refilling occurs in field-grown maize (Zhang et al., 1995; McCully et al., 1998).

In this study, we investigate the ecophysiological properties of two woody bamboo species in Iguazu National Park, located in Misiones Province, Argentina, situated within the largest continuous remnant of Atlantic Forest. Four bamboo species, *Chusquea ramosissima*, *Merostachys claussenii*, *Guadua trinii*, and *Guadua chacoensis*, are common at this site. *C. ramosissima* is the most aggressive of this group, colonizing canopy gaps and land cleared for agriculture, and attaining culm densities up to approximately 25,000 stems ha^{-1} (Campanello et al., 2007). Here, we focus on the hydraulic properties of *C. ramosissima* Lindman (hereafter *C. ramosissima*) and *M. claussenii* Munro (hereafter *M. claussenii*) with the goal of understanding what aspects of bamboo physiology might explain their ecological success. Specifically, we ask whether (1) the two focal species differ in xylem hydraulic capacity; (2) their vasculature is protected against or susceptible to drought-induced cavitation; and (3) root pressure allows either species to recover from catastrophic xylem failure by refilling embolized vessels.

RESULTS

Xylem Hydraulic Conductivity

Xylem hydraulic conductivity (K_S) and leaf-specific conductivity (K_L) of *C. ramosissima* culms was more than 1 order of magnitude higher than the same parameters measured in *M. claussenii*. Mean K_S was 43.7 ± 4.92 (mean ± SE) for *C. ramosissima* and 3.1 ± 0.53 kg m^{-1} s^{-1} MPa^{-1} for *M. claussenii* ($n = 12$ for each species). K_L for *C. ramosissima* and *M. claussenii* was 33.9 ± 1.0 × 10^{-4} and 1.1 ± 0.06 × 10^{-4} kg m^{-1} s^{-1} MPa^{-1}, respectively.

Vulnerability to Drought-Induced Cavitation

C. ramosissima culms were highly vulnerable to drought-induced cavitation, exhibiting greater than 50 percent loss in conductivity (PLC) at −1 MPa (Fig. 1A). In contrast, *M. claussenii* was much more resistant to cavitation, with a P50 value of ≤3 MPa (Fig. 1B). The mean midday leaf water potential experienced by *C. ramosissima* was −1.7 to −1.5 MPa, values predicted to induce >50 PLC. Midday leaf water potentials in *M. claussenii* varied from to −2.2 to −1.7 MPa, corresponding to PLC values of approximately 20.

Leaf Hydraulic Conductance

Leaf tissue properties were quantified by analyzing pressure-volume data (Fig. 2A). Turgor loss for *C.*
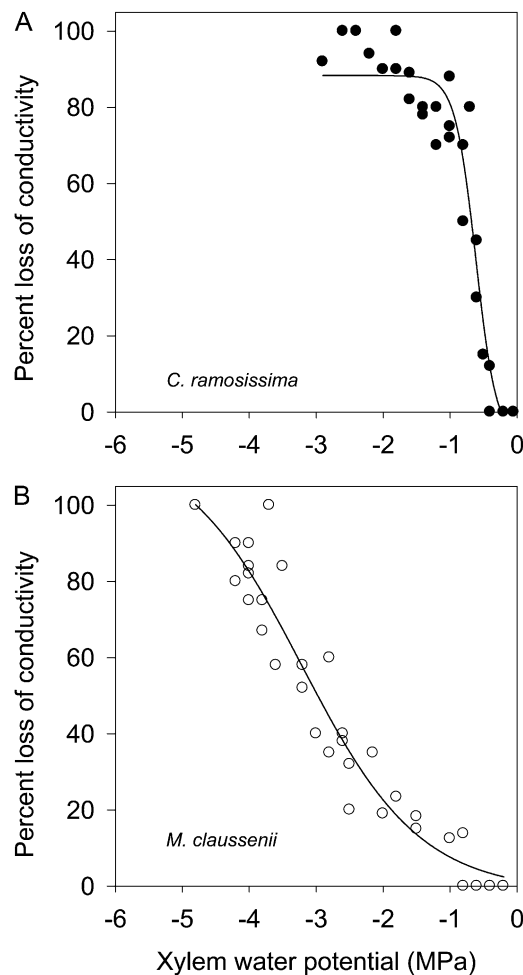
Figure 1. Vulnerability of culm xylem to drought induced by bench drying. Vulnerability curves were produced by fitting a third-order sigmoidal curve, PLC = 100/{1 + exp [$a(\Psi - b)$]} to the data with 50% loss occurring at ≥1 and −3 MPa for *C. ramosissima* (A) and *M. claussenii* (B), respectively.

