ORIGINAL PAPER

A survey of root pressure in 53 Asian species of bamboo

**Fusheng Wang · Xinli Tian · Yulong Ding ·
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Abstract

· *Introduction* Root pressure is a potentially important mechanism for dissolving embolisms in previously cavitated vessels, but the occurrence of root pressure is not a universal property in plants.

· *Material and methods* We suggest that root pressure might be more common in monocots than dicots because in dicots, cambial growth can replace embolized vessels but monocots have no secondary growth and hence need mechanisms for repair of embolized vessels. In this paper, bubble manometers were used to investigate 53 bamboo species from 10 genera.

· *Results* A survey of root pressure in 53 Asian species of bamboo revealed that all possessed root pressure and in some species root pressure was high enough to cause guttation of liquid from leaves at predawn. In contrast, in woody vines were we might expect root pressure to be common because of reduced cambial growth, root pressure

is comparatively rare. Xylem exudate and guttation fluid had an osmotic pressure greater than root pressure and this can be explained in terms of a low reflection coefficient in context of how root pressure is generated according to the composite membrane model of roots.

· *Conclusion* We conclude that the next logical step is to survey bamboo species to determine how common cavitation evens are and to determine if refilling of vessels occurs by root pressure.

Keywords Root pressure · Osmotic pressure · Asian species of bamboo

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1 Introduction

Bamboo is an important renewable resource of economic importance in the tropics and subtropics. Bamboo is a woody monocotyledonous perennial grass that can be used in furniture building and manufactured into laminate flooring which is claimed by retailers to be more durable than oak and maple. Bamboos provide a sustainable wood resource because they can be grown to harvestable size and quality in 4–6 years in subtropical climates versus 50–100 years for harvestable oak and maple in temperate climates.

Bamboo, like all monocots, has no secondary growth; hence, the xylem vessels in bamboo stems have to remain water filled and functional for many years otherwise shoots or whole plants will die. Bamboo shoots can survive 5–20 years and regenerate asexually from rhizome which potentially could be much older; hence, the vessels must remain functional for a rather long time. In contrast, trees with secondary growth can replace functional xylem annually. Because water stress and freeze–thaw events can embolize vessels (Tyree and Zimmermann 2002), many

people have wondered about the possible role of root pressure in refilling embolized vessels with water either on a daily basis or annually in early spring in temperate regions. Hence a number of people have surveyed trees and woody vines for the occurrence of root pressure (Ewers et al. 1997; Fisher et al. 1997). So far, the only known report of root pressure in bamboo was in a vine-like species (*Rhipidocladum racemiflorum*, see Cochard et al. 1994).

Bamboos are much more common in tropical and subtropical ecosystems than in temperate ecosystems, but the reasons for this are unknown; however, it is possible to speculate why. Wide xylem vessels are susceptible to freeze–thaw-induced embolism (Cochard et al. 1994; Sperry and Sullivan 1992; Sperry et al. 1994) when vessels are >40 μm diameter. When water freezes, the air dissolved in it comes out of solution and forms air pockets between the ice crystals. The risk of embolism thus arises when the ice melts leaving many tiny air bubbles mixed with liquid water. These bubbles must dissolve before the water is again under tension due to renewed transpiration otherwise the bubbles will seed an embolism. In large vessels (>40 μm), the small bubbles tend to combine into larger bubbles that take longer to dissolve and are more likely to seed embolisms. Many bamboo species have vessels >40 μm and hence are likely to cavitate when they freeze/thaw. Hence, species that grow in temperate areas probably need root pressure to refill embolized vessels in the same way as wild-grape vine, which has negligible secondary growth. In one study, wild grape was found to be fully embolized over winter but produced root pressures up to 100 kPa to refill in spring (Sperry et al. 1987). The lumina of the bamboo vessels occupy only 6–8% of a culm cross-section area, in comparison with about 30% for rattans, 30% for diffuse–porous hardwoods, and about 70% for softwoods (Liese and Kumar 2003). Another strategy for survival in cold climates might be the propensity of bamboos to regrow from rhizomes following winter kill of shoots. Nevertheless, without secondary growth, the vessel refilling after cavitation could be crucial for the flora.

