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Research paper

Recovery of diurnal depression of leaf hydraulic conductance in a subtropical woody bamboo species: embolism refilling by nocturnal root pressure

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Despite considerable investigations of diurnal water use characteristics in different plant functional groups, the research on daily water use strategies of woody bamboo grasses remains lacking. We studied the daily water use and gas exchange of *Sinarundinaria nitida* (Mitford) Nakai, an abundant subtropical bamboo species in Southwest China. We found that the stem relative water content (RWC) and stem hydraulic conductivity (K_s) of this bamboo species did not decrease significantly during the day, whereas the leaf RWC and leaf hydraulic conductance (K_{leaf}) showed a distinct decrease at midday, compared with the predawn values. Diurnal loss of K_{leaf} was coupled with a midday decline in stomatal conductance (g_s) and CO_2 assimilation. The positive root pressures in the different habitats were of sufficient magnitude to refill the embolisms in leaves. We concluded that (i) the studied bamboo species does not use stem water storage for daily transpiration; (ii) diurnal down-regulation in K_{leaf} and *gs* has the function to slow down potential water loss in stems and protect the stem hydraulic pathway from cavitation; (iii) since K_{leaf} did not recover during late afternoon, refilling of embolism in bamboo leaves probably fully depends on nocturnal root pressure. The embolism refilling mechanism by root pressure could be helpful for the growth and persistence of this woody monocot species.

Keywords: cavitation, daily water balance, hydraulic conductivity, refilling, root pressure.

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Introduction

Bamboos, an extremely diverse group of ~1500 species in 80 genera all over the world, are distributed across a wide range of tropical and subtropical habitats, from alluvial plains to high mountains (Ohrnberger 1999). With >500 species in 39 genera, China has the richest bamboo resources in the world (Lei 2001). Bamboos play an important role in the succession of forest ecosystems (Griscom and Ashton 2003), and support the diversity of forest ecosystems by providing food for a variety of animals, including the Giant Panda (McNeely 1996). Bamboo species are also a non-timber forest product of major cultural and economic importance, and a valuable resource for ecosystem services (Singh and Singh 1999, Virtucio and Roxas 2003, Zhou et al. 2005). In some subtropical forest ecosystems, bamboo species can also be invasive species inhibiting gap phase regeneration (Montti et al. 2011). Despite their ecological and economical importance, and widespread distribution, little is known about their water relations and photosynthesis, which would be crucial in understanding their ecological performance and in improving the efficiency of bamboo cultivation.

As woody monocotyledonous perennial grasses, bamboos have unique structures that may distinguish their daily water use characteristics from other plant groups. Unlike dicotyledons, bamboos not only lack the capacity for secondary growth

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and exhibit rapid growth, but also have large numbers of rhizomes, large xylem vessels in the stems, abundant parenchyma tissues in the xylem tissue and complex anatomical structures in nodes (Liese 1998). Bamboos cannot produce new xylem to replace conduits embolized by seasonal water deficit or freeze–thaw cycles. However, bamboos are known to have root pressure (Wang et al. 2011), which has been proposed to be at least partially responsible for embolism repair in some bamboo species (Cochard et al. 1994, Saha et al. 2009). Recent studies suggest that water storage (Goldstein et al. 1998, Scholze et al. 2007) and diurnal down-regulation of leaf hydraulic conductance (Brodribb and Holbrook 2004, Zhang et al. 2009) are of great adaptive significance for tree daily water use, but to our knowledge, it is unknown whether woody bamboos would exhibit similar patterns as trees. The abundant parenchyma tissues in the xylem tissue of bamboos (Liese 1998) would favor the use of water storage to buffer daily transpiration, which has never been tested.

Sinarundinaria nitida is an understorey bamboo species in the evergreen broadleaf forest of Ailao Mountain, SW China, and also widely distributed in the open areas of the forest edge. Using this species as a representative taxon, the main objectives of this study were to understand (i) the coordination between stem/culm and leaf water transport systems in bamboos, and the function of root pressure in bamboo hydraulics, (ii) the effect of the amount of irradiance on bamboo daily water use and carbon assimilation, and (iii) the contribution of water storage in maintaining daily water use balance in bamboo species.