ramosissima occurred at −1.98 ± 0.14 MPa, π_{ft} (osmotic potential at full turgor) was −1.68 ± 0.19 MPa, ε_{ft} (modulus of elasticity at full turgor) was 2.62 ± 0.21 MPa, whereas R_a (relative water content of tissue apoplasm) was 0.33 ± 0.07. *M. claussenii* lost turgor at −2.12 ± 0.21 MPa, π_{ft} was −1.58 ± 0.16 MPa, ε_{ft} was 1.49 ± 0.11 MPa, and R_a was 0.37 ± 0.04. Leaf area normalized C_{leaf} at pre- and post-turgor loss points were 181.8 ± 22.60 and 401.0 ± 46.74 mmol m^{-2} MPa^{-1}, respectively, for *C. ramosissima*, and 347.6 ± 38.61 and 533.5 ± 64.28 mmol m^{-2} MPa^{-1}, respectively, for *M. claussenii*. Maximum area-normalized hydraulic conductance of leaves (K_{leaf}) was 8.4 and 4.2 mmol m^{-2} s^{-1} MPa^{-1} for *M. claussenii* and *C. ramosissima*, respectively (Fig. 2B). In both species, K_{leaf} declined with decreasing Ψ_L, with a marked drop slightly preceding the turgor loss point.
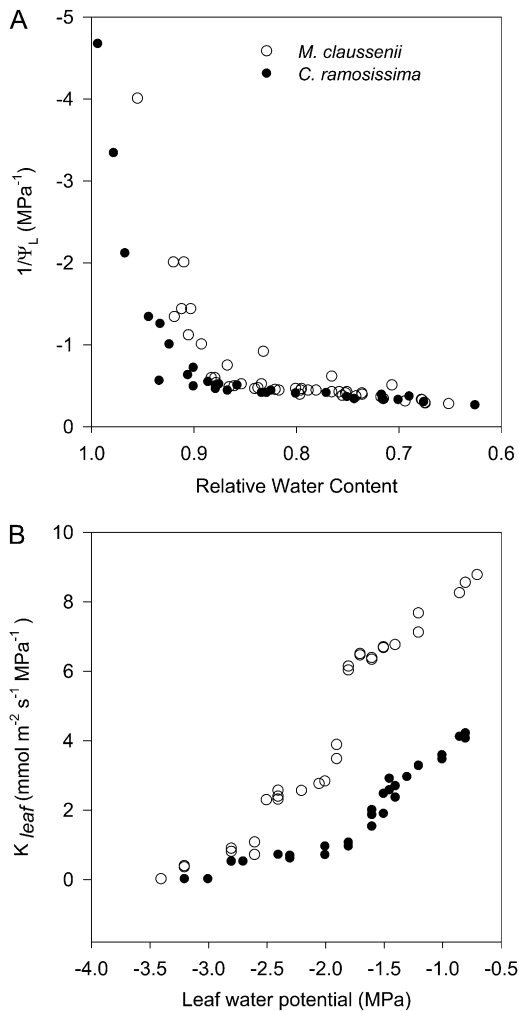
Figure 2. A, Pressure volume curves ($1/\Psi_L$, MPa^{-1}/relative water content) on single leaves of bamboo. These data were used to determine leaf capacitance (C) normalized by leaf area. B, Vulnerability of K_{leaf} (mmol m^{-2} s^{-1} MPa^{-1}) to drought-induced depression in Ψ_L induced by bench drying the leaves.

Diurnal Patterns of Leaf Water Potential, PLC, Stomatal Conductance, and Chlorophyll Fluorescence

Diurnal measurements of hydraulic and photosynthetic parameters were made in April and June, 2004. In terms of environmental parameters, April was warmer and less humid compared to June (Fig. 3, A and B). Leaf water potential for *C. ramosissima* ranged from −0.7 to −1.9 MPa through the day in April (Fig. 4A) and −1.0 to −1.5 MPa in June (Fig. 5A). In both cases, the minimum water potentials were sufficiently negative to cause losses in xylem conductivity of >50%, as estimated from measured vulnerability curves. In *M. claussenii*, leaf water potentials were between −0.5 and −2.2 MPa in April (Fig. 4A) and −0.5 and −2.0 MPa (Fig. 5A) in June. In both species, leaf water potentials in April approached the turgor loss point, although visible signs of wilting were not

observed. In June, both species exhibited leaf water potentials more positive than the turgor loss point (Fig. 5A).

