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LETTER

The maximum height of grasses is determined by roots

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Abstract

Grasses such as bamboos can produce upright stems more than 30 m tall, yet the processes that constrain plant height in this important group have never been investigated. Air embolisms form commonly in the water transport system of grasses and we hypothesised that root pressure-dependent refilling these embolisms should limit the maximum height of grass species to the magnitude of their root pressure. Confirming this hypothesis, we show that in 59 species of bamboo grown in two common gardens, the maximum heights of culms of 67 clones are closely predicted by the maximum measured root pressure overnight. Furthermore, we demonstrate that water transport in these bamboo species is dependent on root pressure to repair hydraulic dysfunction sustained during normal diurnal gas exchange. Our results established the critical importance of root pressure in the tallest grass species and provide a new basis for understanding the limits for plant growth.

Keywords

Embolism, height, plant size, refilling, root, root pressure, xylem.

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INTRODUCTION

The fact the trees do not grow taller than around 130 m is a topic that has fascinated biologists for hundreds of years, but only recently has the water transport system been invoked as possible general explanation (Ryan & Yoder 1997). The so-called hydraulic limitation hypothesis proposes that increases in both the resistance to water flow in the water transport system (the xylem) and hydrostatic tension as plants grow taller produces a limit above which sufficient water cannot be delivered to the leaves for net photosynthetic gain to occur. For the world's tallest woody trees, the conifers *Sequoia* and *Pseudotsuga* and angiosperm *Eucalyptus* the hydraulic hypothesis is supported by observed physiological and anatomical gradients in the tree (Koch *et al.* 2004; Domec *et al.* 2008; Petit *et al.* 2010), but there is little information from other tall-growing plant groups that might support a general rule for height growth limits of all plants. Grasses such as bamboo can also grow up to 32 m in height (Scurlock *et al.* 2000), but they have very different anatomy in their water transport tissues compared with woody plants, raising the possibility that factors other than water transport efficiency may limit their maximum height growth.

Central to the theory of hydraulic limitation of tree height is the fact that once the water tension in the xylem exceeds a certain limit, individual xylem conduits begin to pull air rather than water into their lumens (a process called cavitation), which renders them non-functional (Zimmermann 1983). Increasing the vertical distance required to deliver water to the crown of tall trees increases the risk of cavitation and a consequent rapid loss of water supply, theoretically producing a height limit above which water transport fails. Cavitation cannot be repaired in tall conifers and angiosperms because refilling processes cannot develop sufficient pressure to dissolve embolisms (Tyree & Zimmermann 2002) but in grasses, embolisms appear to be readily reversed by positive water pressure generated in the roots. This root pressure is generated when ions are pumped across a suberised sheath in the root, causing water to flow along an osmotic gradient from the soil into the xylem, thereby generating a positive water pressure. By pumping water from the soil back into air-filled conduits, root pressure dissolves emboli and restores xylem function (Stiller *et al.* 2003; Kaufmann *et al.* 2009; Saha *et al.* 2009). Efficient restoration of hydraulic supply by root pressure in grasses appears to be linked to a high susceptibility of grass xylem to tension-induced cavitation and as such, grasses are thought to represent one extreme in the complex trade-off between xylem transport efficiency, xylem cost and cavitation resistance (Holloway-Phillips & Brodribb 2011).

The apparent dependence on root pressure for xylem repair in grasses (Miller 1985; Ogata *et al.* 1985; Tyree *et al.* 1986; Neufeld *et al.* 1992; Cochard *et al.* 1994; Macduff & Bakken 2003; Stiller *et al.* 2003; Saha *et al.* 2009) raises the possibility that plant height in this group may be limited by the capacity of roots to pump water to the plant apex. Supporting this concept, high root pressures have been reported for tall monocotyledonous plants such as palms (Davis 1961; Fisher *et al.* 1997) and bamboos (Cochard *et al.* 1994; Ewers *et al.* 1997; Saha *et al.* 2009), but a link between plant height and root pressure has never been demonstrated in any plant group. We hypothesised that root pressure-dependent refilling of vessels in stems and leaves may limit the maximum height of grass species to the magnitude of their root pressure. Although still centered on limitations of the water transport system, the idea that plant height may be limited by below-ground processes in grasses suggests a radically different mechanism from that suggested to limit the maximum height of woody plants.