Root pressure may be quite common among bamboos. It was reported that the stumps of bamboos exuded for days following harvest operations in the growing season. In old Chinese literature, guttation of bamboos was described as rain in bamboo forest when relative humidity is high in warm spring mornings; therefore, bamboos could have very strong root pressure. Tyree and Cochard have personally experienced bamboo rain in Panama while working during sunny early morning hours under the canopy of *R. racemiflorum*, when root pressures typically reached 80 kPa overnight (Cochard et al. 1994). The purpose of this study was to survey the occurrence of root pressure in many different species of bamboo.

2 Material and methods

The observations were made at Nanjing, China (32.0°N, 118.5°E), which has a subtropic monsoon climate, annual average temperature of 16°C, and annual precipitation of 1,106 mm. All bamboo species were cultivated in a bamboo botanical garden used for scientific research. The complete list of observed species is given in Table 1 with their growth habits and dimensions. There are two major types of rhizome of bamboos based on the branching habit of the rhizomes: leptomorph and pachymorph (McClure 1966). While leptomorph and pachymorph rhizomes are species-dependent, a few species of bamboos have both types of rhizomes in the same species so McClure named them metamorph rhizomes. Bamboos with leptomorph rhizomes form groves or extensive tracts of rather evenly spaced culms because of the running nature of the underground system. In bamboos with pachymorph rhizomes, the culms are usually close together and form discrete clumps. Rhizome types usually refer to their growth habit. Leptomorph is common in bamboos of subtropic and temperate regions, such as *Phyllostachys* and *Indosasa*. Pachymorph rhizomes are common in bamboos of warm, tropic regions, such as *Bambusa*.

All measurements were made in August–September 2006, and March–April 2007. The late summer in Nanjing is usually very hot and humid and is still high season for plant growth. However, it is cool overnight and relatively dry in the early spring. Both humidity and temperature in the early spring had greater variation than in the late summer (see Table 2 for detail).

Xylem pressure measurements were made with bubble manometers which were made following the description and a diagram by Fisher et al. (1997). The manometers were made from glass micropipettes sealed at the distal end by flame. The distal half was filled with air while water filled the basal half. The base was connected to the cut stem or branch with a tight-fitting vinyl tube (using a hose clamp if necessary).

Stems of all small bamboo species (diameters of the culms of <2 cm at breast height) were cut near the base. For big bamboos (diameters of the culms of ≥2 cm at breast height), the first branches were used to measure the xylem pressure and to collect exudate. All cut surfaces were shaved with a new razor blade before bubble manometers were attached to measure xylem pressure or vinyl tubes sealed with Parafilm to collect exudate. All bubble manometers or collecting tubes were installed in the evening. After allowing the system to equilibrate overnight, the bubble length (L_{pd}) in the manometer was measured at pre-dawn. The vinyl tube was then cut and the bubble length (L_{atm}) was measured at atmospheric pressure. Each evening, the cut surfaces were reshaved and the manometer

Table 1 Bamboo species examined for root pressure with their growth habits and dimensions

