RESEARCH

Do karst woody plants control xylem tension to avoid substantial xylem cavitation in the wet season?

Dayong Fan[1*] , Shouren Zhang[2*], Hui Yan[2,3], Qian Wu[2], Xinwu Xu[2,4] and Xiangping Wang[1]

Abstract

Background: Plants have been hypothesized to maintain strong control over xylem tension by closing stomata and to operate at a water potential above or near the critical potential at which cavitation commences. An alternative hypothesis holds that cavitation temporarily relieves water stress and stomatal closure is insufficient to prevent short term "run-away" cavitation.

Methods: The objectives of this study were to investigate the leaf conductivity loss at noon (*Loss*) of 13 woody species differing in leaf phenology at two sites on karst topography in the wet season in southwestern China; the hydraulic architecture of woody species has rarely been reported previously. *Loss* was predicted from minimum field leaf water potentials (Ψ_{min}) and laboratory-generated vulnerability curves. We also measured the maximum quantum efficiency of photosystem II using chlorophyll *a* fluorescence (F_v/F_m) and other associated leaf traits.

Results: *Loss* in the field varied substantially, from 1.39% in evergreen *Itea chinensis* to 90.07% in deciduous *Sapium sebiferum*. However, the *Loss* did not significantly decrease the efficiency of photosystem II. The water potential at which a 50% loss in leaf conductivity occurred (Ψ_{50}) was not correlated to Ψ_{min}. The co-occurring evergreen and deciduous species differed significantly in some stem hydraulic and associated leaf traits. Deciduous species had higher hydraulic conductance, photosynthetic rate, stomatal conductance, lower cavitation-resistance and minimum water potential than co-occurring evergreen species.

Conclusions: There was no sign that karst woody species in southwestern China could control xylem tension above the threshold to avoid substantial xylem cavitation in the wet season. There was no association between *Loss* and F_v/F_m among the studied species. This "isohydric" regulation behaviour, as well as abundant rainfall in the wet season, may explain why large variations of *Loss* existed across karst woody species in southwestern China.

Keywords: Karst forest, Leaf conductivity loss, Leaf phenology, Photochemistry efficiency of photosystem II

Introduction

Cavitation-induced decrease in the hydraulic conductance of plant stems, roots, and leaves has long been suggested to lead to stomatal closure, thereby preventing the increase in xylem tension that can induce run-away xylem cavitation (Jones and Sutherland 1991; Nardini and Salleo 2000; Domec et al. 2006; Guyot et al. 2012; Daniela et al. 2016; Xiong et al. 2018). Because embolized xylem cells can reduce hydraulic conductivity and

greatly retard photosynthesis and growth, plants would be expected to have strong control over xylem tension and typically operate at a water potential above or near the critical potential at which cavitation commences (Sperry 2000). This hypothesis has been evidenced by tight associations between minimum water potential and hydraulic resistance in various ecosystems (e.g., Pockman and Sperry 2000; Markesteijn et al. 2011b; Gadow et al. 2016). For instance, Nardini and Salleo (2000) demonstrated that 11 tree species in a Mediterranean ecosystem suffered an average of 10% cavitation before stomata began to close. A survey of the hydraulic architecture of 13 tropical dry forest species in Bolivia showed that the

* Correspondence: dayong.fan@anu.edu.au; zsr@ibcas.ac.cn
[1]College of Forestry, Beijing Forestry University, Beijing 100083, China
[2]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
Full list of author information is available at the end of the article

average loss of hydraulic conductivity corresponding to minimum leaf water potential was about 20% in the wet season (Markesteijn et al. 2011b).

However, the functional association between minimum water potential and hydraulic safety does not prove that plants can control embolisms, because the loss of hydraulic conductivity is not a linear function of water potential. In fact, a detailed analysis of published data has shown that there exists a large variation among species at the same site in native embolism rates during a day (Pockman and Sperry 2000; Markesteijn et al. 2011a, 2011b). For example, re-analysis of data from Markesteijn et al. (2011a, 2011b) revealed that daily conductivity loss ranged from 5%–63% of maximum conductivity. The embolism rate varied widely, from 11%–95% in the dry season and from 11%–93% in the wet season, across 12 Sonoran desert species (Pockman and Sperry 2000).

Johnson et al. (2009) hypothesized that there may exist two different strategies for the daily maintenance of hydraulic conductivity: 1) a "radical" strategy of substantial loss and subsequent recovery and 2) a more conservative strategy of loss avoidance. Such a hypothesis, we believe, should be assessed broadly in different global ecosystems for a more comprehensive understanding of the role of cavitation in plant water balance. Furthermore, the two strategies might have different impacts on photosynthesis. The conservative strategy requires that plants close their stomata before catastrophic hydraulic failure occurs. As soon as stomata close, photosynthesis would suffer from a shortage of CO_2 and absorbed light would exceed photosynthetic requirements; consequently, photosystem II (PSII) would be temporarily or chronically photo-inactivated, which could be reflected by a decrease in maximum quantum efficiency of PSII photochemistry (F_v/F_m) (Baker 2008). On the other hand, the radical strategy, which allows massive temporary cavitation with stomata open, would not affect PSII photochemistry, because ambient CO_2 could diffuse into leaf intercellular spaces, particularly if such massive cavitation temporarily relieved water stress (Holtta et al. 2012); therefore its F_v/F_m should be higher than that in the conservative strategy. This expectation, to our knowledge, has not yet been tested.