Materials and methods

Study site and plant material

This study was carried out in an old-growth forest near the Ailao Station for Subtropical Forest Ecosystem Studies (24°32′N, 101°01′E, 2450 m above sea level), located in central Yunnan Province, Southwest China. Mean annual temperature is 11.3 °C. Mean annual rainfall is ~1840 mm and >85% of rainfall occurs in the wet season between May and November. All measurements were performed in April, prior to the beginning of the wet season.

Sinarundinaria nitida (Mitford) Nakai (Bambusoideae, Gramineae), a dominant understorey species in subtropical evergreen broad-leaved forest on the Ailao Mountains, was chosen for this study due to its ecological and economic importance. *Sinarundinaria nitida*, a subalpine evergreen, monocarpic species ~4 m in height and with a sympodial subterranean stem–root system (scattered sympodial type), is found in both open (forest edge) and shaded (understorey) areas. Six mature individuals relatively far away from each other were selected from each area (forest edge and understorey) for physiological measurements. In order to be comparable with trees, the term stem was used to represent the culm of the woody bamboo in the rest of the present paper.

Leaf water releasing curves and relative water content of leaves and stems

For leaf water releasing curves, the terminal branches from six mature individuals of *S. nitida* from both open and shaded habitats were cut in late afternoon. The cut ends were immediately recut under water and transported to the laboratory for rehydration overnight in humid conditions. Following rehydration, mature leaves were cut and weighed to obtain the fresh weight at saturation (FW_s), then air-dried and re-weighed to obtain fresh weight (FW) every 2 min for 30 min, and afterwards every 2 h for a total of 60 h. Leaves were dried at 70 °C for 48 h in an oven to obtain the dry weight (DW). The relative water content (RWC) of leaves was calculated as

$$\mathrm{RWC} = (\mathrm{FW} - \mathrm{DW}) / (\mathrm{FW_s} - \mathrm{DW}) \times 100\% \qquad (1)$$

Ternstroemia gymnanthera (Wight et Arn.) Sprague (Theaceae), a dominant evergreen species in the same forest, was used for comparison. Their leaves were also treated as described above. Leaf water releasing curves were obtained by plotting RWC against time.

At predawn (06:00 h) and midday (13:00 h), bamboo leaves and stem segments were sampled and weighed immediately to obtain the FW and placed in water to rehydrate for 24 h. They were then reweighed to obtain the FW_s and dried at 70 °C for 48 h in an oven to obtain the DW. The RWC of leaves and stems were calculated as above.

Stem specific hydraulic conductivity and leaf hydraulic conductance

For predawn and midday stem hydraulic conductivity (K_h) measurement, six stems from different individuals per site were collected at predawn (between 06:00 and 07:00 h) and midday (between 13:00 and 14:00 h) on sunny days. Stem hydraulic conductivity was measured using a hydraulic conductivity apparatus (Tyree and Sperry 1989). Stem segments were longer than the longest vessel length. Maximum vessel length was estimated according to the 'air' injection method (Zimmermann and Jeje 1981). A raised reservoir of distilled and de-gassed water was attached to the stem to generate a gravity-induced pressure head of ~6 kPa. The water flow rates through the stem, following a short equilibration period, were monitored as the total volume per second. Hydraulic conductivity (K_h, kg m s^{-1} MPa^{-1}) of the stem segment was calculated as

$$K_h = FL / \Delta P \qquad (2)$$

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where F is the flow rate (kg s^{-1}) through the stem segment, ΔP is the pressure drop (MPa) along the stem segment and L is the length (m) of the stem segment. Upon completion of the measurements, the segment was perfused with 0.01% of Safranin dye to determine the cross-sectional area of the active xylem. Specific hydraulic conductivity (K_s, kg m^{-1} s^{-1} MPa^{-1}) was obtained as the ratio of stem hydraulic conductivity (K_h) and the cross-sectional area of the active xylem.

Predawn, midday and late afternoon (18:00 h) leaf hydraulic conductance (K_{leaf}, mmol m^{-2} s^{-1} MPa^{-1}) was determined by assessing the rehydration kinetics of leaves after detachment (Brodribb and Holbrook 2003). Leaf hydraulic conductance (K_{leaf}, mmol m^{-2} s^{-1} MPa^{-1}) was calculated from the equation:

$$K_{leaf} = C \times \ln(\Psi_o / \Psi_f) / t \qquad (3)$$

where C is the leaf capacitance per leaf area (kg MPa^{-1} m^{-2}), Ψ_o is the leaf water potential prior to rehydration and Ψ_f is the leaf water potential after rehydration for t s. Six branches were cut at dawn, noon and dusk, respectively. These branches were then sealed into black plastic bags with wet paper towels for 30 min to ensure that stomata were closed and leaf water potential (Ψ_L) was homogeneous among leaves. Two leaves were then harvested and measured to estimate initial leaf water potential (Ψ_o), and two additional leaves were allowed to absorb water for 10 s, and then were measured for leaf water potential (Ψ_f) using a pressure chamber (PMS 1000, Corvallis, OR, USA).