Significant diurnal variation in PLC was observed in both species. PLC was assumed to be zero at dawn due to the abundant guttation from leaves and positive root pressures (see below). In both species, PLC was highest in the afternoon, but declined by 1,700, coincident with the measurement of positive root pressures. In April, maximum PLC in *C. ramosissima* was 60% to 70%, whereas for *M. claussenii* it was 30% to 40% (Fig. 4B). In June, PLC was between 20 and 40 for both species (Fig. 5B). The fact that *M. claussenii* exhibited greater PLC than expected from the tensions generated in leaves during midday may reflect the difficulty in measuring hydraulic conductivity in this species due to rapid wounding that reduced flow rates through excised culm segments (see "Materials and Methods").
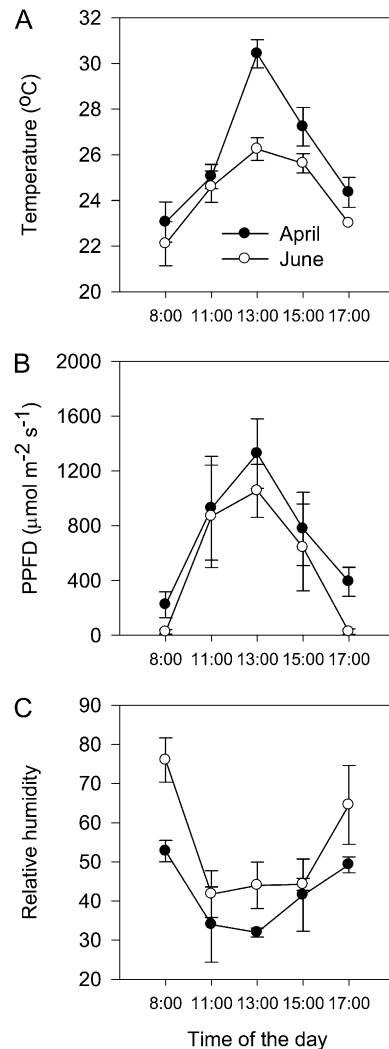
Figure 3. Diurnal microclimatic variation. A, Mean ambient temperature. B, Relative humidity. C, PPFD at the study site.
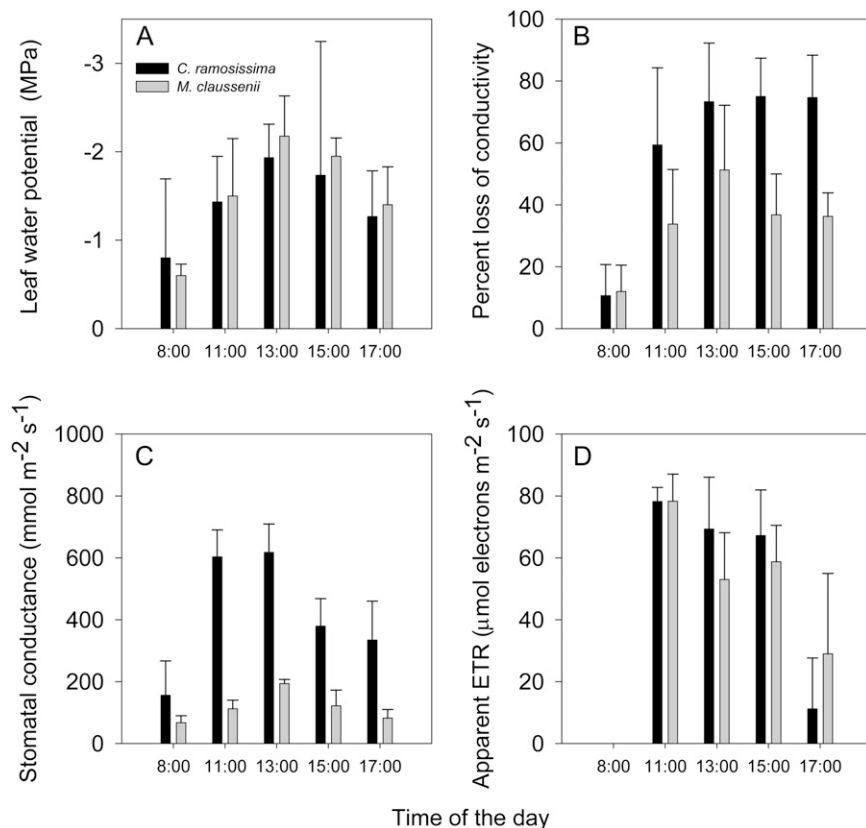
Figure 4. Diurnal variation in leaf water potential (Ψ_L; A), PLC (B), stomatal conductance (C), and apparent ETR (D) measured in *C. ramosissima* and *M. claussenii* in April 2004 (April 8–11). Mean ± 95% confidence intervals are presented for $n = 5$ individuals per sampling time.