Species	Growth habit	Height (m)	Diameter (cm)
Bambusa multiplex cv. fernleaf Young	Pachymorph	3–6	0.8
B. multiplex Raeuschel ex Schultes & Schultes	Pachymorph	4–7	1
B. multiplex var. riviereorum Maire	Pachymorph	1–3	0.5
B. remotiflora Kuntze	Leptomorph	8–12	0.5
B. subaequalis Fung & Sia	Leptomorph	8–12	0.5
Bashania fargesii Keng & Yi	Leptomorph	5–8	0.6
Indocalamus decorus Dai	Leptomorph	0.4–0.8	0.5
I. latifolius McClure	Leptomorph	1–2	0.5
Indosasa sinica Chu & Chao	Leptomorph	10	2.5
Menstroucalamus sichuanensis Yi	Leptomorph	2–4.5	1
Phyllostachys atrovaginata Chao & Zhou	Leptomorph	7–8	3
P. aurea Carrière ex Rivière & Rivière	Leptomorph	8–12	1.2
P. aureosulcata McClure *f. pekinensis* Lu	Leptomorph	7–9	1.2
P. aureosulcata McClure *f. spectablis* Chu & Chao	Leptomorph	5–9	0.5
P. aureosulcata McClure, *f. aureocaulis* Wang & Ma	Leptomorph	9	1.2
P. bambusoides f. lacrima-deae Keng et Wen	Leptomorph	5–15	1.5
P. bambusoides Siebold & Zuccarini	Leptomorph	5–15	1.2
P. bambusoides var. castillonis Makino	Leptomorph	7–13	1.8
P. bissetii McClure	Leptomorph	3–5	2.5
P. concava Yu & Wang	Leptomorph	5–7	0.8
P. dulcis McClure	Leptomorph	6–8	3.5
P. glauca f. yunzhu Lu	Leptomorph	6–18	0.8
P. glauca McClure	Leptomorph	6–18	3.5
P. iridescens Yao & Chen	Leptomorph	6–12	3.5
P. meyeri McClure	Leptomorph	5–11	1
P. nidularia Munro	Leptomorph	10	2
P. nigra (Loddiges ex Lindley) Munro	Leptomorph	5–10	1.2
P. nigra var. henonis (Mitford) Stapf ex Rendle	Leptomorph	5–15	1
P. nuda f. localis Wang et Yu	Leptomorph	5–10	0.8
P. nuda f. luteosulcata Chu & Chao	Leptomorph	6–9	0.6
P. platyglossa Wang & Yu	Leptomorph	8	1
P. praecox Chu & Chao	Leptomorph	8–10	1.5
P. praecox f. viridisulcata Zhang	Leptomorph	7–11	2.5
P. prominens Xiong	Leptomorph	10	3.5
P. pubescens Mazel ex H de Leh	Leptomorph	10–20	8
P. sulphurea f. houzeau Chu & Chao	Leptomorph	6–15	0.8
P. sulphurea var. Robert Young McClure	Leptomorph	6–15	3
P. sulphurea var. viridis Young	Leptomorph	6–10	1.5
P. vivax McClure f. aureocaulis Ma	Leptomorph	5–15	4.5
P. vivax McClure f. huangwenzhu Lu	Leptomorph	5–15	1.5
Pleioblastus amarus Keng	Metamorph	3–7	1.5
P. chinensis f. hisauchii Makino	Leptomorph	2–3	1.2
P. gramineus f. monstrispiralis Muroi et Hamada	Leptomorph	2–4	1.8
P. kongosanensis f. aureostraus Muroi et Yuk	Metamorph	0.5–1.0	0.5
P. maculatus (McClure) Chu & Chao	Leptomorph	3–8	0.8
Pseudosasa amabilis (McClure) Keng	Metamorph	6–13	1.5
P. japonica (Sieb & Zuc ex Steu) Makino ex Nakai	Leptomorph	3–5	0.8
P. japonica var. Tsutsumiana Yanagita	Leptomorph	1–2	0.5
Sasa argenteastriatus Camus	Pachymorph	0.3–0.5	0.3

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Table 1 (continued)

Species	Growth habit	Height (m)	Diameter (cm)
S. auricoma Camus	Pachymorph	0.2–0.8	0.5
S. fortunei Fiori	Pachymorph	0.1–0.5	0.5
S. pygmaea Camus	Leptomorph	0.2–0.4	0.5
Shibataea chinensis Nakai	Leptomorph	1	0.3

The dimensions of bamboos were measured in a bamboo garden collection on the campus of Nanjing Forestry University, Nanjing. Nanjing is not the natural distribution zone for some of the species; therefore, some bamboos might grow to different heights in their natural distribution zone

was reconnected to the plant organ with a new vinyl tube. The operation and measurement were repeated over three consecutive days. Measurements were made on at least two individual culms. The xylem pressure (P_x in kilopascal) was calculated from a relation derived from the ideal gas law:

$$P_x = P_s \left[\left(L_{atm}/L_{pd} \right) - 1 \right], \tag{1}$$

The value P_s is the atmospheric pressure in kilopascal at the time of measurement of L_{atm} and L_{pd}; however, P_s is normally given a constant value of 103 kPa.