Leaf capacitance per area (C) was calculated from the slopes of leaf pressure volume relationships. The relationship between Ψ_L and RWC in the leaf was quantified using the bench drying technique (Tyree and Hammel 1972, Tyree and Richter 1981). Bamboo branches with leaves were cut underwater at dusk and rehydrated overnight. Leaves were removed from the shoot by cutting at the base of the petiole with a fresh razor blade, and then leaf weight and leaf water potential (Ψ_L) were measured periodically during slow desiccation of sample leaves in the laboratory. Desiccation of leaves continued until leaf water potentials nearly stopped falling. The turgor loss point was the inflection point of the graph of $1/\Psi_L$ versus RWC. The slopes of these curves yielded the leaf capacitance function in terms of RWC.

Leaf hydraulic vulnerability curves

The vulnerability of leaf hydraulic conductance to decreases in leaf water potential was also measured. Twenty branches from 10 individuals of *S. nitida* were cut early in the morning and dehydrated at 20 °C in the laboratory for different time periods from 10 to 480 min to generate a range of leaf water potentials. After desiccation, each stem was enclosed in a black plastic bag with wet paper towels for 30 min to ensure that stomata closure and homogeneous leaf water potential across the branch was obtained. K_{leaf} was then measured for two leaves from each branch, as described above. Leaf vulnerability curves were plotted as K_{leaf} against the initial leaf water potential (Ψ_o) before rehydration.

Leaf gas exchange and leaf water potential

Net photosynthetic rate (P_n) and stomatal conductance (g_s) were monitored in *S. nitida* leaves with a Li-6400 potable photosynthetic system (LI-COR, Lincoln, NE, USA) every 2 h from 07:00 h to 19:00 h from leaves of the bamboo stems grown in the shaded and open habitats.

Six to ten fully developed mature leaves from both microhabitats were selected to measure leaf water potential (Ψ_L) every 2 h between 07:00 and 19:00 h on two consecutive sunny days using the pressure chamber (PMS 1000, Corvallis, OR, USA).

Root pressure

Root pressure dynamics were monitored at the base of six *S. nitida* culms in each habitat for three consecutive nights. The bamboo culms were cut ~3 cm above the soil when guttation (the exudation of liquid water from the margins of the bamboo leaves) was observed. The cross-section of the culm stump was re-cut with a fresh razor blade and connected to a plastic tube filled with distilled water and fitted with an electronic pressure transducer (PX26-100DV, Omega Engineering, Stamford, CT, USA). Root pressure was then measured at 10 min intervals automatically with a data logger (CR10X, Campbell Scientific, Logan, UT, USA) until 09:00 h the next morning.

Results

Leaf water releasing curves and hydraulic vulnerability curves

Compared with leaves of *T. gymnanthera*, a dominant evergreen tree species, the water loss of *S. nitida* leaves was considerably faster. For *S. nitida*, both in open and shaded areas, it took ~330 min for the RWC to drop to 50%, whereas it took 1360 min for *T. gymnanthera* under the same laboratory condition (Figure 1).

The water transport system in leaves of *S. nitida* was highly vulnerable to embolism. Leaf hydraulic conductance (K_{leaf}) decreased rapidly with decreasing (more negative) leaf water potentials (Ψ_L) (Figure 2). In shaded areas, a 50% loss of K_{leaf} was induced by $\Psi_L = -1.2$ MPa, close to the midday Ψ_L of −1.29 MPa. For leaves from the open area, K_{leaf} was reduced by 50% at $\Psi_L = -0.6$ MPa, while minimum daily Ψ_L reached −2.28 MPa, consistent with the substantial decrease of K_{leaf} observed at midday (Figures 2 and 4b).

