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Water relations of a tropical vine-like bamboo (*Rhipidocladum racemiflorum*): root pressures, vulnerability to cavitation and seasonal changes in embolism

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Abstract

The occurrence of root pressure, the vulnerability of xylem vessels to drought-induced cavitation, and the seasonal changes in hydraulic conductivity due to embolism were studied in the culms of *Rhipidocladum racemiflorum* (Steud.) McClure, a tropical vine-like bamboo from central Panama. Positive hydrostatic potentials up to 120 kPa occurred only during the wet season when the transpiration rate of the plant was low, i.e. at night or during rain events. Although the xylem vessels were large and efficient for conducting water, they were highly resistant to cavitation. Xylem water potentials lower than -4.5 MPa were required to induce 50% loss of hydraulic conductivity in culms. The minimum water potential reached -3.75 MPa at the end of the 1993 dry season, so loss of hydraulic conductivity due to embolism remained <10%. The species is adapted to drier habitats both by way of a low vulnerability to xylem cavitation and by root pressures in the wet season that could refill vessels that became embolized during a severe dry season.

Key words: *Rhipidocladum racemiflorum*, root pressure, cavitation, embolism, water relations.

Introduction

Xylem conduits are now known to be vulnerable to drought-induced embolism (Tyree and Sperry, 1989).

When xylem pressure potential, Ψ_{xp}, becomes sufficiently negative, the water columns may cavitate, impairing water flow through the plant. This situation is critical for the plant, so adaptations or mechanisms must exist to prevent or repair it. Vulnerability to cavitation may be particularly serious for woody monocotyledons like palms or bamboos because (1) they lack secondary xylem—all the vessels of the stipe or the culm are formed only once at the beginning of the life of the organ and can not be replaced; (2) the vessels are large, which confers to the xylem a high efficiency in water conduction, but also, as suggested by Zimmermann (1983), a reduced 'safety'; and (3) these species usually are shallow-rooted.

We report experiments made on *Rhipidocladum racemiflorum* (Steud.) McClure, a vine-like bamboo native from the tropical moist forest in the lowlands of Panama. Central Panama has a seasonally dry habitat; during the 4-month dry season, the upper layers of the soil become dry (Becker *et al.*, 1988). These plants are thus likely to experience low water potential. We studied the daily and seasonal progression of xylem embolism and Ψ_{xp} in the culms of this species. We also measured the vulnerability of the vessels to drought-induced cavitation along with the occurrence of positive hydrostatic potentials due to root pressures. Root pressure might provide a mechanism to refill cavitated vessels in a species not capable of forming new vessels by secondary growth. We discuss the results in terms of adaptation of *Rhipidocladum* to drought.

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Materials and methods

Plant material and sites

Experiments on *Rhipidocladum racemiflorum* (Steud.) McClure, Poaceae, were conducted from October 1992 to May 1993 on Barro Colorado National Monument (9° 7.5′ N; 79° 52′ W), central Panama. Because plant sampling was restricted on Barro Colorado Island, culms were collected around the laboratory clearing at three sites. *R. racemiflorum* is a vine-like bamboo with 5–10 m long culms. The culms form dense clumps up to 1 m in diameter (Croat, 1978). The culms are 10–30 mm diameter at the base and 5–10 m long; they droop under their own weight or obtain support from adjacent plants. On each culm, leafy branches 0.2–0.5 m long are attached in dense whorls at each node; the nodes are spaced approximately every 0.5 m along the stems. For this study we assumed that each clump represented one individual.

Average precipitation in the wet season (mid-April to mid-December) is 2400 mm, and 215 mm in the dry season (mid-December to mid-April; Windsor, 1990). The dry-season humidities rarely fall below 65% RH at midday. Wet season humidities are generally >90%. Temperatures, all seasons, range from 23 to 33 °C daily minimum and maximum, respectively. The 1993 dry season had about 50% more precipitation than usual. Rainfall for the 4 months starting in January 1993 was 101.3, 34, 67.5, and 124.3 mm.

Positive xylem pressure potential

Positive xylem pressure potential (Ψ_{xp}) in the culms of *Rhipidocladum* was measured with electronic pressure transducers (Omega Engineering Inc., Stamford, CT; 0.5 kPa accuracy)[6]. The culms were cut 5 mm above a node where the stem is not hollow or brittle. The cross-section of the culm stump was recut with a fresh razor blade and connected to a pressure transducer with 30-mm-long rigid plastic tubing that was filled with distilled water at the beginning of the experiment. The pressure transducer was connected to a data logger (model DT100, Datataker, Zi-Tech Corp., Mountain View, CA) and readings were made continuously every 10 min over 2–3 d. At the end of that period, the culm was recut one node below or a new culm was selected, and the transducer reapplied. Measurements were made on 15 culms from four individuals of *Rhipidocladum*. Most of the measurements were made at the base of the culms, less than 0.5 m above ground level. Ψ_{xp} also was measured at a height of 5 m where the culm reached the highest point above the ground, or in other cases near the apex of the drooping culms, which ranged from 0–4 m above the soil level.