To test the relationship between maximum height and root pressure in grasses we examined species from the tallest of the grasses, the

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bamboos. Bamboos are a critically important group of plants both ecologically and economically, yet little is known about their physiology. Bamboo species provide an excellent opportunity to examine the relationship between plant height and root pressure because they are highly speciose and encompass an enormous size range, from dwarf species <1 m tall to tropical species reported to reach heights of almost 40 m. Using two of the most comprehensive live collections of bamboo in China we were able to determine if root pressure-dependent refilling is an important part of the diurnal water relations of bamboo, and whether species and individuals are height-limited by the magnitude of their root pressure.

MATERIALS AND METHODS

Study site

Experiments were undertaken in two bamboo common gardens in Southern China. The first was Xishuangbanna Tropical Botanical Garden (XTBG – 21°41′ N, 101°25′ E) in southern Yunnan Province, where 42 culms of 34 species with clumpy clonal growth were measured from a large common garden. The second garden was Anji Bamboo Expo Park (ABEP – 30°37′ N, 119°41′ E) in Zhejiang Province, where 25 culms from 25 bamboo species with the runner clonal growth form were measured (see Table S1 for details). Because both gardens have monsoonal climates all measurements were made during the rainy season to avoid variation in soil water availability. Maximum root pressures were measured at both gardens, while diurnal gas exchange measurements were conducted from tall and dwarf bamboo species at XTBG.

Diurnal gas exchange and root pressure

To establish whether bamboo species undergo diurnal cycles of hydraulic dysfunction that might require root pressure repair we sampled a tall bamboo *Bambusa vulgaris* and a dwarf bamboo *Bambusa multiplex* at XTBG. In these two species, we measured gas exchange on a clear day using an open flow gas analyzer (Li-6400; Licor, Lincoln, NE, USA) on six leaves from three individuals approximately every 120 min starting predawn at 0630 h and finishing at 1630 h. Temperature, CO_2 concentration, light and humidity in the leaf cuvette were set to match ambient environmental conditions. A crane was used to access the canopy of the tall bamboo to ensure healthy sunlit leaves were measured.

In the same two species, we measured the nocturnal development of root pressure using digital pressure transducers (PX26-100DV, Omega Engineering, Stamford, CT, USA) linked to a data logger (CR10X, Campbell Scientific, Logan, UT, USA) to log pressures for every 10 s. A single transducer was fitted to each individual by cutting a small branch close to the ground and fitting the transducer to a short piece of water-filled tubing attached to the branch by zip-ties. Care was taken to select branches with intact septa between nodes such that root pressure could not dissipate into the hollow centre of the stem.

Shoot hydraulic conductance

In parallel with gas exchange measurements, we sampled shoot (combined terminal branch and leaf) hydraulic conductance to determine whether diurnal patterns of embolism were evident. At approximately the same time, gas exchange measurements were made on three small shoots from where the same culms were cut and transported to the adjacent laboratory wrapped in plastic. Shoots were approximately 20 cm in length with 3–5 leaves and intact septa between nodes. A rehydration technique was used (Brodribb & Cochard 2009) whereby flow into shoots was measured on a flowmeter and recorded every 5 s on a datalogger (CR1000, Campbell Scientific Inc.) to capture the flow rate at the time of disconnection. After approximately 60 s of rehydration, shoots were removed into a humid plastic bag to prevent dehydration of the shoot and leaf water potential (Ψ_{leaf}) was determined, using a pressure chamber (SKPM 1400, Skye Instruments Ltd, Lladrindod Wells, UK) and leaf area was determined with a leaf area meter (LI-3000A, Licor). Shoot conductivity (K_{shoot} – including the terminal part of the shoot and the leaves) was calculated from the flow rate and leaf water potential using (eqn 1):

$$\mathrm{K}_{\text{shoot}} = -\frac{I}{A_l \psi_{leaf}} \tag{1}$$

where I = instantaneous flow rate into the leaf (mmol s^{-1}); A_l = projected leaf area.