The karst topography is characterized by shallow soils with low water-retention capacity and high porosity of the underlying limestone rock. Compared to other karst areas at similar latitudes, the karst area in southwestern China is unique because of its abundant precipitation, with rainfall concentrated in the growing season (from May to September) (Wu et al. 2003), mainly due to the rise in elevation of the Qinghai–Tibet Plateau. Previous studies have shown that the water potential at which a 50% loss in hydraulic conductivity occurs (Ψ_{50}) in 31 woody species in this area was only − 1.27 MPa (Fan et

al. 2011), compared with high resistance in Mediterranean (Tognetti et al. 1998) and Central American karst regions (McElrone et al. 2004). Xylem tension measurements in the wet season have shown that woody plants experienced average midday leaf water potentials (Ψ_{min}) of about − 1.5 MPa (Yu et al. 2002; Liu et al. 2012), suggesting that, on average, more than 50% embolism will occur in the field. Unfortunately, the Ψ_{50} and Ψ_{min} measurements were made either separately or across different species; therefore, whether karst woody plants in southwestern China can control xylem tension above a critical threshold remains unknown. This knowledge is also crucial to better evaluate the suitability of plant species to site-specific reforestation programs in the karst area in southwestern China, which has suffered serious degradation due to intensive human disturbances.

The objectives of present study were to 1) investigate variation in native embolism in branches and its relationship to leaf traits in 13 woody species (six evergreen and seven deciduous) at two sites in the karst area of southwestern China; 2) examine whether there are associations between *Loss* and PSII's photochemistry among woody species; and 3) investigate the relationship between native embolism and leaf phenology. Because many studies have demonstrated that evergreen species have larger safety margins (the difference between Ψ_{min} and the water potential at which cavitation occurs), higher cavitation resistance, and lower daily minimum water potential (Choat et al. 2005; Chen et al. 2009; Markesteijn et al. 2011b; O'Brien et al. 2017) than co-occurring deciduous species, we expected that evergreen species would lose less conductivity than deciduous species on sunny days.

Materials and methods
Study area
The study was conducted at two sites in Guizhou Province, southwest China. The Huajiang site (HJ; 25°42'N, 105°35′E, 900 m a.s.l.) and the Puding site (PD; 26°15′N, 105°44′E, 1200 m a.s.l.). The two sites were 60 km from each other, in the southwestern and western parts of the province and have mean annual temperatures 18.4 °C and 15.1 °C, respectively. Both sites have very few days with temperatures below 0 °C in winter (Wu et al. 2003).

The Huajiang site has a warm temperate climate, with a mean annual precipitation (MAP) of 1100 mm, 83% of which occurs during the growth season between May and October. Vegetation in this region is characterized by sparsely distributed secondary deciduous trees and shrubs on bare rocks. The Puding site is dominated by a humid monsoon climate. The MAP is 1398 mm, 60%–70% of which occurs between May and October. The Puding site has a well-developed secondary evergreen

and deciduous broad-leaved mixed forest growing in yellow lime soil.

Plant materials

We sampled 13 common canopy and sub-canopy woody angiosperm species in 12 plant families in August (Table 1). We sampled saplings or young trees 2–4 m tall that occurred either in canopy gaps created by natural disturbance or near clearings associated with forest roads to ensure that all samples experienced similar light environments. All 13 species were dominant tree species at the two sites.

In situ photosynthetic gas exchange and chlorophyll *a* fluorescence measurements

A branch (0.4–0.7 m long) from each tree was detached from the top or middle of the sunny (south-facing) side of the canopy using pruning shears mounted on a 5 m pole. The detached branch was immediately immersed in a water-filled bucket. Then, the end of each branch was re-cut twice under water, ensuring continuum of the xylem conduit.

Theoretically, g_s is coupled to leaf specific hydraulic conductivity (K_{lnoon}) and Ψ_{min} at noon as follows (Oren et al. 1999):

$$g_s = \frac{K_{lnoon} \times (\Psi_{min} - \Psi_s)}{D}$$

Where D is vapour pressure deficit and Ψ_s is soil water potential.

To obtain g_s under similar conditions of D, we measured g_s of new, fully expanded leaves on detached branches using a LI-6400 photosynthesis system (LI-COR, Lincoln, NE, USA) in a blue-red light source

leaf chamber with 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ light intensity, 25 °C–30 °C leaf temperature (ambient temperature ranged from 25 °C–32 °C), an airflow rate of 400 $\mu mol \cdot s^{-1}$, and 50%–70% relative humidity (ambient, 40%–80%) to maintain D between 0.8 and 1.2 kPa. Instantaneous photosynthetic rate (P_n) under similar conditions of D was also recorded at the same time. Measurements were conducted at midday, around 11:30–14:00 Beijing Standard Time.

Chlorophyll *a* fluorescence, F_o, and F_m (minimum and maximum fluorescence yields corresponding to open and closed reaction centre traps, respectively) were measured in the same leaves used to measure g_s with a handy-PEA portable fluorometer (Hansatch Instruments, Norfolk, UK) operated at 100% maximum excitation light intensity. Before measurements, the leaves were darkened for at least 30 min. The maximum quantum efficiency of PSII photochemistry, F_v/F_m (= $(F_m - F_o)/F_m$), can provide a simple and rapid way of monitoring stress (Baker 2008). Non-stressed plants have an F_v/F_m ratio of 0.75–0.85 (Araus and Hogan 1994; Ogaya et al. 2011).

Leaf water potential

The midday leaf water potential (Ψ_{min}) was determined for each species at the two sites using a PSYPRO Water Potential System (Wescor, Logan, UT, USA). The measurements were carried out between 11:30 and 14:00 h Beijing Standard Time on leaves from the detached branches.