Vessel anatomy

When a transpiring plant is cut in the air, the sap in the xylem conduits is sucked into the vessel lumina until the meniscus encounters and stops at an intervessel membrane. It is therefore important to know the length of the vessels and the extent of the culm that becomes air-filled after excision to measure the native-state percentage loss of hydraulic conductivity (*PLC*) prior to cutting of culms. Current methods to determine vessel length are inaccurate and may be misleading (Tyree, 1993). We determined the length of the culm that became embolized after excision by measuring directly the decrease in *PLC* due to

embolism along the culm. At the excision point, *PLC* should be the highest (close to 100%) because all the vessels are air-filled, and should decrease down to the native-state level for a length more than that of the longest cut vessel. Three representative unstressed culms, 10 m long, were excised at a node near ground level and allowed to dehydrate for 30 min. This period was presumed to be long enough to suck the sap the full length of the cut vessels without inducing extra cavitation in intact vessels. The *PLC* was measured at each node acropetal of the excision over a distance of 4.5 m by the following technique.

Seasonal progression of negative Ψ_{xp} and PLC

The seasonal progression of Ψ_{xp} and *PLC* was measured periodically from November 1992 (end of the rainy season) to May 1993 (beginning of the new rainy season); Ψ_{xp} was measured with a pressure chamber on 3–5 branches collected randomly on different culms from the same individuals. Immediately after sampling, the branches were enclosed in a plastic bag and Ψ_{xp} was measured in the laboratory within 30 min. The native-state *PLC* was assessed by the methods of Sperry *et al.* (1987a). For each sampling date, one culm, 5–10 m long, was excised in the air at ground level and brought to the laboratory where it was immediately recut under water >2.5 m distal of the base. The part of the culm where the *PLC* was affected by air sucked in after the cutting was discarded (see Results). Ten segments, 0.1 m long, were then excised under water from the remaining culm. Each segment was centred on a node because the internodes of *Rhipidocladum* have a hollow pith. All branches attached to the node were excised under water, leaving 20 mm of leafless segments. Air was then removed from the hollow pith of the samples and the cross-section was recut with a new razor blade. The initial hydraulic conductivity, K_i, was determined by measuring the flow rate through each sample with a 2 kPa pressure difference. Such a low pressure was necessary because higher pressures were found to displace air from most of the embolized vessels. After determination of K_i, the samples were perfused for 5 min with degassed distilled water at 0.1 MPa pressure difference. One perfusion usually was sufficient to remove the embolism in the vessels. The maximum conductivity, K_m, was then measured. *PLC* was calculated from:

$$PLC = (1 - K_i/K_m) \times 100.$$

Vulnerability curve

The vulnerability curve is the relation between minimum Ψ_{xp} reached during a dehydration and the corresponding *PLC* induced by dehydration. This relation was obtained by successively air-dehydrating 11 excised culms over different periods. At the end of each dehydration period Ψ_{xp} of one culm was measured on 5 branches chosen randomly. These were enclosed in an airtight plastic bag at the beginning of the experiment for equilibration with the xylem water potential of the culm. After Ψ_{xp} was measured, the culm was enclosed overnight in a large, black, airtight plastic bag. *PLC* in the xylem was then assessed with the method described earlier.

Results and discussion

Figure 1 shows the daily progression of Ψ_{xp} measured with the pressure transducers and representative of the
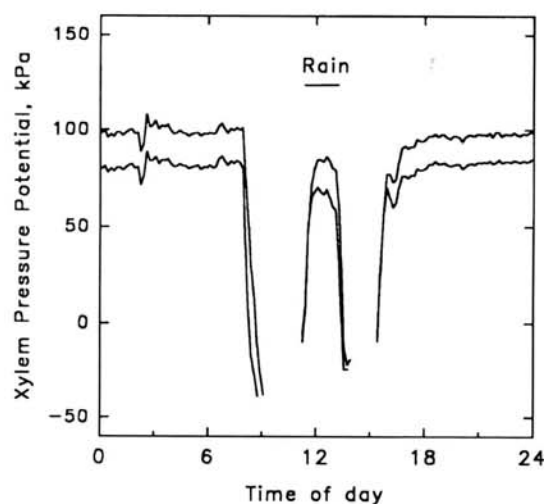