Additional shoots were sampled for K_{shoot} from the same six individuals measured above. Samples from these two species were taken throughout the day as leaf water potential declined naturally, thus allowing the relationship between Ψ_{leaf} and K_{shoot} to be determined as shoot water content varied throughout the day.

Root pressure among bamboo species

To investigate the relationship between maximum root pressure and plant height, we examined a total of 67 clones from 59 species from the two botanical gardens. Species were selected to span the full range of sizes observed in bamboos from dwarf to tall and encompassing different clonal types (running and clumping varieties). Initially, the dynamics in root pressure were monitored for 12 representative bamboo species in XTBG from 2030 h to mid-morning the next day using the same method of pressure transducer attachment as described above. These representative root pressure dynamics were then used to determine to appropriate time to measure maximum root pressure. Maximum root pressure measurements were conducted in September and October 2010 in XTBG and November 2011 in ABEP. Maximum root pressures of 42 clones from 34 bamboo species in XTBG and 25 clones of 25 species in ABEP were determined between 0200 and 0500 solar time, when bamboos maintained maximum root pressure. Root pressure was measured as above with a pressure transducer but rather than remaining fixed to the culm all night, the transducer was attached and allowed to come into equilibrium with the xylem pressure (typically over 5–10 min) after which the pressure was recorded. We attempted only to measure culms that had achieved their maximum size, and this was assessed visually based on the criterion that lateral branches bore leaves all the way until the apex. Maximum root pressure was calculated as the pressure measured at the cut end, plus the hydrostatic pressure generated by the water column from the ground to the cut end.

Additionally, in four plants of four bamboo species, we examined the hydrostatic decline of root pressure up the culms of large bamboo plants. For xylem pressure at different heights, a crane was used to reach different heights, and xylem pressures were measured with the pressure transducer between the hours of 0200 and 0500 h. The height of the tallest individual of each clone of the species taller than 3 m was determined with a clinometer (Vertex Laser VL402, Haglof, Sweden) and a tape, and defined as maximum clonal height. The maximum height of the bamboo species shorter than 3 m was measured with a stick and a measuring tape.

RESULTS

Diurnal variation in gas exchange, root pressure and shoot conductance

Diurnal gas exchange in both the tall *Bambusa vulgaris* and the dwarf *Bambusa multiplex* species were highly sensitive to declining leaf water potential during the day despite the abundant availability of soil water during the rainy season. Strong depression in stomatal conductance (g_s) after a peak between 1000 and 1100 h led to a dramatic decline in assimilation and transpiration in both species despite increasing atmospheric vapour pressure deficit (Fig. 1). Shoot conductance and leaf water potential (Ψ_{leaf}) fell in parallel between the hours of 0600 and 1200 h after which both remained stable, but remarkably low, with $K_{shoot} < 1$ mmol m^{-2} s^{-1} MPa^{-1} and $\Psi_{leaf} < -2.5$ MPa. At this point, stomata were almost closed and remained so for the rest of the day resulting in assimilation rates <20% of maximum. This type of feed-forward stomatal closure is thought to be associated with a loss of hydraulic conductivity, and indeed the extremely high vulnerability of shoot and leaf xylem suggests this was the cause of the depressed gas exchange in the latter part of the day for both bamboo species (Fig. 2). In both the species, we found that the shoot water transport system was very vulnerable to dysfunction (presumably by embolism) when water tension exceeded mild values of −0.4 MPa in the shoot. Both species had a relatively high maximum mean K_{shoot} of approximately 10 mmol m^{-2} s^{-1} MPa^{-1} but this fell rapidly to 1 mmol m^{-2} s^{-1} MPa^{-1} at water tension between −0.7 MPa (*B. vulgaris*) and −1.2 MPa (*B. multiplex*) (Fig. 2). In culms monitored overnight, we observed the K_{shoot} recovered each night. Accompanying the recovery of K_{shoot} was a large magnitude pulse of nocturnal root pressure. Positive xylem pressure appeared in most species around 2100 h, rising to peak values between 0100 h and 0500 h, before declining to zero at dawn (Fig. 3). This pulse of root pressure was hypothesised to be essential for repairing the dramatic diurnal decline observed in K_{shoot}.