Hydraulic conductance and vulnerability to xylem cavitation

In early morning, branches near those used to measure g_s were collected to measure K_l and the vulnerability curve. Briefly, four to nine sun-exposed shoots (2–4

Table 1 Characteristics of the 13 tree species from the karst area of southwestern China included in this study

Species	Family	Leaf phenology	Location	Site
Alangium chinense (Lour.) Harms subsp. *chinense*	Alangiaceae	D	HJ	HJ
Carpinus pubescens Burkill	Betulaceae	D	PD	PD
Daphniphyllum oldhami (Hemsl.) Rosenth.	Daphniphyllaceae	E	PD	PD
Ficusbenguetensis Merrill	Moraceae	E	HJ	HJ
Itea chinensis Hook. & Arn.	Saxifragaceae	E	PD	PD
Ligustrum lucidum W. T. Aiton	Oleaceae	E	PD	PD
Lindera communis Hemsl.	Lauraceae	E	PD	PD
Lithocarpus glaber (Thunb.) Nakai	Fagaceae	E	PD	PD
Mallotus japonicus (L. f.) Müll. var. *floccosus*	Euphorbiaceae	D	HJ	HJ
Picrasma quassioides (D. Don) Bennett	Simaroubaceae	D	HJ	HJ
Platycarya longipes Wu	Juglandaceae	D	PD	PD
Sapium sebiferum (L.) Roxb.	Euphorbiaceae	D	HJ	HJ
Stachyurus obovatus (Rehder) Handel-Mazzetti	Stachyuraceae	E	PD	PD

D Winter deciduous, *E* Evergreen, *HJ* Huajiang site, *PD* Puding site

years old) of 0.4–0.7 m were cut, immediately wrapped in moist paper towels, and carried to the laboratory, where they were re-cut to 17–19 cm lengths under water for hydraulic measurement. In an air-conditioned laboratory (26 °C), maximum flow rate was measured with a precision balance (Sartorius, BP221S, Göttingen, Germany) under 8 kPa hydrostatic pressure after air emboli were clear by perfusion with 110 kPa distilled water (filtered to 0.2 μm) for 30 min. Measurements were not initiated until after ~ 2 min, when the flow rates stabilized. The efflux changes were measured every 30 s to obtain the flow rate. The K_l (kg·m^{-1}·MPa^{-1}·s^{-1}) was calculated by dividing maximum flow rate by the leaf area distal to the measured sample and by pressure gradient. Leaf area was measured and calculated with a scanner and WinFOLIA software (Regent Instruments, Quebec City, Canada).

Vulnerability of the xylem to cavitation was characterized using a vulnerability curve as described by Sperry and Saliendra ([1994](#)). Stems were inserted into a collar and sealed with both ends protruding. Air was injected into the collar to a desired pressure, which was maintained for 15 min and then slowly decreased to 0.1 MPa. Afterwards, hydraulic conductivity was re-measured. This procedure was repeated until more than 90% loss in conductivity was reached. The percentage loss of conductivity (*PLC*) following each pressurization of the chamber was calculated as $PLC = 100 \times (K_h - K_{hi})/K_h$, where K_{hi} is the hydraulic conductivity of the sample measured after each chamber pressurization. Vulnerability curves were fitted with an exponential sigmoidal equation (Pammenter and Vander Willigen [1998](#)):

$$PLC = \frac{100}{1 + e^{a(\Psi - b)}}$$

where Ψ is the negative of the injection pressure and a and b are coefficients estimated by non-linear regression in SPSS 10.0 (IBM, Chicago, IL, USA). The coefficient b represents Ψ_{50}.

The 15–17 cm long stem as applied in the present study, may cause an open-vessel artefact. To check this possibility, firstly we traced the book *Woods in China* (Cheng et al. [1992](#)), in which the data of the sampled species showed that the maximum vessel element's length ranged from 150 (*Picrasma quassioides*) to 2000 μm (*Daphniphyllum oldhami*). Secondly, to measure the VC curve, we applied a 0.1 MPa in the collar to re-measure hydraulic conductivity to minimize the possible open-vessel artefact (Cochard et al. [1992](#)). Further, some studies showed that generally the current-year branches of woody species (diffuse-porous and ring-porous) have the maximum vessel length less than 16 cm in different forest ecosystems (eg. Cochard et al.

[1990](#); Sperry et al. [1994](#); Hacke et al. [2006](#); Jacobsen et al. [2008](#)). However, we also noticed some woody species (eg. *Quercus rubra*) have vessels with length of more than 1 m in the literature (Ennajeh et al. [2011](#)), which means there is a little chance that some branch samples in the present study may have open-vessels at both ends.

We calculated the daily maximum percentage loss of leaf hydraulic conductivity (*Loss*), as well as K_l at noon (K_{lnoon}), by using field water potential measurements and the vulnerability curve (Johnson et al. [2009](#)). It has been reported that xylem embolism is likely a critical element for the decrease of leaf hydraulic conductance during the daytime (Kikuta et al. [1997](#); Woodruff et al. [2007](#); Johnson et al. [2010](#)).

Data analysis

We tested the differences between evergreen and deciduous species using ANOVA and Multivariate ANOVA (MANOVA), the latter using either the identity or contrast response design (both with indistinguishable results) and using the Pillais Trace statistic test. When necessary, data were log-transformed to meet normality assumptions. Pearson correlation analysis was conducted among investigated traits. All analyses were performed using SPSS 10.0. For investigation on the relationship between Ψ_{min} and Ψ_{50}, data from this study as well as previously-published literature cross different ecosystems (Pockman and Sperry [2000](#); Choat et al. [2005](#); Hao et al. [2008](#); Markesteijn et al. [2011b](#)) were compiled.