Fig. 1. Daily course of xylem pressure potential, Ψ_{xp}. Ψ_{xp} was measured with pressure transducers attached to the base of two cut culms of the same individual. The line above the midday rise in Ψ_{xp} indicates a rainy episode. Missing data (a break in the line) indicates when Ψ_{xp} was negative enough to suck air into the linkage between the stem and the pressure transducer and thus the pressure readings were no longer valid.
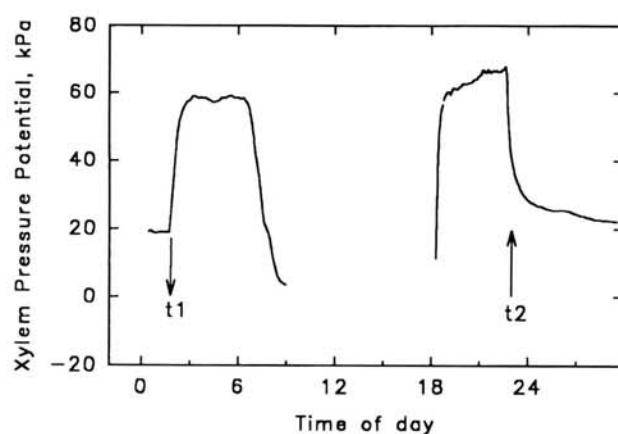

Fig. 2. Gravitational-induced changes in hydrostatic potential. A pressure transducer was mounted at the apex of a flexible, 5 m culm. After 1 h of measurement, the culm was bent 4.5 m down (t1). The second night, the apex was moved back to its initial position 5 m above ground (t2). Changes in hydrostatic potential closely agreed with the changes due to gravitational potential. Breaks in the line are for the reason indicated in Fig. 1.

rainy season. Shown are the Ψ_{xp} at ground level for two culms from the same individual. Positive Ψ_{xp} was observed each night and during the day only during rainstorms. Ψ_{xp} was constant at night and ranged from 80–120 kPa, larger culms tending to generate higher Ψ_{xp}. These values are comparable to those generated during the spring by *Vitis vinifera* (up to 100 kPa, Sperry *et al.*, 1987*b*) or at the base of *Acer saccharum* trees (56 kPa, Sperry *et al.*, 1988). Some other grasses (Poaceae), which are larger than *Rhipidocladum*, can generate considerably higher pressures, for instance, 200 kPa in *Bambusa arundinaceae*, another vine-like bamboo in Panama (Cochard, unpublished data), and 300 kPa in sugarcane, *Saccharum* spp. (Neufeld *et al.*, 1992). Both sugarcane and *Zea mays* appear to undergo xylem embolism during the day and vessel refilling at night by means of root pressure (Tyree *et al.*, 1986).

Transitions from positive to negative ranges were rapid (30–60 min). After Ψ_{xp} became less than −20 to −40 kPa, Ψ_{xp} tended to come back to the atmospheric value. For such tensions the plastic tubing connecting the pressure transducer to the culm cavitated and became air-filled, the hydrostatic potential of water in the tubing thus was decoupled from the Ψ_{xp} in the xylem sap. Positive Ψ_{xp} values were not observed in the dry season.

The Ψ_{xp} value measured depended on the height above ground of the point at which Ψ_{xp} was measured on the culm. This is illustrated by the experiment represented in Fig. 2 in which the apex of a culm was moved up and down on successive nights during the rainy season. A pressure transducer was connected to the apex of a culm 5 m above ground. In that position the Ψ_{xp} stabilized at 20 kPa on the first night. At 2 a.m., the apex of the

flexible culm was bent down 4.5 m; Ψ_{xp} rapidly increased up to 60 kPa until dawn. The next night the reverse experiment was performed: the tip of the culm was raised 4.5 m and the Ψ_{xp} dropped about 45 kPa. The observed change in Ψ_{xp} was approximately the expected amount from the gravitational potential effect on total water potential, Ψ. The value of Ψ should be the same everywhere within a plant under a condition of zero water flow, i.e. independent of height. As the transducer is raised to a height of h m, the gravitation potential component of Ψ will rise $\rho g h$ where g is the acceleration due to gravity and ρ is the density of water; for an increase in h of 4.5 m, $\rho g h$ equals 45 kPa, so Ψ_{xp} must decrease by a corresponding amount.