Root pressure and plant size

Testing the possibility that root pressure acts as a source of hydraulic pressure to repair xylem damaged during daytime gas exchange, we examined the relationship between plant height and root pressure in a large sample of bamboo species in the two common gardens. Peak root pressures sampled in the predawn ranged from 22 kPa in the dwarf bamboo (*Pseudosasa japonica* var. *tsutsumiana* Yanagita) to the maximum value of 195 kPa at the base of the tall bamboo species (*Dendrocalamus latiflorus* Munro). In tall bamboo culms, the decline in nocturnal xylem pressure measured from the base to the apex of individual culms was very close to the gradient expected by hydrostatic pressure, particularly if the apical pressure was not included (Fig. 4, insert), confirming that the origin of the nocturnal xylem pressure was at the root. Xylem pressures at the apex of sampled culms were close to zero or slightly below zero.

When comparing species, we found that in 67 clones of 59 bamboo species, the maximum height of culms was closely predicted by the maximum measured root pressure overnight ($r^2 = 0.81$, $P < 0.0001$; Fig. 4). Although the species with clumpy clonal growth (from XTBG) tended to be larger than those with runner clonal growth (from ABEP), both groups produced similar relationships between height and root pressure (Fig. 4). The relationship between maximum plant height and maximum root pressure was very close to the predicted relationship if maximum height was exactly constrained by the capacity to refill the entire xylem network by root pressure (Fig. 4). Under this constraint, individual plants could not exceed heights where nocturnal apical xylem pressure was below zero, and hence maximum height should equal the maximum root pressure divided by the hydrostatic pressure gradient produced by gravity (9.8 kPa m^{-1}). The regression between height and root pressure in all species showed that in most species a small positive margin existed between height and root pressure such that culms were slightly shorter than the maximum allowable (root pressure constrained) height. Culms that exceeded the maximum root pressure-constrained height were infrequent, and only did so by a small margin (Fig. 4). Plants exceeding the maximum predicted height were found to produce anomalously low-water potentials at their apex (*Dendrocalamus brandsii* and *D. longaminnis*; Fig. 4) suggesting incomplete xylem repair.

DISCUSSION

Our data provide strong support for the hypothesis that maximum size in bamboo species is determined below ground by the maximum pressure that can be generated in roots overnight. This remarkable observation puts an entirely novel perspective on the processes that limit plant size, particularly in grasses, and places considerable emphasis on the importance of root pressure for the function and development of plant species.