Guttation from leaves was observed before sunrise. The observation was only successfully made in the dry season because the guttation was hard to distinguish from dew water in the wet season. The guttation water was collected into an Eppendorf tube and capped and also further sealed with Parafilm. The tubes were stored in −20°C until the osmotic pressure of the guttation fluid was measured with an osmometer (Wescor 5220). Exudates were also collected in early mornings from the cut stems. The collection, storage, and measurement of the exudation liquid were the same as the guttation water. In this paper, osmotic pressure is reported as a positive quantity=minus the solute potential.

Macerations of portions of stems and branches rich in vascular tissue were prepared with Jeffrey's Fluid (Johansen 1940). Briefly, stem and branch portions were cut into small slices about 3 mm thick. The slices were macerated in a solution of equal parts of 10% chromic acid and 10% nitric acid and incubated for 24 h. Macerations were spread onto glass slides and examined with a microscope. The diameters of 50 vessels were randomly measured.

The minimum pressure, critical water pressure (P_c, kilopascal), required to dissolve an embolism is:

$$P_c = -(4\tau/D)10^3 \tag{2}$$

Where τ is the surface tension of water=0.072 Pa m and D is vessel diameter in μm and 10^3 is a conversion factor to get P_c in kilopascal (Tyree et al. 1994; Ewers et al. 1997).

When P_x exceeds P_c, the air in the embolism is above atmospheric pressure and can dissolve as dictated by Henry's law (Tyree et al. 1994). Since roots have to push water against a gravity gradient of −10 kPa m^{-1}, the critical height (H_c, m) for the dissolution of an embolism reversal, assuming equilibrium static conditions, is:

$$H_c = H + (P_x - P_c)/10. \tag{3}$$

Where H is the height at which the stem or branch was cut for measuring xylem pressure.

3 Results

Positive xylem pressure was observed in all 53 bamboo species from ten genera in at least one of the two seasons (Table 3). In the summer of 2006, all other 52 species had positive xylem pressure between 2 and 68 kPa except for *Phyllostachys bambusoides* which had a negative value. In the spring of 2007, 51 species had positive root pressure

Table 2 Air temperature and relative humidity are shown in this table as means and standard deviations for each of the two periods of 10 days each

	2006, Aug–Sept	2007, March–April
Relative humidity (%)	74.6±3.8	53.9±9.6
Maximum temperature (°C)	31.0±2.3	21.9±5.5
Minimum temperature (°C)	24.8±1.4	9.6±4.6

The relative humidity and daily maximum and minimum temperatures in the air were collected in every morning (8–9 am)

Table 3 Maximum, mean, and SD of pre-dawn xylem pressure (*n*=6 per mean); mean and SD of osmotic pressure of exudation or guttation fluid (*n*=5 per mean; guttation fluid values shown in bold)