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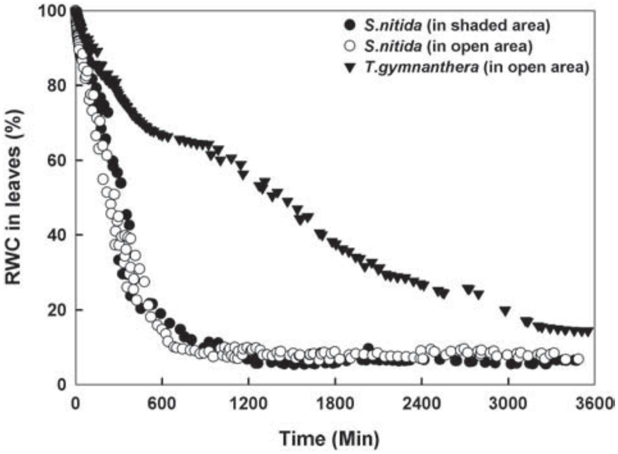

Figure 1. Leaf water releasing curves of *S. nitida* in shaded and open areas and *T. gymnanthera* showing changes of RWC with time after excision. Points were means calculated from six leaves of different individuals.

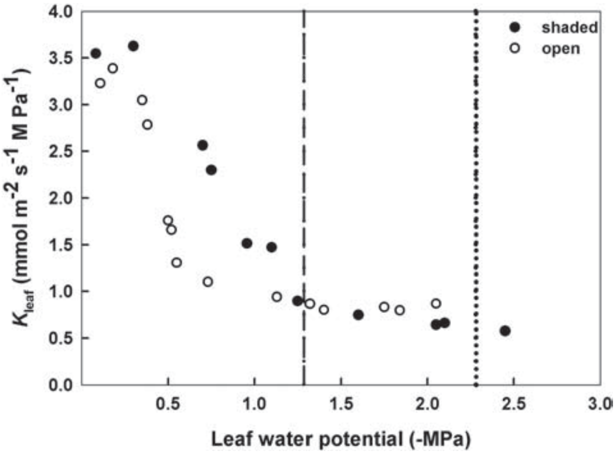

Figure 2. Hydraulic vulnerability curves of leaves measured in *S. nitida* in shaded and open areas. The vertical long dash line and the vertical dotted line indicated the midday leaf water potential observed in shaded and open areas, respectively.

Daily changes in water status of stems and leaves, hydraulic conductivity and gas exchange

Stem RWC of *S. nitida* did not differ between predawn and midday in both habitats (Figure 3a, $P > 0.05$). However, a significant midday decrease in RWC was observed in leaves in both open and shaded habitats. Leaf RWC at midday was 73.4 and 80.6%, compared with 93.3 and 94.9% of predawn values in open and shaded areas, respectively (Figure 3b, $P < 0.01$).

When leaf water potential reached its daily minimum value at noon, stem specific hydraulic conductivity (K_s) in shaded and open areas did not differ significantly from predawn K_s (Figure 4a, $P > 0.05$). Leaf hydraulic conductance (K_{leaf}), however, significantly decreased from 3.55 to 1.71 mmol m^{-2} s^{-1} MPa^{-1} in the shaded areas and from 3.22 to 1.16 mmol m^{-2} s^{-1} MPa^{-1} in the open areas (Figure 4b, $P < 0.01$). In the late afternoon, K_{leaf} maintained a low value, but it recovered to its maximum value in the following morning (Figure 4b).

Maximum net photosynthetic rate (P_n) in open areas was 5.51 µmol CO$_2$ m^{-2} s^{-1}, whereas in shaded areas it was 1.29 µmol CO$_2$ m^{-2} s^{-1} (Figure 5a). Leaves in open areas also exhibited higher maximum stomatal conductance (g_s) (Figure 5b). For bamboos in open areas, midday depression of photosynthesis was correlated with the low stomatal conductance (g_s) and low K_{leaf}.

The diurnal course of leaf water potential (Figure 5d) exhibited similar patterns under different light regimes; however, the lowest water potential of the individuals in the shaded area occurred later compared with those in the open area. Predawn leaf water potential did not differ significantly between the two habitats, whereas minimum leaf water potentials in the open (13:00 h) and shaded areas (15:00 h) were −2.28 and −1.29 MPa, respectively. Leaf turgor loss points of these bamboos from the open and shaded areas were −2.26 ± 0.15 and −1.28 ± 0.13 MPa, respectively, which are nearly equal to the daily minimum leaf water potential observed in the field.