In bamboos, we found that a nocturnal pulse of root pressure is critical for repairing embolisms that accumulate during normal diurnal gas exchange under non-stressed conditions. Our sample of bamboo species, similar to other grass species, was highly vulnerable to xylem dysfunction (Fig. 2) such that cavitation during normal photosynthetic gas exchange appears to be a typical part of xylem operation even under conditions of high soil water availability (Fig. 1). Observations of bamboo stems indicate that they may be more resistant to dysfunction under water-stress than the shoots we measured here (Cochard 2002). This observation suggests that the xylem dysfunction observed here is probably isolated to the distal branches or leaves. Based upon direct observations of cavitation in grass species (Pate & Canny 1999; Facette *et al.* 2001), the diurnal loss of xylem function in bamboos is most likely associated with cavitation and not the collapse of xylem conduits, although it should be noted that the collapse of conduits has been observed in the roots of a grass (Kaufmann *et al.* 2009). Hence the accumulation of embolisms during the day requires repair of K_{shoot} from the depressed levels recorded in the period after 1200 h to restore the capacity to photosynthesise the next morning (Fig. 1). Very low K_{shoot} at the end of the day could only support very low levels of photosynthesis the following day if K_{shoot} was not repaired overnight (Brodribb 2009). This repair process in bamboo species and other grass species appears to rely on root pressure to dissolve embolisms during the night while stomata are closed and humidity close to 100%. Alternative processes of refilling embolised xylem have been proposed (Holbrook & Zwieniecki 1999), but we did not see any evidence of K_{shoot} recovery in the bamboo species during the daylight hours, and furthermore the observation of positive xylem pressures throughout