C. ramosissima exhibited greater maximum stomatal conductance rates compared to *M. claussenii* during both April (Fig. 4C) and June (Fig. 5C), with the higher values reported for *C. ramosissima* reflecting the amphistomatous character of this species. Stomatal conductance declined in the afternoon for both species and overall both species exhibited higher stomatal conductance in June than in April.

Quantum yield of photosynthesis and apparent electron transport rate (ETR) exhibited trends parallel to stomatal conductance, decreasing in response to declining photosynthetic photon flux density (PPFD) values in the afternoon (Figs. 4D and 5D). Maximum mean ETR increased from April to June for both species; Figs. 4D and 5D), whereas the mean midday light levels ranged from 1,300 μmol m^{-2} s^{-1} in April to 1,100 μmol m^{-2} s^{-1} in June. Species differences may be due to *C. ramosissima* leaves having greater exposure to the sun due to greater self-shading in *M. claussenii*.

Root Pressure

Abundant guttation demonstrated the existence of positive xylem pressures in both species, which we quantified during both April and June, 2004. Systematic monitoring of root pressure using pressure transducers showed that both species exhibited positive root pressure for a shorter time span in April than in June (Fig. 6A). *C. ramosissima* exhibited a buildup of

positive root pressure between 9 PM and 7 AM in April compared to 5 PM and 9 AM during June (Fig. 6A). The average root pressure built by *C. ramosissima* culms spanning entire sampling time was 13.46 ± 2.68 kPa in April and 19.58 ± 4.54 kPa in June, although the temporal patterns were different across seasons. Maximal root pressure was recorded at 3 AM in April, whereas in June the root pressure peaked at 9 PM followed by a slow decline (Fig. 6, A and B). *M. claussenii* generated positive pressure only between 3 AM to 7 AM during both sampling periods (Fig. 6, A and B).

The root pressures measured in *C ramosissima* were of sufficient magnitude to generate positive pressures throughout the culms of the sampled individuals, whose stature was approximately 3 to 4 m above the ground. This level of root pressure, however, would not be sufficient to raise the water potentials of the entire xylem above atmospheric pressure in larger plants. It is possible that larger individuals of *C. ramosissima* produce greater root pressures or that the diffusion of air into embolized conduits is slowed by the dense fiber matrix surrounding each vascular bundle such that the vapor pressure of the emboli is <0.1 MPa. Alternatively, the values measured in this study may underestimate the actual pressures in the xylem as a result of small leaks introduced when the apparatus was attached to the culm. The situation for *M. claussenii* suggests that this may be the case because

Figure 5. Diurnal variation in leaf water potential (Ψ_L; A), PLC (B), stomatal conductance (C), and apparent ETR (D) measured in *C. ramosissima* and *M. claussenii* in June 2004 (June 18–23). Mean ± 95% confidence intervals are presented for $n = 5$ individuals per sampling time. Stomatal conductance, ETR, and Ψ_L could not be measured at 8 AM in June because the leaves were covered with water deposited as a result of condensation and profuse guttation.
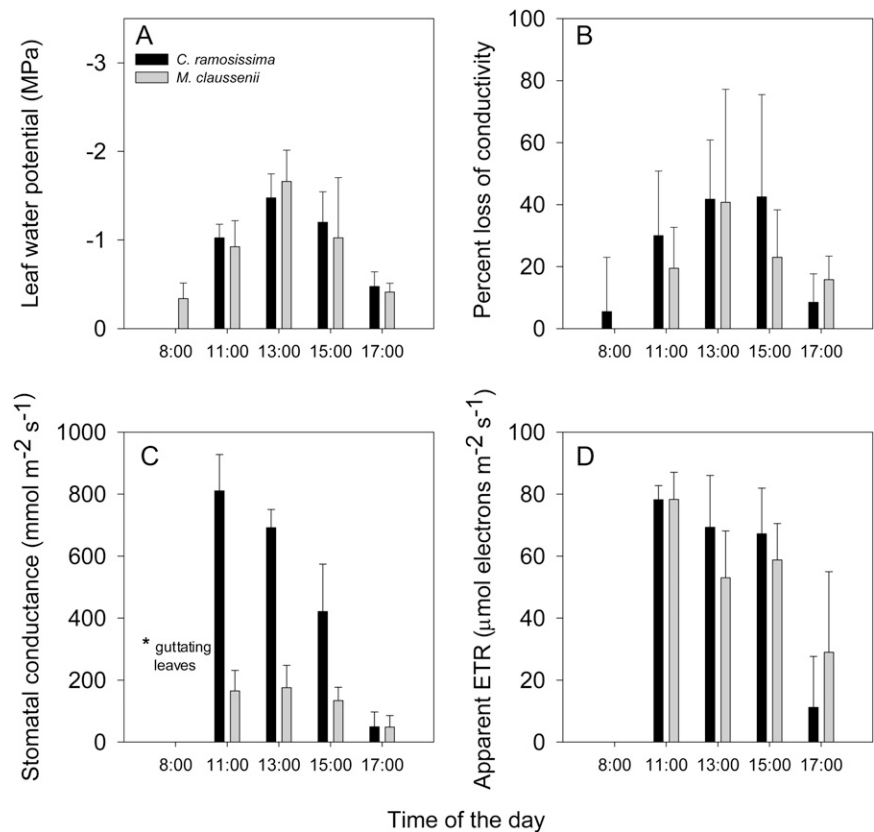
measured pressures were too small to account for visible guttation that was regularly observed in this species at heights above 2 m.