Results

Values of Ψ_{min} ranged from -0.96 MPa in *Stachyurus obovatus* (an evergreen species at the PD site) to -1.61 MPa in *Mallotus japonicus* (deciduous; HJ site), a difference of only 0.65 MPa (Table [2](#)). These values corresponded closely to data collected by Liu et al. [2012](#)) at the same sites. On the contrary, there were wide variations in vulnerability curves and Ψ_{50} across the 13 species (Table [2](#), Fig. [1](#)). In this study, *S. obovatus* was the species most resistant to xylem cavitation; its Ψ_{50} of -4.31 MPa was seven-fold more negative than the least resistant species, *Daphniphyllum oldhami* (evergreen; PD). The *Loss* at noon, calculated using field water potential measurements and the vulnerability curve, varied substantially in the field, from 1.39% in *Itea chinensis* (evergreen; PD) to 90.07% in *Sapium sebiferum* (deciduous; HJ) (Table [2](#)). As an extension of the study by Johnson et al. ([2009](#)), we compiled from the literature a large dataset on embolism of native woody species across various ecosystems (Pockman and Sperry [2000](#); Bucci et al. [2003](#); Nardini et al. [2003](#); Brodribb and Holbrook [2004](#); Meinzer et al. [2004](#); Choat et al. [2005](#); Brodribb and Holbrook [2006](#); Bhaskar et al. [2007](#); Hao et al. [2008](#); Johnson et al. [2009](#); Markesteijn et al. [2011b](#); Guyot et

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Table 2 Summary parameters for the 13 woody karst species from southwestern China examined in this study. Minimum leaf water potential (Ψ_{min}, MPa), photosynthetic rate (P_n, $\mu mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (g_s, $mol \cdot m^{-2} \cdot s^{-1}$), leaf specific conductivity (K_l, $kg \cdot m^{-1} \cdot MPa^{-1} \cdot s^{-1}$), xylem tension at 50% cavitation (Ψ_{50}, MPa), leaf specific conductivity at noon (K_{lnoon}, $kg \cdot m^{-1} \cdot MPa^{-1} \cdot s^{-1}$), loss percentage of K_l at noon (*Loss*, %), maximum quantum efficiency of photosystem II (F_v/F_m), and hydraulic safety margin (Margin, Mpa) were assessed for each species. Standard errors were shown in parentheses

Species	Ψ_{min}	P_n	g_s	K_l	Ψ_{50}	K_{lnoon}[a]	*Loss*[a]	F_v/F_m	Margin[b]
Alangium chinense ssp. *chinense*	−1.50 (0.25)	10.55 (1.24)	0.38 (0.10)	6.06 (1.13)	−1.08 (0.23)	1.94	67.95	0.75 (0.01)	−0.42
Carpinus pubescens	− 0.99 (0.32)	6.90 (2.96)	0.23 (0.08)	2.68 (0.88)	−1.39 (0.15)	1.77	33.82	0.78 (0.02)	0.4
Daphniphyllum oldhami	−1.12 (0.21)	4.05 (0.71)	0.11 (0.03)	0.91 (0.32)	−0.62 (0.08)	0.09	89.84	0.79 (0.01)	−0.5
Ficus benguetensis	−1.15 (0.62)	5.12 (0.23)	0.13 (0.05)	2.17 (1.27)	−0.66 (0.09)	0.42	80.68	0.80 (0.01)	−0.49
Itea chinensis	−0.99 (0.18)	7.46 (1.65)	0.14 (0.02)	1.40 (0.49)	−2.54 (0.26)	1.38	1.39	0.76 (0.02)	1.55
Lindera communis	−0.98 (0.06)	9.86 (0.53)	0.21 (0.01)	0.51 (0.21)	−0.85 (0.12)	0.20	60.13	0.79 (0.02)	−0.13
Lithocarpus glaber	−1.08 (0.18)	9.71 (3.79)	0.17 (0.12)	1.70 (0.53)	−1.57 (0.32)	1.16	31.69	0.81 (0.01)	0.49
Ligustrum lucidum	−1.09 (0.16)	11.49 (1.23)	0.32 (0.15)	1.44 (0.19)	−3.67 (0.60)	1.13	21.37	0.80 (0.01)	2.58
Mallotus japonicus var. *floccosus*	−1.61 (0.23)	7.03 (0.66)	0.34 (0.12)	3.53 (0.63)	−1.12 (0.12)	0.95	73.19	0.77 (0.03)	−0.49
Platycarya longipes	−1.07 (0.19)	10.71 (0.82)	0.31 (0.05)	2.46 (0.55)	−1.50 (0.04)	1.59	35.56	0.76 (0.01)	0.43
Picrasma quassioides	−1.38 (0.05)	10.49 (0.66)	0.30 (0.08)	5.60 (0.49)	−0.93 (0.13)	0.20	87.84	0.77 (0.01)	−0.77
Stachyurus obovatus	−0.96 (0.56)	5.42 (2.09)	0.14 (0.03)	0.86 (0.19)	−4.31 (0.39)	0.74	14.07	0.80 (0.02)	3.35
Sapium sebiferum	−1.42 (0.31)	10.37 (1.71)	0.23 (0.02)	4.52 (0.82)	−0.65 (0.08)	0.45	90.07	0.84 (0.02)	−0.77

[a], calculated using laboratory-generated vulnerability curve and field water potential measurements. [b], calculated as the difference between Ψ_{50} and minimum water potential

al. 2012). *Loss* values for a total 75 species were bimodally-distributed (Fig. 2, Additional file 1: Table S1). The K_l and K_l at noon (K_{lnoon}) each varied by more than 10-fold. On average, the evergreen species displayed significantly higher Ψ_{min} and lower K_l than the deciduous species, but the differences in K_{lnoon} between groups was not significant (Table 3). Evergreen species also tended to exhibit lower loss (42.7%) of K_{lnoon} and lower Ψ_{50} than deciduous ones (Table 3).

The F_v/F_m ratios of all 13 species were above 0.75 (Table 2), suggesting that no physiological stress was experienced at noon. When the species were classified into two groups based on daily maintenance of hydraulic conductivity (10%–40% and 60%–90%; Johnson et al. 2009), no significant differences in F_v/F_m ratio was detected between the groups (Fig. 3). There were substantial variations among species in g_s at noon measured under constant vapour pressure deficit (Table 2). The P_n varied among species by a factor of about three, whereas variation in g_s was each several times greater. On average, evergreen species had significantly lower g_s, and higher hydraulic safety margin than deciduous ones. A MANOVA using the Pillais Trace statistic revealed that the two groups, on the whole, was not significantly different for the 8 leaf traits (Table 3).