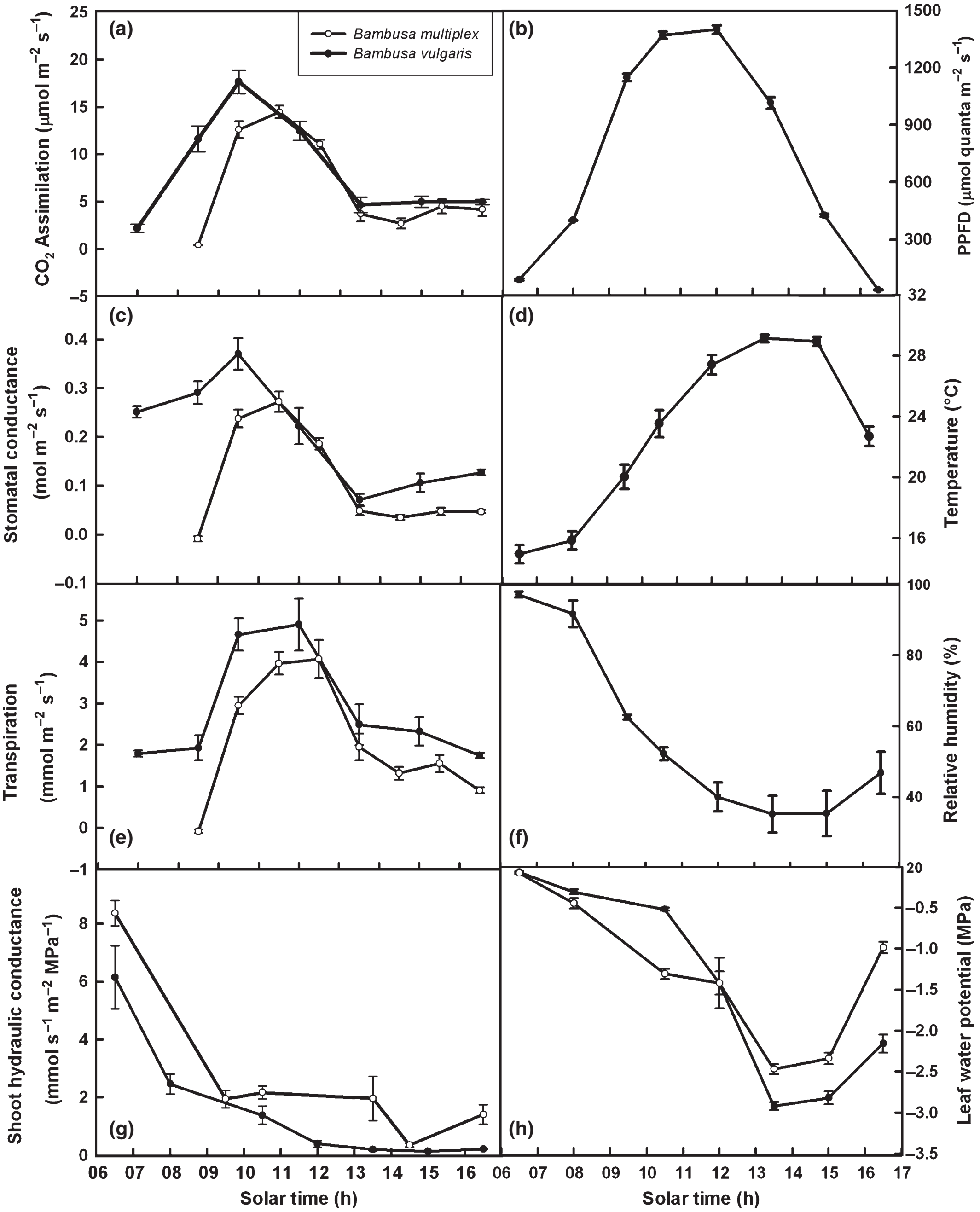

Figure 1 Diurnal photosynthetic gas exchange and shoot hydraulic conductance in a tall (*Bambusa vulgaris*) and short (*Bambusa multiplex*) representative bamboo species. In both species, photosynthesis (a), stomatal conductance (c) and transpiration (e) rose to a peak between 1100 and 1200 h, while at the same time shoot hydraulic conductance (g) fell to very low levels. Low leaf water potential (h) and shoot hydraulic conductance in the after noon led to a strong depression in leaf gas exchange despite favorable light (b) and temperature (f) conditions, and an abundance of soil water.

the culm overnight obviates the need for metabolic processes in the stem capable of refilling the xylem under mild tension.

If a dependence on root pressure for refilling was universal amongst bamboo species, this would then constrain the maximum size of bamboo plants to the magnitude of the root pressure generated. The pressure required to pump water against the force of gravity is proportional to the height of the water column and hence we predicted a proportional relationship between root pressure at the base of culms and the height of their apical leaves. Xylem supplying leaves above this maximum height would not be repaired overnight and would either provide very limited photosynthetic function, or be damaged by desiccation. Measurements of 59 species of bamboos strongly supported our predictions, providing a clear link between xylem embolism, root pressure and plant stature. We found a remarkably strong correlation between the height and the maximum nocturnal root pressure of individual culms, and more importantly, that the slope of this relationship was very close to the hydrostatic limit produced by gravity (Fig. 4). Some shoots were observed to slightly exceed the hydrostatic limit for refilling, but in a sample of two such species, we found that root pressure did not quite propagate to

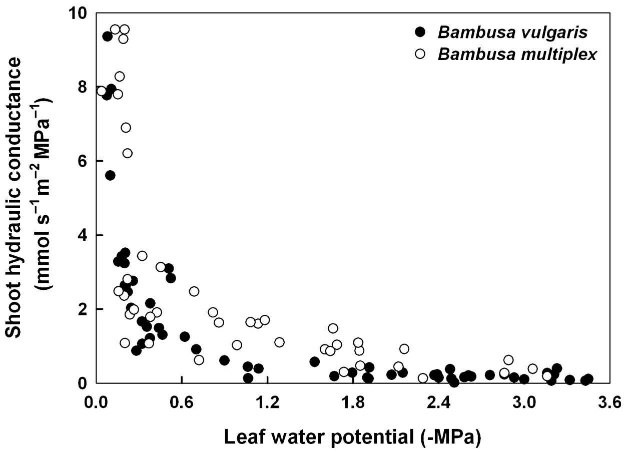

Figure 2 Vulnerability of bamboo shoot xylem to dysfunction under water tension. In the same tall and short bamboo representatives measured in Fig. 1, shoot hydraulic conductance was very sensitive to declining water potential in the leaf. Shoots were sampled throughout the day during the wet season and hence the minimum water potentials shown represent minimum diurnal water potentials in the field.