The xylem anatomy of *R. racemiflorum* was typical of woody monocotyledons. Each vascular bundle contained two large vessels with an average diameter of 196 μm (sd = 55, n = 424) comparable to many lianas species. As a consequence the stems were efficient for water conduction. For instance, the hydraulic conductivity of a culm 5 mm in diameter was about 2×10^{-4} kg m s^{-1} MPa^{-1}. This was comparable to other lianas species (Ewers, 1985), but 10 times as much as similar diameter stems of *Schefflera morototoni* or *Acer saccharum* (Tyree *et al.*, 1991) and 100 times more than *Thuja occidentalis*.

Figure 3 shows the changes in hydraulic conductivity along the culms that were cut in the air and dehydrated for 30 min. As predicted, the loss of conductivity was nearly 100% in the first node close to the cut and then decreased linearly over the first 2.2 m, probably because of the random distribution of the vessel ends. For the nodes situated further than 2.2 m from the initial cut, the loss of conductivity was not significantly different from the native-state level. Consequently, the basal 2.5 m of
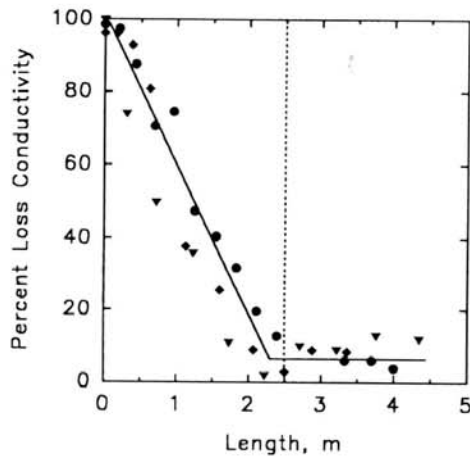
Fig. 3. Loss of conductivity versus distance from the base of cut culms. Three culms (different symbols) were cut in the air and left to dehydrate for a short period. The loss of hydraulic conductivity due to air embolism was then measured on each node starting at the cut end (length = 0). Nodes situated at a distance > 2.5 m from the cut end (vertical line) displayed a degree of embolism not significantly different from the native-state level.

the culms was always recut under water and discarded for all the following measurements of hydraulic conductivity.

The minimum Ψ_{xp} of the leafy branches of *Rhipidocladum* were significantly reduced during the dry season and reached -3.75 MPa at the end of the dry season (Fig. 4). But the native *PLC* due to embolism remained below 10% over the entire period; no new embolism developed during the 1993 dry season because the xylem vessels of this species were remarkably resistant to cavitation.
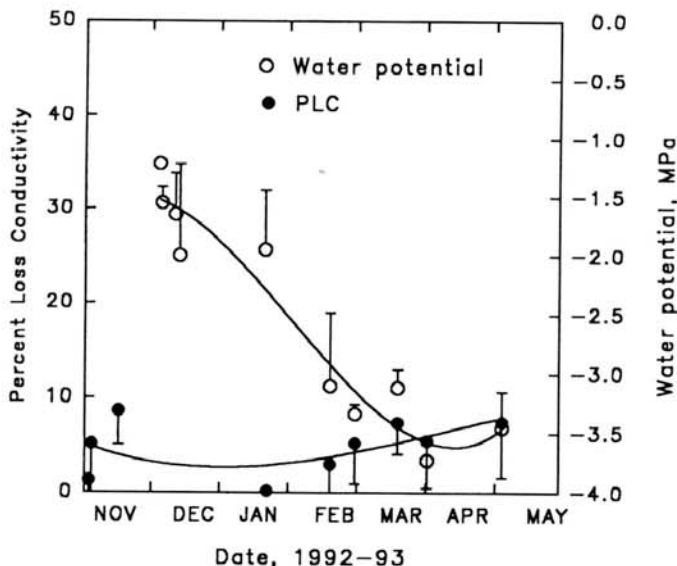
The vulnerability curve of the culms of *Rhipidocladum* to air embolism is shown on Fig. 5. *PLC* increased in the xylem vessels only when Ψ_{xp} reached values below -4 or -4.5 MPa. Then the *PLC* increased steeply and the culms were fully embolized for Ψ_{xp} equal to -5 MPa. Thus this species is more resistant than many tracheid-bearing species (Cochard, 1992) and many diffuse-porous species (Cochard *et al.*, 1992). Some authors have suggested that there could be a trade-off between the xylem efficiency and its safety (Zimmermann, 1983) or between the vessels' diameter and their vulnerability to drought-induced cavitation (Salleo and LoGullo, 1986, 1993). This is not the case for *Rhipidocladum*, whose xylem is efficient for water transport, but is one of the most resistant species to cavitation that we have studied (Zotz *et al.*, 1994).