Daily pattern of root pressure

Sinarundinaria nitida from different habitats exhibited a similar diurnal pattern in root pressure, which lasted from 21:00 to 09:00 h (Figure 6). At 05:00 h, the root pressure in open and shaded areas reached the peak value of 62.2 and 47.9 kPa, respectively. The root pressure of individuals in open areas was higher than that of shaded individuals. Individuals in both habitats maintained root pressure at maximum values from 03:00 to 05:00 h (Figure 6). The positive root pressures were of sufficient magnitude to raise the water potential of the entire xylem above atmospheric pressure in this relatively short-stature species (3–4 m).

Discussion

Our results reveal the mechanisms that bamboo species use to cope with daily water deficits from transpirational water loss. Unlike trees and palms, this studied bamboo species did not use stem water storage to buffer transpirational water loss, despite possessing abundant parenchyma tissues in their stems/culms. Bamboo leaves were vulnerable to water loss so that there was a strong decline in hydraulic conductance at midday. The decline in K_{leaf} and gas exchange protected stem xylem from embolism formation, and embolism refilling in leaves depends on nocturnal root pressure.

Leaf water loss and stem water storage

The leaves of the studied bamboo species lost water very quickly relative to their leaf capacitance or leaf water storage.

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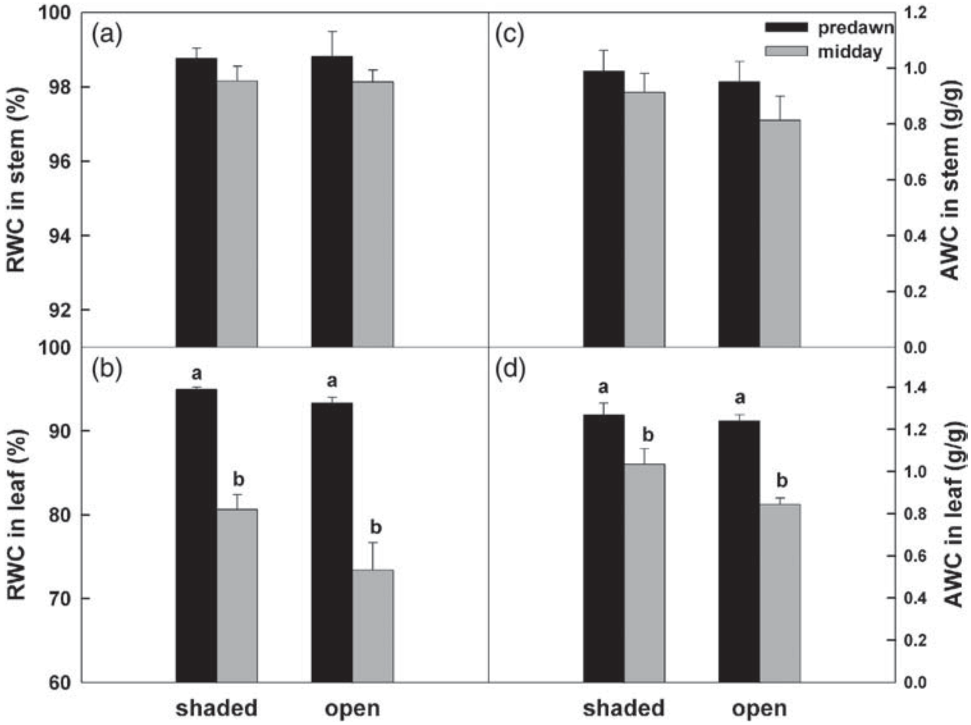

Figure 3. Predawn and midday value of RWC and AWC in stem and leaf measured in *S. nitida* in shaded and open areas. The means ± SE were calculated from six plants. Letters a and b indicated that significant differences between predawn and midday RWC ($P < 0.01$) and AWC in the leaves were found ($P < 0.01$).

The water loss rate of bamboo leaves was much higher than the co-existing evergreen broadleaf species, and did not decrease until the RWC reached 20% (Figure 1). Consequently, leaf RWC and absolute water content (AWC) decreased significantly at midday. This rapid water loss suggests a weak capability of bamboo leaves in controlling water loss, which is probably because of their very thin leaf waxy cuticle. Therefore, bamboos have to either replace leaf water loss quickly or employ other mechanisms to prevent leaf desiccation during the day. Additionally, turgor loss in the bulliform cells, which are large and bubble-shaped epidermal cells on the upper bamboo leaf mesophyll (Liese 1998), also appear to induce leaf rolling and folding at midday (unpublished observation), which may help to reduce light exposure and evaporation from the leaf adaxial surface.