DISCUSSION

C. ramosissima and *M. claussenii* exhibit distinct traits with regard to their water transport properties. *C. ramosissima* has exceptionally high K_S and highly vulnerable xylem that cavitates and refills on a diurnal basis. *M. claussenii*, on the other hand, has lower K_S and more cavitation-resistant xylem. Compared to another bamboo species, *R. racemiflorum*, which has a P50 of −4.5 MPa (Cochard et al., 1994), both *C. ramosissima* and *M. claussenii* exhibit greater vulnerability to cavitation. Vulnerability of *C. ramosissima* xylem to cavitation and nighttime refilling using root pressure parallels the daily cycle of xylem failure followed by refilling exhibited by rice cultivars (Stiller et al., 2003).

Hydraulic differences between the two species are paralleled by differences in anatomical structure. The density of vascular bundles is higher in *C. ramosissima*, approximately 1,000 vascular bundles cm^{-2} as opposed to approximately 225 cm^{-2} in *M. claussenii* (Rúgolo de Agrasar and Rodríguez, 2003). The basal portions of *C. ramosissima* culms have vessel lengths of up to 1 m, whereas the entire *M. claussenii* vasculature is characterized by short (<20 cm) vessels. *C. ramosissima*

leaves are amphistomatous, as opposed to *M. claussenii* leaves, which have stomata only on the abaxial side.

Comparison with xylem hydraulic measurements on dicotyledonous woody stems shows that *M. claussenii*'s maximum K_S falls squarely within the range of values for dicotyledonous saplings growing at the same site (1.0–8.8 kg m^{-1} s^{-1} MPa^{-1}; Campanello et al., 2008), whereas *C. ramosissima*'s maximum K_S is higher than typical tree values, falling in the lower range of values reported for topical lianas (25 to >100 kg m^{-1} s^{-1} MPa^{-1}; Tyree and Zimmermann, 2002). The maximum measured K_L for both species, however, places *C. ramosissima* in the middle of reported values for temperate angiosperms, whereas *M. claussenii*'s K_L value sits at the low end of values reported for angiosperms (Tyree and Zimmermann, 2002). The reason for this is that both species of bamboo support large leaf areas relative to their cross-sectional area of their culms. The mean ratio of leaf area to culm cross-sectional area was $1.43 \times 10^4 \pm 1.26 \times 10^3$ for *C. ramosissima* and $3.6 \times 10^4 \pm 3.77 \times 10^3$ for *M. claussenii*; more than 1 order of magnitude larger than the range of values reported for 1.5-cm-diameter stems of temperate angiosperm trees (Tyree and Zimmermann, 2002). These values, however, are similar to those reported for dicotyledonous saplings (<1 m height) native to Iguazu National Park (Campanello et al., 2008).

The modest ETR$_{max}$ and low K_{leaf} measured for both species suggest that realized photosynthetic rates are
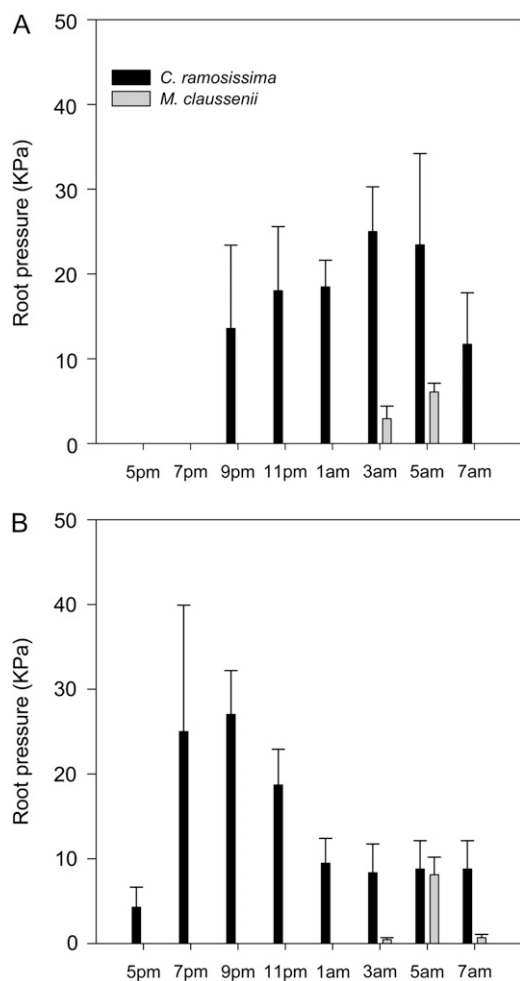
Figure 6. Root pressure measured on five culms at each sampling time, measured every 2 h (April 10–15; A and June 19–24; B). Error bars = mean ± 95% confidence intervals ($n = 15$) per sampling time.