Species	Height (cm)	Root pressure (kPa)				Osmotic P (kPa)	
		2006		2007		2006	2007
		Max	Mean ± SD	Max	Mean ± SD	Mean ± SD	Mean ± SD
Bambusa multiplex cv. Fernleaf	5	67.5	46.4±12.5	28.3	17.5±9.3	163±27	–
B. multiplex	5	42.6	35.3±4.9	16.4	14.2±2	143±21	–
B. multiplex var. riviereorum	5	30	25.6±2.7	4.5	3.1±0.8	153±41	–
B. remotiflora	5	8.3	4.8±1.9	10	4.9±3.5	176±54	–
B. subaequalis	5	52.3	32.8±15.6	5.5	3.6±1.2	141±39	**226±64**
Bashania fargesiii	5	19.6	8.3±6.4	23.6	17.1±6.1	–	336±44
Indocalamus decorus	5	26.9	26.2±0.7	50.8	45.4±6	151±59	–
I. latifolius	5	43.5	37.5±4.1	12.7	7.5±3.4	160±33	**316±45**
Indosasa sinica	120	3.4	3.2±0.1	5.9	4.4±1.4	154±59	–
Menstroucalamus sichuanensis	5	26	23.2±2.1	3.4	3.2±0.5	158±54	**314±81**
Phyllostachys atrovaginata	135	27.8	23.6±6.8	9.6	5.5±2.3	159±66	189±41
P. aureae	5	4.8	3.4±0.7	15.8	8.9±3.7	161±32	336±66
P. aureosulcata f. pekinensis	5	3.1	1.8±0.6	13.9	7.8±3.4	168±88	–
P. aureosulcata f. spectablis	5	3.1	3±0.1	8	4.1±2.1	169±48	–
P. aureosulcata f. aureocaulis	5	16.9	10.6±4.9	5.6	5.1±0.8	146±37	212±48
P. bambusoides f. lacrima-deae	5	43.5	20.8±13.8	27.4	22.9±3.8	159±43	336±44
P. bambusoides	5	−2.9	−4.8±3.2	10.7	6.1±2.8	134±32	276±88
P. bambusoides var. castillonis	5	15.5	6.5±5.2	7.1	5.1±1.1	161±74	351±37
P. bissetii	125	44.4	38.5±4.4	5.7	4.1±1	146±32	–
P. concava	5	4.8	4.1±0.8	8	5.4±1.8	162±51	–
P. dulcis	125	11.9	8.7±1.5	3.4	2.6±0.6	168±57	**460±48**
P. glauca f. yunzhu	5	4.7	3.3±1.2	11.8	7.2±2.6	190±81	–
P. glauca	85	53.3	40±10.6	4.2	3.4±0.7	163±41	212±57
P. iridescens	150	4.8	3.3±0.8	36.4	22.9±7.8	143±21	–
P. meyeri	5	15.5	7.4±5.1	7.4	4.8±1.6	166±13	171±48
P. nidularia	120	11.1	4.7±3.2	20	7.8±6.9	173±53	–
P. nigra	5	10	7.6±1.7	4.3	3.2±0.7	156±32	288±65
P. nigra var. henonis	5	3.2	2.8±0.6	3.7	2.9±0.7	–	–
P. nuda f. localis	5	4.5	3.4±0.6	5.9	3.9±1.1	193±50	–
P. nuda f. luteosulcata	5	8.1	3.9±2	−2.2	−2.8±0.5	168±50	–
P. platyglossa	5	6.3	4.4±1.2	15.4	7.6±4.7	161±44	–
P. praecox	5	6	4.5±1	11.1	5.4±3.4	162±33	–
P. praecox f. viridisulcata	80	4.5	3.1±1	8.4	6.2±1.4	157±28	–
P. prominens	150	37.5	31.6±4.5	11.3	8.2±2.1	167±33	–
P. pubescens	180	4.6	3.6±0.8	29.1	24.3±3.6	164±46	**309±77**
P. sulphurea f. houzeau	5	6.5	3.6±1.4	6.5	4.2±1.5	165±60	–
P. sulphurea var. Robert Young	120	4.8	3.7±0.8	13	9.1±2.7	162±41	–
P. sulphurea var. viridis	5	6	4.6±1	–	–	128±48	128±48
P. vivax McClure f. aureocaulis	120	44.4	36.9±8.7	6.4	3.8±1.5	150±28	–
P. vivax f. huangwenzhu	5	1.6	1.5±0.1	7.1	4.4±1.8	138±41	156±54
Pleioblastus amarus	5	10.2	4.9±3.4	6.7	4.1±1.5	142±38	–
P. chinensis f. hisauchii	5	3.2	2.8±0.6	7.1	5.2±1.4	199±57	**349±63**
P. gramineus f. monstrispiralis	5	3.4	3.2±0.2	14.7	9.7±4.8	168±30	**359±53**
P. kongosanensis f. aureostraus	5	12.3	8.8±2.1	18.7	7.8±7.9	142±89	–
P. maculatus	5	6.3	2.8±1.9	30.3	18.8±6.4	176±32	–

Table 3 (continued)