The relatively high (~60%) parenchyma content in bamboo stems (Liese 1998) was expected to increase water storage to buffer variation in transpiration and mitigate limitations in the hydraulic systems, as in trees (Goldstein et al. 1998, Scholze et al. 2007, Dierick et al. 2010) and palms (Holbrook and Sinclair 1992). However, the lack of significant changes in stem RWC and AWC observed in this study indicates that leaves were not utilizing stored water from the stem parenchyma on a daily basis. Instead, stomatal closure and turgor loss resulted in decrease in transpiration; these are mechanisms used by woody bamboos to avoid further water loss during the day.

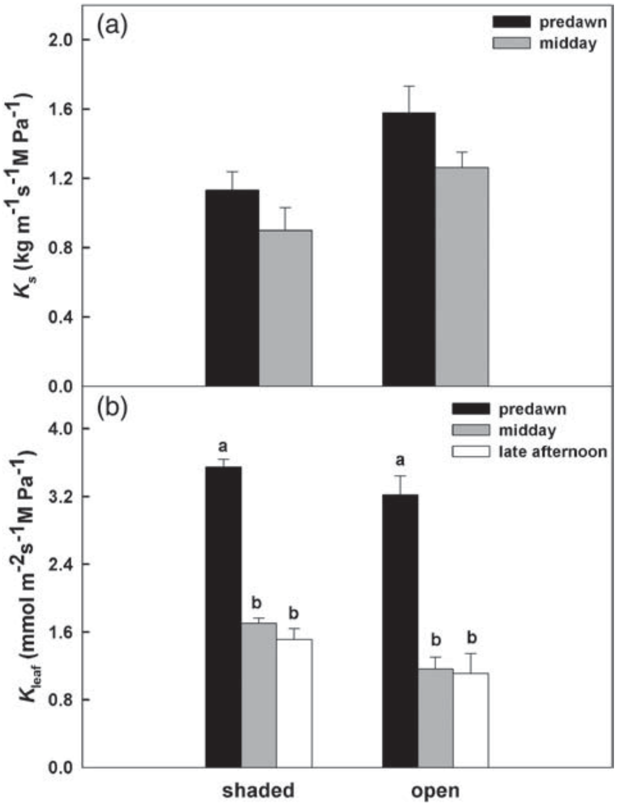

Figure 4. Diurnal variation of K_s and K_{leaf} measured in *S. nitida* in shaded and open areas. Bars are means ± SE ($n = 6$). Significant differences were indicated by different letters ($P < 0.01$).