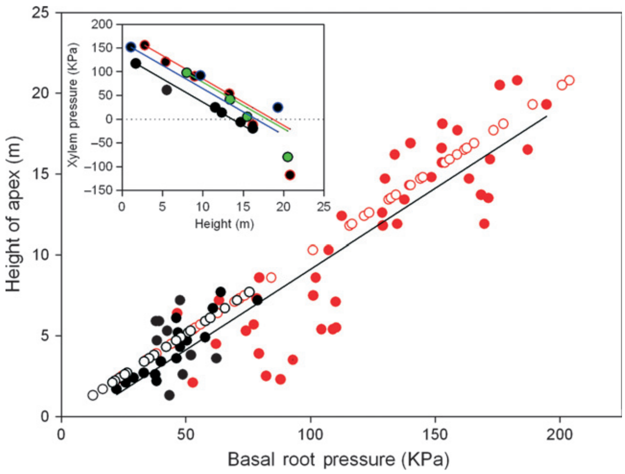

Figure 4 Maximum nocturnal root pressure in 59 species (67 clones) of bamboo from two common gardens (XTBG – red, and ABEP – black) was strongly correlated with the height of the apex of the culm ($r^2 = 0.81$). Maximum heights according to our root-pressure–limited hypothesis are shown (open symbols) and these predictions agreed closely with the observed maximum bamboo heights. Xylem pressure (insert) declined with height above the soil in four species of tall bamboos (red border – *Dendrocalamus longilaminis*; green – *Dendrocalamus brandisii*; blue – *Dendrocalamus latiflorus*; black – *Bambusa vulgaris*) according to the hydrostatic pressure gradient (shown as coloured lines for each species) such that xylem pressure was close to zero at the apex.

the apex of the culm, resulting in a larger-than-hydrostatic decline in pressure at the plant apex (Fig. 4, insert). Anomalously, low pre-dawn xylem pressures in the apex of these individuals may indicate incomplete xylem repair and may render these apical portions non-functional. Alternatively, it is possible that small amounts of transpiration may have been occurring in the apical parts of some plants at the time they were measured early in the morning. Any transpiration would quickly lead to xylem tension developing in apical parts of the plant.

It remains to be seen whether the coordination between height and root pressure shown here represents correlated evolution of root and stem traits, or whether root pressure actively regulates shoot height during the rapid phase of shoot expansion. Given the extraordinary rate of shoot elongation in many bamboo species, it seems possible that rapid expansion of cells in the basal meristems of these species may require positive pressure to sustain growth. Contrary to this simple explanation of how root-shoot coordination may take place, are observations in *Phyllostachys nigra* indicating no effect on stem elongation of substantial root pruning (Porterfield 1935). It is possible however, that rapid wound healing or hydraulic compartmentalisation in bamboos may prevent the leakage of root pressure away from the meristem. Environmental variation on the other hand does support a direct interaction between root pressure and stem height, with strong influence of soil moisture on stem height probably via its effect on root pressure (Liu *et al.* 2004). Further work is required to determine whether the root pressure–shoot height linkage in bamboo is the product of a mechanistic interaction or trait coordination. A first step might be to determine the effects of physical or chemical impairment of root pressure on shoot elongation. Regardless of the process, it is clear that bamboo demonstrates a fundamental association between physiology and stature, apparently linked through the need to sustain hydraulic connection with the soil.