Species	Height (cm)	Root pressure (kPa)				Osmotic P (kPa)	
		2006		2007		2006	2007
		Max	Mean ± SD	Max	Mean ± SD	Mean ± SD	Mean ± SD
Pseudosasa amabilis	5	5	2.6±1.4	16.9	10.7±4.3	138±22	207±57
P. japonica	5	3.2	2.5±0.8	42.6	28.8±9.8	151±46	310±85
P. japonica var. Tsutsumiana	5	47.7	23.7±20.1	19.7	15.4±3	133±59	277±75
Sasa argenteastriatus	5	7.7	6.8±1.2	16	7.3±5.7	172±67	–
S. auricoma	5	5.1	4.5±0.7	21.6	17±3.6	161±92	**302±32**
S. fortunei	5	4.6	3.4±0.6	22.7	15.5±7.9	164±51	345±51
S. pygmaea	5	7.7	6.4±1.4	15.6	9.3±5.5	140±22	–
Shibataea chinensis	5	11.1	7.3±2.4	4.5	3.4±0.7	155±54	–

The stems of all small bamboo species (diameters of the culms of <2 cm at breast height) were cut near the base. For big bamboos (diameters of the culms of ≥2 cm at breast height), the first branches were used for the air bubble manometer to measure the xylem pressure and collecting exudate

between 3 and 51 kPa with data for one species (*Phyllostachys sulphurea* var. *viridis*) missing, and with one species (*Phyllostachys nuda f. luteosulcata*) having negative xylem pressure. It is interesting to see that *P. bambusoides* had a negative xylem pressure in the summer of 2006, however exhibited positive 11 kPa xylem pressure in the spring of 2007. In contrast, the xylem pressure of *P. nuda f. luteosulcata* was positive in the summer and negative in the spring.

The stumps made in the summer of 2006 produced more exudates than those in the spring of 2007. More species produced enough exudate for osmotic pressure measurements from their stumps in the summer 2006 than in the spring of 2007 (Table 2). When the root pressure was too low, not enough liquid was collected for osmotic pressure determination, which is the reason for missing values in Table 2. The mean osmotic pressure of exudates in the summer of 2006 was 158 kPa and was significantly ($p<0.001$) lower than that in the spring of 2007 with 252 kPa (Table 3). Guttation was observed in eight species in the spring of 2007. The species with guttation all had positive xylem pressure. The guttation osmotic pressure was significantly ($p=0.023$) higher than that of exudates in 2007 (331 vs. 262 kPa, respectively).

The mean vessel diameter was 79 μm (Table 4), and smaller than the average range of 140–180 μm reported by others (Cochard et al. 1994; Liese and Kumar 2003). Of the 15 species measured, near half had their H_c for vessel refilling higher than or equal to the maximum height of the specimen (H_s) (Table 4). The H_c in another half was less that the H_s. However, it is interesting to find that two species (*Bambusa subaequalis* and *Phyllostachys pubescens*) had guttation though their H_c values were respectively less than the height of the plants (Table 3).

4 Discussion

The purpose of this research was to survey the occurrence of root pressure in a large number of species of bamboo, and this was motivated by an interest in how bamboos might refill embolized vessels. A full review of how root pressure might contribute to refilling of embolized vessels is beyond the scope of this paper. However, a few comments on this subject will put the results into context for the general reader.

Embolized vessels have air bubbles trapped inside the vessel lumens. Air can be expelled through dry pits at the apex of plants by the advance of water from the base driven by root pressure, if vessel walls and hence pit membranes in the walls are very dry (dehydrated). This mechanism accounts for about half the refilling in grape vines in spring because vine stems become very dehydrated over winter (Sperry et al. 1987). But when vessels are embolized by drought-induced cavitation events, the walls are still saturated with water and the surface tension of water in pit membranes prevents the passage of bulk air. Under these circumstances, bubbles are trapped in place and must dissolve into the surrounding water and the gas must diffuse away. Readers should consult Tyree and Yang (1992) and Yang and Tyree (1992) for details of the mechanisms involved which are explained by the combine influence of surface tension, Henry's law, and Fick's law.