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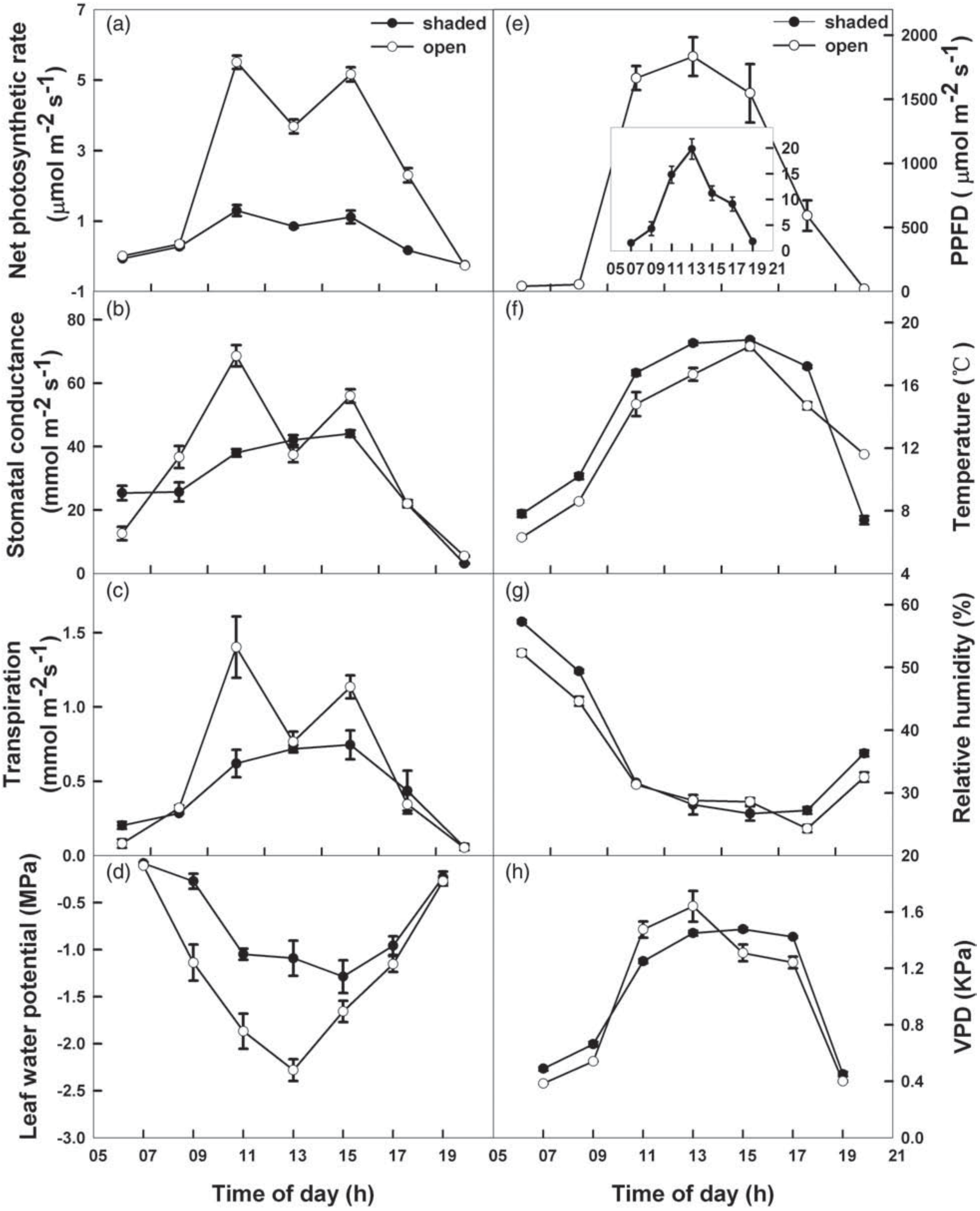

Figure 5. Daily variation of photosynthesis, stomatal conductance, transpiration and leaf water potential measured in *S. nitida* in shaded and open areas. The means ± SE were calculated from six plants. The relevant environmental parameters (photosynthetic photon flux density (PPFD), temperature, relative humidity and vapor pressure deficit (VPD)) were shown on the right side.

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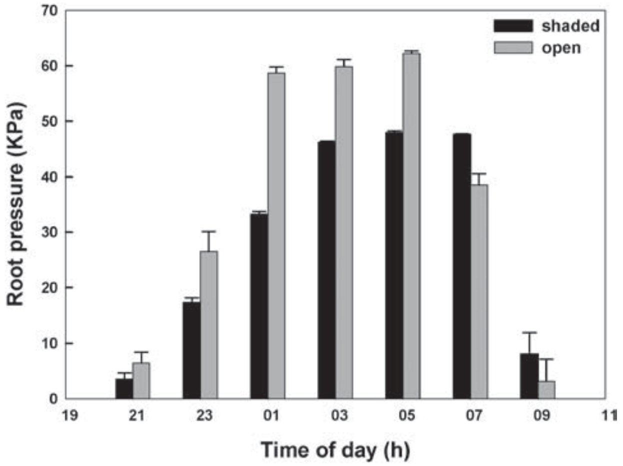

Figure 6. Daily variation of root pressure measured on six culms of *S. nitida* in shaded and open areas, respectively. Values were measured every 2 h, from 21:00 to 09:00 h in three consecutive days. Bars were means ± SE of six culms.

Coordination between water transport systems in bamboo leaves and stems

Diurnal depression in leaf hydraulic conductance suggests that vessels in bamboo leaves experience daily cycles of cavitation and refilling. Although the diurnal depression in K_{leaf} in conifers could be partially explained by changes in conduit dimensions under cycles of tension increase and tension release (Cochard et al. 2004), more evidence indicates that embolism formation is responsible for diurnal depression in K_{leaf} (Lo Gullo et al. 2003, Woodruff et al. 2007, Johnson et al. 2009). In contrast, no significant reduction in bamboo stem hydraulic conductivity (K_s) suggests that embolism did not occur in stem xylem during the day. This pattern (K_s did not change significantly between dawn and midday) is consistent with a Neotropical savanna tree (Zhang et al. 2009). Midday depression of K_{leaf} has also been reported in tropical rain forest trees (Brodribb and Holbrook 2004), and may constitute a hydraulic signal involved in normal daily stomatal regulation to prevent further water loss and embolism in stems (Brodribb and Holbrook 2003, Zhang et al. 2009). The coordination between leaf and stem hydraulic systems for preventing embolism in stems was also found in three eastern US tree species (*Acer rubrum* L., *Liriodendron tulipifera* L. and *Pinus virginiana* Mill.) in recent research (Johnson et al. 2011).