The values of g_s were positively correlated with K_l across species ($P = 0.013$), while K_{lnoon} was not significantly associated with g_s ($P = 0.073$; Fig. 4). A strong association between Ψ_{min} and Ψ_{50} across different ecosystems was demonstrated; species with lowest Ψ_{min}

were most resistant to drought-induced cavitation (Fig. 5). However, no significant relationship was detected from data pooled from this study alone (Fig. 5, Table 4). Ψ_{50} was only marginally positively associated with K_l (Table 4, $P = 0.08$), consistent with previous results either across many vegetation types (Maherali et al. 2004) or within specific ecosystems (e.g., temperate forest; Maherali et al. 2006). There was no association between *Loss* and F_v/F_m (Table 4, $P = 0.58$).

Discussion

The loss of leaf conductivity in the field, most likely due to leaf or stem xylem embolism (Domec et al. 2006; Woodruff et al. 2007; Johnson et al. 2009; Blackman et al. 2017), can be accurately predicted from field measurements of leaf water potentials and laboratory-generated vulnerability curves (Brodribb and Holbrook 2004; Johnson et al. 2009). The 13 species in this study varied substantially in *Loss* in the field, from 1.39% in the evergreen *I. chinensis* to 90.07% in the deciduous *S. sebiferum* in the field. The large variation in *Loss* in the karst area in China argued against the hypothesis that plants control xylem tension above threshold for cavitation. Interestingly, *Loss* in the current study did not significantly depress the efficiency of PSII and/or the photosynthetic rate, suggesting that photosynthetic capacity was not affected by xylem cavitation, even in the extreme case of *S. sebiferum*, which lost 90% hydraulic conductivity at noon.

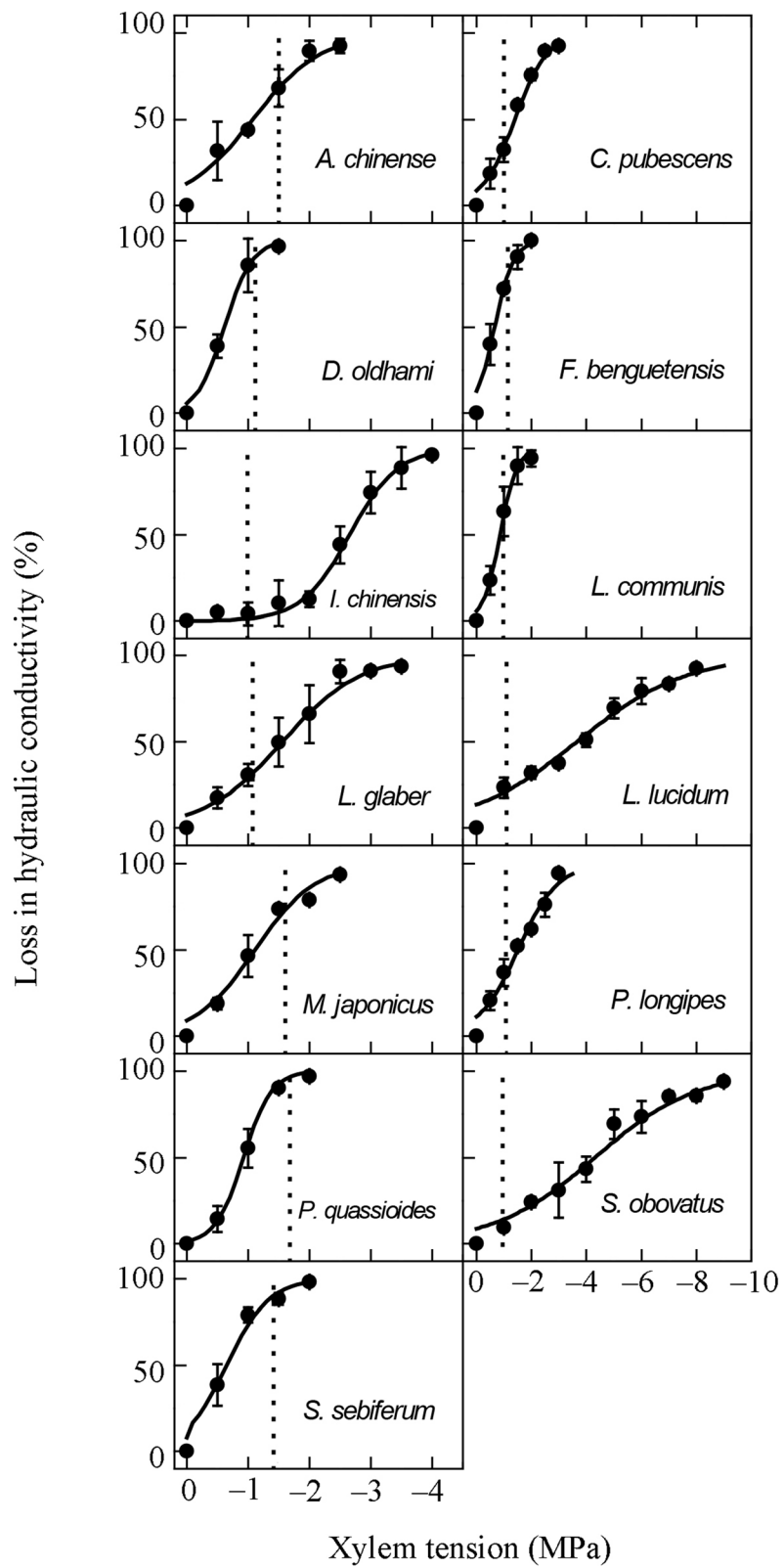*Loss* values for a total 75 species was bimodally-distributed, further supporting the idea that