low. In particular, K_{leaf} values, which are correlated with maximum assimilation rates (Brodribb et al., 2007), fall at the low end of the range (approximately 5–35 mmol m^{-2} s^{-1} MPa^{-1}) reported for angiosperms (Brodribb et al., 2005; Sack and Holbrook, 2006). Before both species exhibited substantial diurnal loss in culm hydraulic conductivity, this suggests that leaf parameters are more closely related to midday hydraulic capacity than to their maximum values. Characteristics of bamboo leaves, such as high silica content (>25% on a dry mass leaves in *Sasa veitchii*; Motomura et al., 2007), relatively low leaf nitrogen concentrations, and slow leaf litter decomposition rates (Singh and Singh, 1999), are consistent with leaves exhibiting lower photosynthetic rates. *C. ramosissima*, however, exhibited surprisingly high stomatal conductance values, which declined during the day as culm hydraulic conductivity decreased due to cavitation. Further studies are needed that explore the photosynthetic properties of this species in relation to patterns of water use. Nevertheless, the ability of the bamboo

growth form to support large leaf areas on their slender culms may, in part, compensate for what appear to be surprisingly low photosynthetic rates for plants that exhibit such rapid growth rates.

L. Montti, P.I. Campanello, and G. Goldstein (unpublished data) argue that the coexistence of multiple life history stages (seedlings, nonflowering and flowering culms) in space and time due to asynchronous flowering allows *C. ramosissima* to achieve monospecific dominance. Our data suggest that structural and hydraulic traits play a role as well. Based on our findings, we hypothesize that a combination of root pressure and high maximum K_S enables *C. ramosissima* to out-compete other growth forms despite its susceptibility to drought-induced cavitation. In contrast, *M. claussenii* occurs primarily in forest gaps, lacks the high K_S of *C. ramosissima*, and exhibits less root pressure. Rapid colonization of space by *C. ramosissima*, whose culms elongate at rates of 0.5 to 1 m d^{-1} (McClure, 1966), may be related to root pressure. Liese (2007) reported high solute (sugars) concentration in rhizomes of *Phyllostachys bissetii* and *Sasa palmate*, which diminished after the carbon was allocated to the culms and leaf tissue during the initial shoot growth. Vascular segmentation, especially between culms and leaves, may help prevent the spread of emboli to the less conductive leaves, whereas a disproportionate allocation to leaves likely contributes to the ability of *C. ramosissima* to colonize disturbed areas.

MATERIALS AND METHODS

Study Site and Species

Annual precipitation at Iguazu National Park is approximately 2,000 mm without a marked dry season, although drought spells of short duration can occur any time of the year and maximum and minimum temperatures are 42°C and 0°C, respectively (Campanello et al., 2007). We sampled from several populations of both species in gaps at different locations in Iguazu National Park. Laboratory measurements were made at the Centro de Investigaciones Ecologia Subtropicales' research facility and the Universidad de Buenos Aires' Laboratorio Ecologia Funcional, both located within the park. The plants sampled in this study ranged from 2 to 4 m in height for both species.

Chusquea ramosissima and *Merostachys claussenii* are running and clump-forming bamboo, respectively. Although both species initially produce erect culms (up to 4 m tall in *C. ramosissima*; Campanello et al., 2007), *C. ramosissima* acquires a scandent habit because it grows culms up to 10 m in height (Clayton et al., 2006). Maximum culm diameter in *C. ramosissima* is 1.5 cm, whereas *M. claussenii* has wider and more robust culms, reaching 3 cm in diameter and attaining maximal culm height of 8 m (L. Montti, P.I. Campanello, and G. Goldstein, unpublished data). Vessel diameters in *C. ramosissima* range from 40 to 60 μm in the central bundles; in *M. claussenii* vessel diameters range from 60 to 90 μm in mature culms (Rúgolo de Agrasar and Rodríguez, 2003). Another notable difference between the two species is that *C. ramosissima* culms are solid as opposed to the hollow culms of *M. claussenii*. *C. ramosissima* and *M. claussenii* are monocarpic, fast growing, and quick to take advantage of gaps, which they colonize rapidly. Populations of *C. ramosissima* flower asynchronously with irregular flowering intervals on the order of 10 to 15 years (L. Montti, P.I. Campanello, and G. Goldstein, unpublished data), whereas *M. claussenii* flowers synchronously. *M. claussenii* clumps can cover an area as large as 250 m^2. Both species are evergreen and exchange leaves continuously.