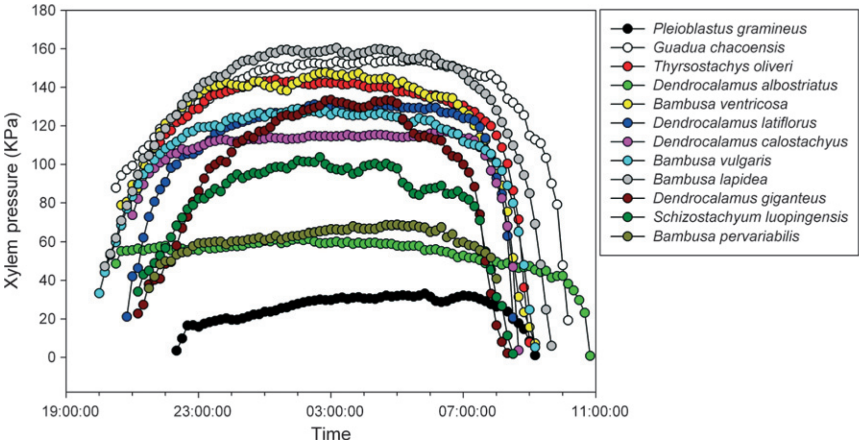

Figure 3 Root pressure dynamics recorded at the bases of 12 representative bamboo species during the rainy season. In all species positive pressures developed soon after 1900 and peaked in the early hours of the morning. Maximum pressures were highly variable between species but pressure dynamics were relatively conserved.

The range of root pressures we recorded among species was extremely large (from 22 to 195 kPa), suggesting that variation in root pressure may provide a rapid means for bamboo species to adapt their size to local conditions. Interestingly, such diversity of root pressure is not confined to tall perennial monocots, and indeed pressures of >150 kPa have been recorded from a number of herbaceous species such as sage and sunflower (Eckerson 1908). In these cases, high root pressure may enable refilling under conditions of mild water stress, and rather than constraining height, root pressure may constrain the minimum soil moisture limits of these species. In stark contrast to our data for bamboo species, studies of woody plants show no significant relationship between plant height and root pressure (Ewers *et al.* 1997) except for some cases of deciduous species where sap must be pumped to the tree apex in spring to refill xylem embolised during winter (Westhoff *et al.* 2008). Indeed the tallest trees on earth (*Sequoia*) show no capacity to generate root pressure at all. However, on the basis of the direct link between plant height and root pressure demonstrated here in bamboo, we proposed that maximum height is constrained by root pressure in grasses, and although it may be common for species to be shorter than their maximum root pressure may allow, we did not find any evidence of plants significantly exceeding the constraints of a root pressure limited maximum size. It is unknown whether the other tall monocot group; the palms, show the same dependence as bamboo on root pressure. Evidence suggests that this group represents an intermediate between the grassy and woody strategies, with both high root pressure (Davis 1961) and cavitation resistance reported among palm species (Holbrook & Sinclair 1992).

Although root pressure appears to occupy a central role in the functioning of the water transport system of many monocot plants, among dicotyledonous species there is no evidence of any reliance upon root pressure for refilling xylem except in some deciduous trees where a burst of root pressure in the spring is used to refill xylem embolised by winter freeze–thaw events (Sperry *et al.* 1987; Cochard *et al.* 2001; Ewers *et al.* 2001). This significant difference between groups may reflect either the fact that dicot species tend to avoid cavitation by closing stomata prior to the development of cavitation in the plant, or that other metabolic refilling processes are present in woody plants. Recent evidence points to the fact that most woody species produce xylem sufficiently resistant to cavitation that they are exposed to significant embolism only under drought conditions (Brodribb & Holbrook 2003). Furthermore, recovery of drought embolised stems in woody plants seems to be associated with xylem replacement rather than refilling (Brodribb *et al.* 2010). In stark contrast, most grass species measured experience significant cavitation even when well watered (Holloway-Phillips & Brodribb 2011). This strategic dichotomy is of major importance, because the two contrasting systems of water transport must invoke different costs and trade-offs. These processes are beginning to be unraveled in woody plants (Lens *et al.* 2011), but little consideration has been given to the ecological significance of root pressure in grasses and other monocots. Investigations into the costs associated with sustaining root pressure in grasses under different soil and atmospheric conditions are required to understand how this critically important group of plants has become so successful.

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AUTHORSHIP

Written by TJB, SJY and KFC, experimental work by SJY, YJZ, TJB and KFC.

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