For bubbles to dissolve, the absolute pressure of the bubble must rise above atmospheric pressure as determined by the critical pressure of the surrounding fluid (Eq. 2). Fluid pressure is driven by the dynamics of water flow in stems, which is pushed from below by root pressure and pulled from above by surface tension at the evaporative sites inside leaves. Evaporation from leaves

Table 4 Maximum pre-dawn xylem pressure (P_x), vessel diameter (D), critical pressure (P_c) for refilling, critical height (H_c) for vessel refilling under static equilibrium conditions, and the maximum specimen height (H_s)

Species	Height (m)	P_x (kPa)	D (μm)	P_c (kPa)	H_c (m)	H_s (m)
Bambusa multipkex cv. Fernleaf	0.05	46.4	100	−2.8	4.97	3.0
B. multipkex Raeuschel ex J. A.	0.05	35.3	82	−3.5	3.93	4.0
B. subaequalis Fung et Sia	0.05	32.8	66	−4.3	3.76	4.5
Bashania fargesii Keng Et Yi	0.05	17.1	103	−2.8	2.04	5.0
Indocalamus latifolius McClure	0.05	37.2	52	−5.5	4.32	1.0
Indosasa sinica Chu et Chao	1.20	4.4	83	−3.4	1.98	10.0
Monstroucalamus sichuanensis	0.05	23.2	66	−4.3	2.8	2.0
Phyllostachys aureosulcata cv. Spectabilis	0.05	4.1	68	−4.2	0.88	5.0
P. nigra Munro	0.05	7.5	70	−4.1	1.21	5.0
P. praecox Chu et Chao	0.05	5.4	101	−2.8	0.87	5.0
P. prominens Xiong	1.50	31.6	129	−2.2	4.88	6.0
P. pubescens Mazelex H. de Lehaie	1.80	24.4	92	−3.1	4.55	10.0
Pleioblastus kongosanensis f. aureostriaus	0.05	8.7	64	−4.4	1.36	1.0
Pseudosasa amabilis Keng	0.05	10.6	104	−2.7	1.38	6.0
P. japonica Makino	0.05	28.8	54	−5.3	3.46	3.0
Sasa argenteastriatus Camus	0.05	7.3	47	−6.0	1.38	0.3
S. auricoma Camus	0.05	16.7	55	−5.2	2.24	0.5

and surface tension can produce quite large negative pressures (≤1,000 kPa at maximum transpiration rates, Tyree 1999). However, the pull from above "dwarfs" the slight additional push provided by roots as explained below.

Solutes are accumulated into vessels of fine roots. Because the root cylinder is a composite membrane leaky to solutes and water (Steudle et al. 1993), soil water can be drawn into root vessels by osmosis and sometimes a positive pressure can develop (root pressure). This root pressure is most when flow is zero and the pressure in minor roots can reach a maximum value equal to $\sigma\Delta\pi$, where σ is the reflection coefficient of the composite membrane to the solutes and $\Delta\pi$ is the osmotic pressure difference between the xylem solution and soil solution. The value of root pressure we measured in this paper was probably $\leq\sigma\Delta\pi$, because flow of water through the bamboo might be non-zero during our measurements. The maximum value we observed was about 70 kPa and all values are likely to be less than the true value in the minor roots by 10 kPa for every meter the manometers were above the fine roots because gravity will diminish the measured pressure. Hence, root pressure is manifested as positive xylem pressure and can play a role in dissolving embolisms only when transpiration is very low. As transpiration increases, fluid pressure becomes more

Fig. 1 Root pressure data on vines (Ewers et al. 1997) compared to bamboos in this study. Among vines (30 species total), 27 had no root pressure and only three hand any. Among the 53 species of bamboo in this study and one in Cochard et al. (1994) all species had some root pressure