Xylem Hydraulic Conductivity

K_S of *C. ramosissima* was measured on six culms each in April and in June. Six culms were sampled for *M. claussenii* in April and five culms in June.

Culms were cut under water from bamboo clumps separated by a minimum distance of 50 m before 7 AM, while stems of *C. ramosissima* were still bleeding water, and leaves were saturated. Measurements were made on culm segments longer than 2.5 m (*C. ramosissima*) and 0.75 m (*M. claussenii*) to avoid vessels open at both ends, with all samples collected from near the base of the culm to minimize the number of nodal branches. Maximum vessel lengths were determined using the air-injection method (Zimmerman and Jeje, 1981).

Bamboo culms and attached leaves were kept in black plastic bags moistened from inside (two to three bags, if necessary) to prevent water loss before being connected to the flow-measuring apparatus. Although we endeavored to use culm segments that did not have any nodal branches, this was not always possible, although in all cases the number of attached leaves was small (<5%) relative to the downstream leaf area. These leaves were removed followed by flushing of stems with distilled water to ensure that no embolisms were present. Cut nodal branches were sealed with cyanoacrylate glue to prevent water from leaking out during the measurement. The cut ends of the *M. claussenii* culms had to be reshaved immediately prior to making measurements as the conductivity of *M. claussenii* culms decreased rapidly with time and within 5 min essentially ceased, probably as a result of response to wounding (Liese, 1998).

This blockage appeared to be located entirely at the cut ends of the segment because reshaving the cut surfaces resulted in an immediate increase in flow that would remain steady for several minutes, after which it slowly declined. In contrast, measurements of *C. ramosissima* remained steady for an hour (the maximal time for which we had left the stem attached for observation) and the flow did not increase in response to reshaving or recutting.

K_S and K_L were calculated as $K_S = JL/\Delta PA_x$ and $K_L = JL/\Delta PA_L$, where J is the flow rate (kg s^{-1}), L is the length of the stem segment (m), ΔP is the pressure drop across the segment (MPa), A_x is the cross-sectional area of the culm (m^2), and A_L is the leaf area distal to the measured segment (m^2). Flow rates were measured using a portable steady-state flow meter as described in Feild and Brodribb (2001) calibrated against a balance (Mettler Toledo AB 104-S, readability of 0.1 mg). Distilled water was used to make a perfusing solution of 20 mM KCL, which was supplied at a delivery pressure of 5 kPa. The entire stem cross-section was considered conductive for *C. ramosissima*, whereas the conductive area (A_x) for *M. claussenii* was estimated by subtracting the area of hollow circular pith from the total area of the culm transverse surface. Leaf area distal to the measured segment was measured using a leaf area meter (LI-COR 3100C). We obtained steady-state values by averaging five measurements, each recorded for 60 s.

Vulnerability to Drought-Induced Cavitation

The vulnerability of the xylem-to-water stress-induced embolism was characterized in both culms and leaves. Vulnerability in culms was quantified by measuring the PLC of increasingly dehydrated segments (Sperry et al., 1993). Culms, 1 m in length, from the upper one-half of the bamboo culms were cut under water. These culms were placed immediately in tightly sealed plastic bags containing wet tissue paper. In the laboratory, the culm segments were removed from the bags and allowed to dehydrate under laboratory conditions (20°C) for between 0 to 5 h. A 20-cm piece consisting typically of one internode was then excised under water and the flow rate through this segment measured using 1-mL pipettes. Following this initial measurement, each test segment was flushed to the maximum flow rate, allowing calculation of PLC. Because vessel lengths decrease toward the culm apex, it is unlikely that air was able to enter into the test segment from either of the cut ends or that a vessel open at both ends was present in the test segment.

Leaf Hydraulic Conductance

K_{leaf} (mmol m^2 s^{-1} MPa^{-1}) was determined by measuring the Ψ_L relaxation rate of leaves detached under water as described in Brodribb and Holbrook (2003): $K_{leaf} = C \ln (\Psi_o/\Psi_f)/t$, where C is the capacitance per leaf area (kg MPa^{-1} m^{-2}), Ψ_o is the leaf water potential prior to rehydration, Ψ_f is the leaf water potential after dehydration, and t is the time of rehydration (s).