Zimmermann (1983) argued that plants with large vessels need relatively few vessels to support transpiration. If a small number of these vessels are lost due to mechanical injury, pathogenic attack, or cavitation it will result in a relatively large loss of hydraulic efficiency. This is especially true of monocots since they lack secondary growth to replace dysfunctional vessels. Root pressure may be an important mechanism in monocots to dissolve drought-induced embolisms, thus regaining functionality of vessels.

Although the 1993 dry season was relatively wet, the minimum water potential reached values close to the threshold water potential that induces embolism (Fig. 5). There is evidence that some species operate near this
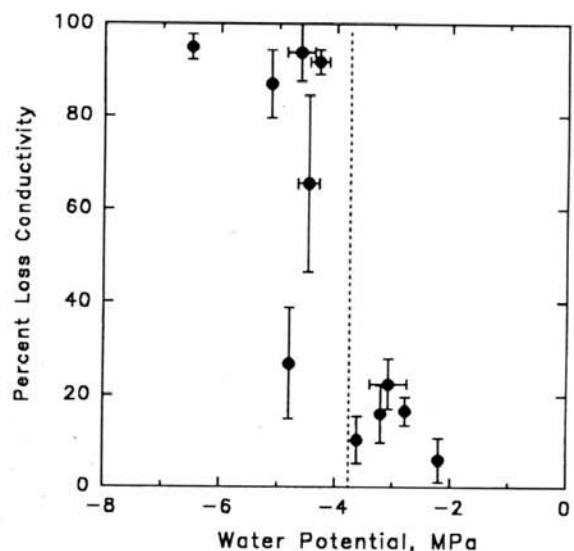

Fig. 4. Seasonal progression of midday water potential and percentage loss hydraulic conductivity, *PLC*. The water potential was measured on five branches chosen randomly on different culms of the same individuals. The loss of hydraulic conductivity is reported as the mean. Vertical error bars represent 1 standard deviation (*n* = 10 segments).

Fig. 5. Vulnerability curve. Each point represents a cut culm dehydrated in the air and whose minimal Ψ_{xp} was measured on five bagged branches. The culm was then rehydrated and loss of conductivity due to embolism measured on segments excised under water. Bars represent 1 standard deviation; vertical error bars are based on means of *n* = 10 segments per culm and horizontal error bars are based on means of *n* = 5 determinations per culm. The vertical line gives the minimal midday Ψ_{xp} observed in the dry season of 1992.

'point of catastrophic xylem dysfunction' (Tyree and Sperry, 1988) and that they cope with the situation in which Ψ_{xp} decreases by regulating water loss (stomatal closure, leaf fall). It seems likely that under the conditions that prevail during most of the dry seasons in central Panama, the minimum water potential of *Rhipidocladum* culms may become much more negative and that embolisms could develop. At the beginning of the rainy season, *Rhipidocladum* would be able to generate up to 120 kPa of xylem pressure for at least 12 h at night and for longer periods with rain during daylight hours. It has been demonstrated that positive Ψ_{xp} can dissolve air embolism in the xylem (Tyree and Yang, 1992). The time it takes for embolisms to dissolve depends on the magnitude of the positive pressure and on the length of the diffusion path from the embolized vessel and the stem surface. The *Rhipidocladum* stem is hollow, possibly an adaptive feature to reduce the path length for diffusion. In a few hours or days, the xylem conductivity would be completely restored, so root pressures may increase the lifespan of the culms. It is unlikely that root pressure may serve as a repairing mechanism on a daily basis in droughted plants because it is produced only during the rainy season, i.e. when Ψ_{xp} is too high to induce cavitation events.

In conclusion, *Rhipidocladum* can be classified as a drought-tolerant species. Because of its shallow rooting patterns, the plant experiences severe drought conditions during the dry season. The plant copes with this situation with xylem vessels that tolerate low Ψ_{xp} without cavitation and with a possible mechanism, root pressure, that repairs embolism during the wet season. At this time, the role of root pressure in embolism dissolution is speculative since we have no evidence of substantial *PLC* during the dry season. Stomatal closure under water stress may well be a 'first-line of defence' against prolonged drought. But stomatal closure can not totally prevent soil dehydration especially if co-occurring species are competing for water at the same site; so root pressure may be the ultimate recourse for survival of *Rhipidocladum*. We know of no other studies of the water relations or general physiology of bamboo species. Further studies of this interesting group of plants may provide valuable insights to understand the strategies taken by diverse taxa in response to a water stress.

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