Fig. 1 Loss of hydraulic conductivity as a function of xylem pressure for 13 karst woody species from China. Dashed lines represent minimum leaf water potential and vertical error bars indicate standard error. Graphs for the 13 species are alphabetically arranged
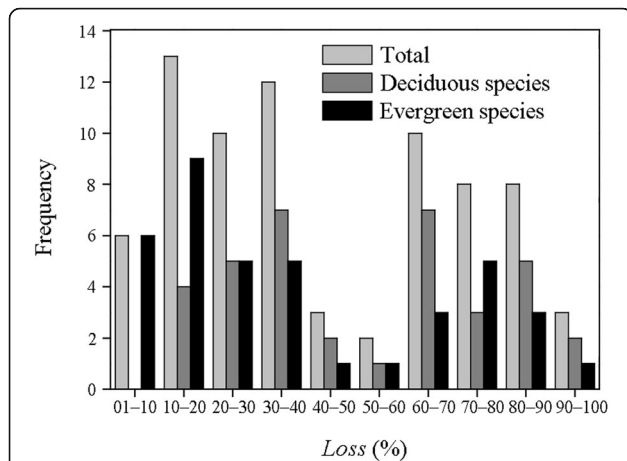
Fig. 2 Frequency distribution of per cent loss of leaf hydraulic conductivity (*Loss*). Data for 75 species (36 deciduous, 39 evergreen) were compiled from this and other studies (see text for references) to expand the analysis of Johnson et al. (2009). Data were binned into intervals of 10% *Loss* (e.g., 0–9%, 10%–19%) for deciduous, evergreen, and total species. Loss in deciduous species was more evenly distributed than in evergreen species, with 18 species having less than 50% and 18 having more than 50% Loss, while evergreen species (25 out of 39) tended to have less than 50% Loss
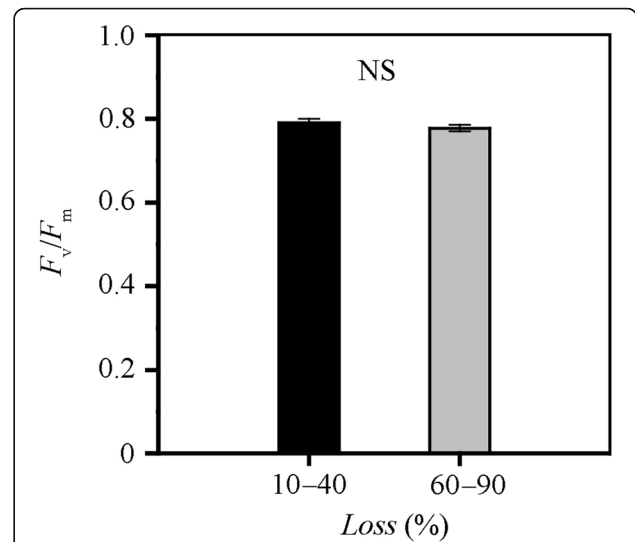

Fig. 3 Maximum quantum efficiency of photosystem II (F_v/F_m) of karst plants at noon. Plants from the karst area of China that maintained leaf hydraulic conductivity loss below 40% of maximum (five species, black column) were compared to those that tolerated more than 60% (six species, grey column). Two extreme cases (*Itea chinensis*, an evergreen species that can maintain 98.61% leaf specific hydraulic conductivity (K_l) and *Sapium sebiferum*, a deciduous species that can tolerate 90.07% loss of K_l at noon) were excluded from the analysis. There was no significant difference in F_v/F_m between these two groups ($P = 0.339$)

plants can adopt two strategies to deal with xylem cavitation: 1) maintain the water potential above the cavitation threshold, or 2) tolerate massive xylem cavitation and subsequent recovery (Jones and Sutherland 1991; Johnson et al. 2009). Some plants can operate well beyond the point of xylem failure via stomata closure, but they sacrifice carbon fixation, because ambient CO_2 cannot diffuse into leaf intercellular spaces. Other plants can tolerate massive cavitation over the short term, allowing photosynthesis to continue. In fact, massive cavitation was experimentally demonstrated to help relieve water stress temporarily by releasing water from

Table 3 Mean values of hydraulic and leaf traits for evergreen and deciduous functional groups and the results of MANOVA to test the effect of leaf phenology on measured traits

Traits	Deciduous	Evergreen
Ψ_{min}*	−1.33	−1.05
P_n	9.34	7.59
g_s**	0.3	0.17
K_l***	4.14	1.28
Ψ_{50}	−1.11	−2.03
K_{lnoon}	1.23	0.73
Loss	64.7	42.7
Margin*	−0.27	0.98
MANOVA	**F**	**P**
Functional group	2.654	0.181

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Trait abbreviations and units as in Table 2. MANOVA was performed using the Pillais Trace statistic (= 0.181)

embolizing conduits to the transpiration stream (Logullo and Salleo 1992; Holtta et al. 2012) and to lower the risk of xylem wall implosion (Pratt et al. 2008).