K_{leaf} was measured for single leaves dehydrated to a range of initial water potentials. Branches were cut early in the morning while Ψ_L was high, and most leaves were removed except for terminal clusters of four to eight leaves. These branches were then allowed to desiccate very slowly to prevent large gradients in Ψ_L from developing. Periodically, branches were bagged and placed in the dark for 30 min to ensure stomata were closed and Ψ_L was homogeneous among leaves. Two leaves were then removed to determine Ψ_o

of the leaves remaining on the branch, after which two further leaves were detached with their pseudopetioles underwater and allowed to rehydrate as described above. The standard rehydration period was between 30 and 45 s. Branches were progressively desiccated during the course of a single day, and K_{leaf} was monitored as Ψ_L dropped.

Leaf capacitance per area was estimated by multiplying the intrinsic capacitance (MPa^{-1}), as calculated from pressure volume curves, by the mass of water per unit leaf area (kg m^{-2}) and the leaf dry mass per unit area (kg m^{-2}). Pressure volume curves were derived from five samples per species using the bench drying technique (Tyree and Hammel, 1972).

Diurnal Measurements of Hydraulic Parameters and ETR$_{max}$

We measured hydraulic properties and photosynthetic capacity of *M. claussenii* and *C. ramosissima* every 2 h starting at 8 AM and continuing until 6 PM on five clumps of each species. Measurements took place over a period of 4 d in April and 6 d in June 2003. The restricted sampling for PLC reflects the greater time required to make these measurements, which limited the number of replicates that could be made between two consecutive sampling times.

Leaf water potential was measured using a pressure chamber (PMS 1000; PMS Instrument Co.). We immediately wrapped the excised leafy shoots in plastic bags until they were inserted in a pressure bomb within 5 min for measuring water potential. Stomatal conductance was measured using a portable steady-state porometer (LI-COR LI-1600). *C. ramosissima* leaves are amphistomatous, whereas *M. claussenii* has stomata restricted to the abaxial surface. Data reported for *C. ramosissima* represent the sum of measurements made on abaxial and adaxial leaf surfaces. Conductance measurements were made within 30 s of placing the leaf in the cuvette while maintaining the humidity inside the porometer chamber near ambient.

Due to its portability and availability, we used a miniPAM portable fluorometer (Waltz) to measure the instantaneous ETR as a measure of photosynthetic capacity at native light levels (1,200–1,800 μmol m^{-2} s^{-1}). We calculated ETR as Yield × PPFD × 0.5 × 0.84 (Björkman and Demmig, 1987; Edwards and Krall, 1992), assuming a constant leaf absorbance value of 0.84 (Schreiber and Bilger, 1987).

We used short culm segments (20 cm) for measurement of PLC due to cavitation. These segments were cut under water and transported to the lab within 5 min of cutting. The cut segments were wrapped in thoroughly wet plastic bags containing wet paper towels to prevent postexcision desiccation. Initial flow rates through these segments was measured at a constant pressure (<3 kPa) using 1.0-mL pipettes to measure volume flow rates using a perfusion solution of 20 mM KCl. Given that xylem diameters ranged from 90 to 110 μm in *C. ramosissima* and 100 to 110 μm in *M. claussenii* (measured with a light compound microscope Wild M20), there was little chance that air bubbles trapped within xylem vessels would be dislodged during the flow measurements under such low delivery pressure.

After the initial flow measurement was made, each sample was flushed at a higher pressure (100 kPa) for 60 to 120 s to remove any air bubbles within the xylem and the flow rate remeasured (J_{max}). PLC was calculated as the difference between the original flow rate measured at low pressure ($J_{initial}$) and the maximum value obtained after high pressure flushes (J_{max}): PLC = 100 $(J_{max} - J_{initial})/J_{max}$.

Root Pressure

Measurements of root pressure were made on three nights per species during April and June 2004. Five bamboo culms per species were cut approximately 3 cm above the soil at 5 PM and the cut end was fitted with a tube connected to a pressure transducer (Omega 236PC100GW, 12VDC, 1 PSI = 1 mV). The tube was filled with water, making sure that no air bubbles were trapped. Pressures were read every 2 h between 5 PM to 7 AM using a multimeter. Because exudation was not observed in *M. claussenii* culms until 4 AM, we cut five different stems every 2 h between 12 to 4 AM and a stiff 2-cm-long tube was connected to the cut end of the culms to facilitate observation of initial exudation. If bleeding was observed at a particular sampling time, we attached the pressure transducer and recorded the pressure within 2 to 3 min.

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