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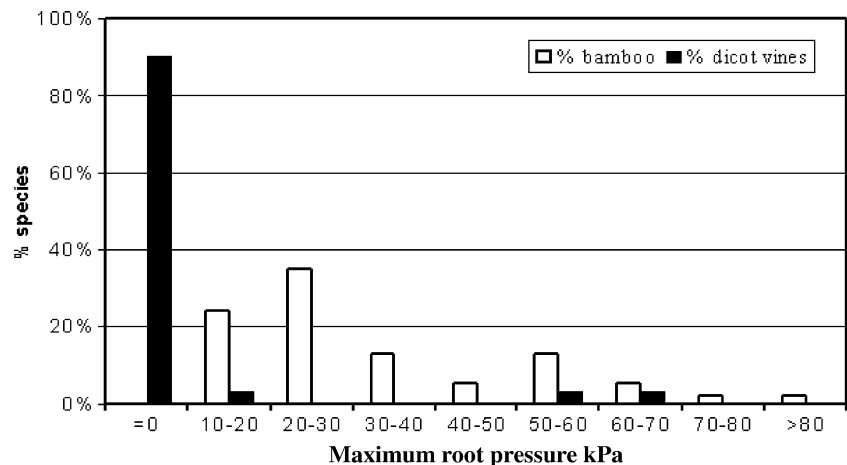
negative in leaves and stems and $\Delta\pi$ decreases because fluid flow into the roots dilutes the solutes accumulated by the root hairs and epidermal cells. The concentration of solutes inside$=J_s/J_w$. J_s is the relatively constant flux of solutes into the root in mole per second, J_w is the flux of water into the root in cubic meter per second which increases with transpiration. Xylem pressure is often negative during the day in all vessels from the fine roots to the leaf veins. Transpiration is very low in leafless dormant plants in spring, but bamboos are rarely leafless so root pressure can contribute to bubble dissolution only overnight when transpiration is minimal.

When the results of the present study were compared to literature values, it is clear that positive xylem pressures were more common in different species of bamboos than reported in different species of woody trees and vines (Ewers et al. 1997; Fisher et al. 1997). Thirty species of the vines in the seasonally dry rainforest of central Panama rarely exhibited root pressure compared to bamboos (Fig. 1) even though one might have speculated that vines would benefit from root pressure as much as bamboos. In a bigger survey of 109 species of vines, shrubs, and trees in Costa Rica and Mexico, Fisher et al. (1997) reported root pressure in 56% of the species. In theory, any species that exhibits root pressure or positive stems pressures could use such pressures to dissolve emboli. In some species of bamboo, the measured root pressure was enough to account theoretically for refilling of vessels up to the full height of the bamboo species. In others, it was only enough to account for partial refilling. At this point, we have no evidence that cavitation events are common in bamboo species and such information must await further studies. So far, seasonal changes in embolism and vulnerability to cavitation have been reported in only one bamboo species (Cochard et al. 1994).

Tables 3 and 4 showed that H_c values of two species were respectively less than the height of the specimens; however, they did exhibit guttation from the lower leaves. The values of osmotic pressure were consistently high values and always more than the root pressure. If the roots are ideal osmometers and if the roots contain the same fluid as in the exudate, then we would expect the root pressure to equal the osmotic pressure. A possible explanation is that the roots may not be ideal osmometers, i.e., that the reflection coefficient, σ, of the roots is much less than 1. Low reflection coefficients have been reported for mineral solutes of the type found in soil solutions roots of monocots and dicots ($\sigma=0.1–0.5$; Steudle 2000). However, the chemical identity of the exudate was not determined and the chemical species is also likely to have a big impact on σ. However, assuming low values of σ then the observed root pressures in Table 3 were consistent with likely values of $\sigma\Delta\pi$. The possibility that the Wescor model 5220

osmometer consistently overestimated osmotic pressure has been eliminated because we measured known samples of NaCl solutions in the range of 20–60 kPa and got the correct instrument reading. The higher values of osmotic pressure in the guttation fluid observed in Table 3 could be explained by evaporation of water prior to collection of the fluid from the leaves.

There were two well-documented cases of vessel refilling in species while xylem pressure was negative in surrounding tissues; one was laurel shrubs (Tyree et al. 1999; Hacke and Sperry 2003) and the other was commercial grape vines (Holbrook and Zwieniecki 1999). While the exact mechanism of this refilling process was not fully established, there was reason be believe that it involved the injection of solutes into embolized vessels (Salleo et al. 2004) from ray and xylem parenchyma cells. We cannot eliminate the possibility that a similar mechanism might occur in bamboo and hence the high osmotic pressures observed in the exudates (Table 3) in our study may indicate refilling by the solute injection process aided by root pressure.

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