There were no sign of physiological stress in the 13 species at noon and no significant differences in F_v/F_m between plants with less than 40% and more than 60% *Loss*. The relationship between *Loss* and F_v/F_m was also not significant. Thus, plants adopting both strategies could maintain PSII efficiency at noon in the karst region of China, possibly via different hydraulic solutions. For example, the radical strategy allowing massive xylem cavitation could temporarily relieve water stress and therefore might maintain photosynthesis for hours before leaf water reserves are exhausted (Logullo and Salleo 1992; Holtta et al. 2012). Such massive embolized conduits could be expected to be fully refilled before the following dawn. In fact, $\Psi_{predawn}$ values of two fig species in the karst region of southwestern China were close to zero (Liu et al. 2012b), suggesting they had fully refilled embolized conduits. However, another survey of 50 karst woody species at forest site demonstrated that $\Psi_{predawn}$ values were about − 1.0 MPa (Liu et al. 2012a), suggesting that embolisms persisted. Such a large discrepancy between two studies at similar sites deserves further investigation. For the conservative strategy, these plants might develop a stronger ability to dissipate excessive absorbed light energy as nonphotochemical quenching
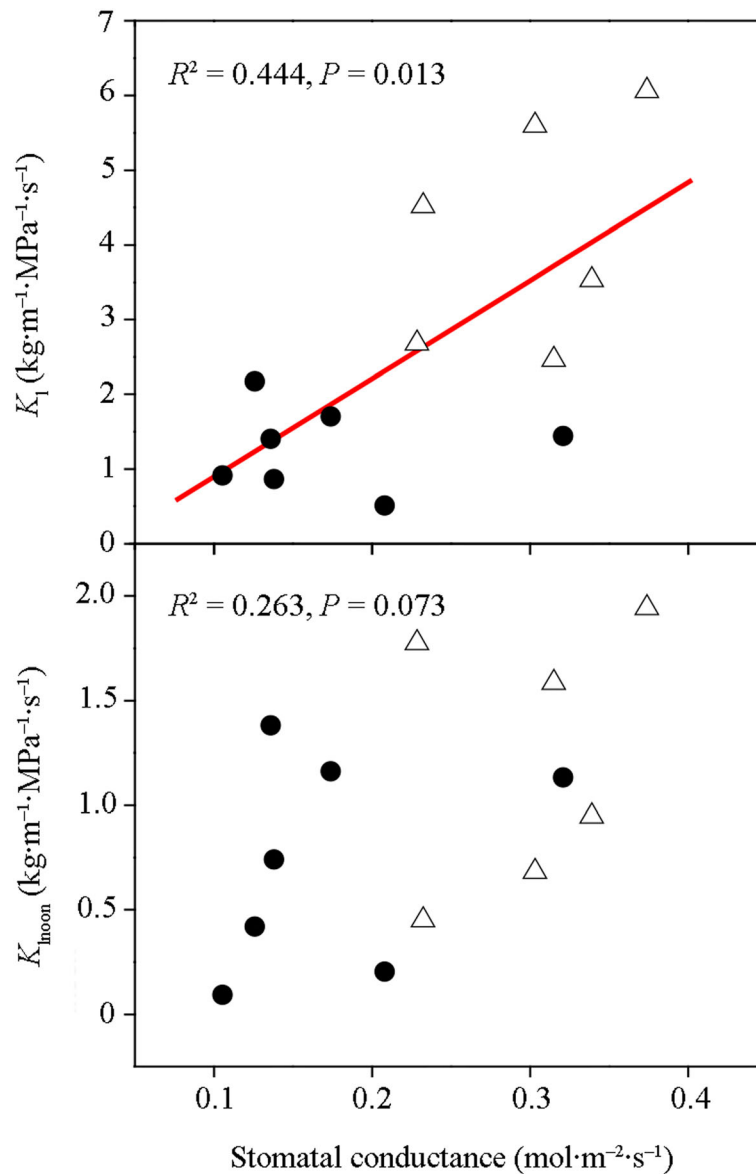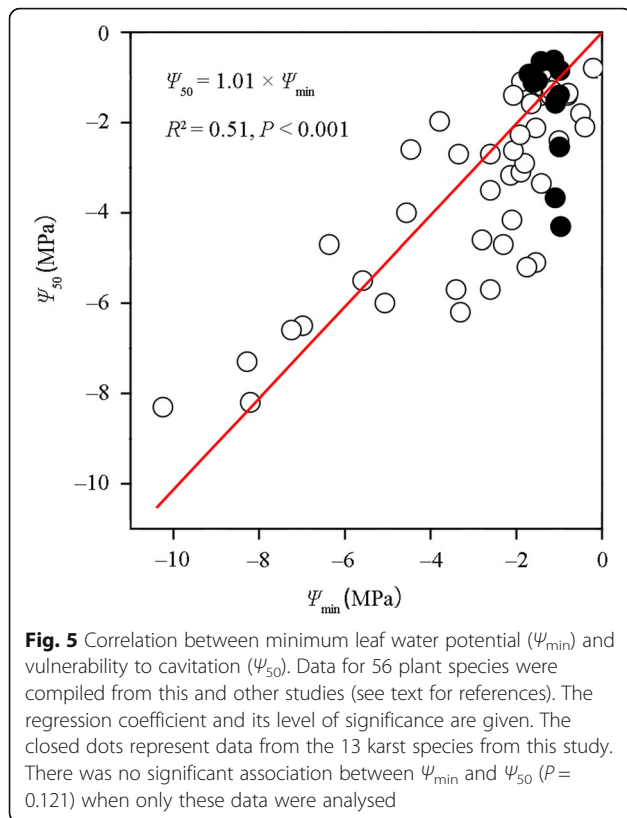
Fig. 4 Stomatal conductance as a function of leaf specific hydraulic conductivity for 13 karst woody species. Both maximum K_l and K_l at noon (K_{lnoon}) were measured at a vapour pressure deficit of 1 kPa for 13 karst woody species in southwestern China. The solid line represents best-fit linear regression. Open triangles and closed dots represent deciduous and evergreen species, respectively

(NPQ) to alleviate excitation pressure at PSII reaction centres and consequently maintain PSII maximum quantum efficiency (Baker 2008). Interestingly, it is noteworthy that g_s had no association with *Loss* (Table 4); possibly whole-plant hydraulic adjustment participates in the regulation of *Loss*, which merit further investigation.