Embolism refilling is possibly easier in leaves than in stems. The hydrostatic pressures needed for embolism refilling in the xylem depend on the conduit size (Hacke and Sperry 2003). A small conduit containing only water vapor can be refilled even when the xylem is under tension. In contrast, a larger air-filled conduit needs more positive pressures to refill. The maximum diameter of these bamboo leaf vessels is close to half of that of stem vessels (unpublished data). Thus, the embolized leaf vessels should be easy to refill, making it beneficial for maintaining stem conductivity at the expense of leaf conductivity. Although the large vessels of bamboo stems can confer the xylem system high efficiency in long distance water transport, they may also require more energy to refill once cavitated. Therefore, the stems of the bamboo species maintain high RWC at midday, and are highly protected during the day from embolism. Plants employ a variety of structural and physiological mechanisms to prevent cavitation (Zimmermann 1983), for example, partially closing stomata and wilting leaves. The investment in a refilling strategy is frequently more expensive than avoiding cavitation, especially in stem xylem with big vessels (Salleo et al. 2009, Secchi and Zwieniecki 2011).

Midday depression in K_{leaf} limits leaf gas exchange in bamboos. Decrease in petiole hydraulic conductance of grapevine is responsible for stomatal closure (Zufferey et al. 2011), and midday depression in K_{leaf} in the studied bamboo species could also be responsible for midday depression in g_s. In addition, leaf turgor loss as well as leaf rolling at midday (unpublished observation) could also be mechanisms against further water loss. Interestingly, K_{leaf} of the bamboos in open areas was more vulnerable to water loss than that of the bamboos in the shade (Figure 2). This could be because bamboos in open areas developed a more conservative water use strategy, owing to higher evaporation demand in the open area. Higher vulnerability of K_{leaf} to water loss will allow quicker stomatal closure to conserve water.

Embolism refilling by nocturnal root pressure

Positive root pressure of bamboo was observed during the night, and the root pressures were high enough to fill up the embolized vessels in the bamboo leaves, assuming that there is little or no cuticular transpiration during the night. Root pressure has been proposed to be responsible for cavitation refilling in some bamboo species (Cochard et al. 1994, Saha et al. 2009). Refilling of vascular systems via positive root pressure at night has also been extensively shown to play an important role in cavitation repair in other species, including grapevine (Sperry et al. 1987), sugarcane (Neufeld et al. 1992), maize (Tyree et al. 1986, Zhang et al. 1995, McCully et al. 1998) and rice (Stiller et al. 2003). The ability to refill cavitated conduits would allow plants to recover conductive capacity and facilitate photosynthetic gas exchange in the morning. Some novel mechanisms under negative pressure were proposed to explain diurnal cavitation refilling (Bucci et al. 2003, Stiller et al. 2005, Zwieniecki and Holbrook 2009). However, K_{leaf} of this bamboo species did not recover during the late afternoon under negative xylem pressure, suggesting that refilling of cavitated vessels in this species may fully depend on nocturnal root pressure.

Conclusion

Our results showed hydraulic segmentation between leaf and stem, wherein stem xylem was highly protected by midday

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down-regulation in K_{leaf} and low g_s. Uncoupling of stem hydraulics from leaf hydraulics prevents stem xylem dysfunction and helps maintain adequate water balance under both high and low light environments. Stem water storage did not appear to be substantially used for daily transpiration in this woody bamboo species. Bamboo leaves lost water very quickly and thus the leaf hydraulic system of bamboo was quite vulnerable to water loss. Midday depression in stomatal conductance and photosynthesis, as well as leaf turgor loss and rolling at midday, may decrease the daily carbon gain for bamboos, but it helps to prevent water loss and stem xylem embolism. Recovery of K_{leaf} did not occur during the day under negative pressure, therefore embolism refilling of this bamboo species may fully depend on root pressure occurring at night.

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Conflict of interest

None declared.

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