The previously reported strong association between Ψ_{50} and Ψ_{min} across species in some ecosystems (e.g., Pockman and Sperry 2000; Markesteijn et al. 2011b; Choat et al. 2012) was not observed by using our data in the current study, suggesting that xylem resistance is not necessarily related to the tensions experienced in the

karst area. In fact, the absence of such an association could be explained by the fact that karst plants maintained a very narrow range of Ψ_{min} (from − 0.96 MPa in *S. obovatus* to − 1.61 MPa in *M. japonicus*) in the present study. Such "isohydric" regulation behaviour may also have been seen in other studies in this area (Yu et al. 2002; Liu et al. 2012a). For example, Liu et al. (2012a) reported a Ψ_{min} range from about − 1 to − 1.8 MPa in the wet season and − 1 to − 2.6 MPa in the dry season (50 tree species), and Yu et al. (2002) reported a Ψ_{min} range from − 0.79 to − 2.2 MPa in the wet season (25 tree species). In other words, plants with isohydric regulation might

Fig. 5 Correlation between minimum leaf water potential (Ψ_{min}) and vulnerability to cavitation (Ψ_{50}). Data for 56 plant species were compiled from this and other studies (see text for references). The regression coefficient and its level of significance are given. The closed dots represent data from the 13 karst species from this study. There was no significant association between Ψ_{min} and Ψ_{50} ($P = 0.121$) when only these data were analysed

$$\Psi_{50} = 1.01 \times \Psi_{min}$$
$$R^2 = 0.51, P < 0.001$$

have larger variations in loss of hydraulic conductivity than "anisohydric" one. For example, a relatively isohydric piñon pine experienced loss of root hydraulic conductivity ranging from 0 to 100% *PLC* during a seven-year observation period, compared with the constant and very small *PLC* of a co-occurring anisohydric juniper (McDowell 2011).

Theoretical assessments of the role of stomatal regulation on hydraulic conductance revealed a positive, linear relationship between g_s and K_l if the whole-plant water pressure gradient and *D* between the leaf and air remain

similar (Sperry et al. 1993; Oren et al. 1999). Given that the species studied here had similar Ψ_{min} and *D*, the close relationship between K_l and g_s found was consistent with previous studies in other ecosystems (Hubbard et al. 2001; Santiago et al. 2004). Interestingly, the K_{lnoon} was not significantly correlated with g_s; similarly, Santiago et al. (2004) reported that the correlation coefficient between K_{init} and g_s was lower than that between K_{lmax} and g_s. The absence of correlation between K_{lnoon} and g_s could have many explanations. For example, leaf capacity may decouple the relationship between K_{lnoon} and g_s.

Evergreen species, with 42.7% *Loss* at midday, tended to maintain xylem conductivity better than deciduous species (with 64.7%) in the current study, although the difference between groups was not significant ($P = 0.221$). This tendency was also seen in the more even distribution of *Loss* frequencies in deciduous than in evergreen species; 18 deciduous species had less than 50% and 18 had more than 50% *Loss*, while more evergreen species (25 of 39) had less than 50% *Loss*. These results were consistent with our expectation that evergreens could avoid massive cavitation at midday better than co-occurring deciduous species.

A MANOVA revealed a non-significant contrast between deciduous and evergreen species in hydraulic and associated leaf traits, which means these two life-history adaptations are likely part of a continuum of strategies (Borchert 1994; Brodribb et al. 2002; Williams et al. 2008; Ishida et al. 2010). On the other hand, deciduous species were geared towards higher hydraulic conductance, photosynthetic rate, stomatal conductance, lower hydraulic safety margin and lower cavitation-resistance and minimum water potential than co-occurring evergreen species, in agreement with previous reports (Gartner et al. 1990; Sobrado 1993; Choat et al. 2005; Chen et al. 2009; Markesteijn et al. 2011b; Fu et al. 2012; O'Brien et al. 2017). The strategy of higher tolerance of

Table 4 Magnitude and statistical significance of Pearson correlations between hydraulic and leaf traits of 13 karst woody species in southwestern China

Trait	Ψ_{min}	P_n	g_s	K_l	Ψ_{50}	K_{lnoon}	Loss	F_v/F_m	Margin
Ψ_{min}	1								
P_n	−0.229	1							
g_s	−0.621*	0.704**	1						
K_l	−0.815*	0.422	0.666*	1					
Ψ_{50}	−0.452	0.000	0.075	0.414	1				
Kl_{noon}	−0.040	0.350	0.513	0.333	−0.237	1			
Loss	−0.654*	−0.067	0.136	0.505	0.804**	−0.519	1		
F_v/F_m	0.125	−0.046	−0.412	−0.247	−0.032	−0.568*	0.168	1	
Margin	0.591*	−0.055	−0.187	−0.541	−0.984**	0.216	−0.853**	0.063	1

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Trait abbreviations and units as in Table 2

hydraulic loss seen in deciduous species might guarantee sufficient carbon gain when water is abundant, or water stress could be relieved temporarily by releasing water from embolizing conduits to the transpiration stream, which might favour fast growth closely associated with a higher photosynthetic rate during the growing season (Santiago et al. 2004; Chen et al. 2009). During droughts or winter, deciduous species minimize transpiration by shedding their leaves, thereby greatly reducing the risk of long-term hydraulic failure (Maherali et al. 2004).

In conclusion, we found no evidence that karst woody species in southwestern China could control xylem tension to avoid substantial xylem cavitation. The variation in loss of leaf conductivity in this study did not significantly depress the efficiency of PSII. Ψ_{50} was not related to Ψ_{min}. The frequency distribution of the loss of leaf hydraulic conductivity due to xylem cavitation at noon in a total of 75 species from this study and the literature supported the idea presented by Johnson et al. (2009) that there may exist two different strategies for the daily maintenance of hydraulic conductivity. The co-occurring evergreen and deciduous woody species of karst in southwestern China differed significantly in some stem hydraulic and associated leaf traits. Under the high variable daily moisture conditions in karst areas in China, the interactions between isohydric regulation behaviour, low cavitation resistance (Fan et al. 2011), and other hydraulic traits (particularly root systems) for maintaining homeostatic water balance in whole plants are worthy of further study. A more sophisticated design of field investigation on a single species in different seasons, to explore the relationship between *PLC*, F_v/F_m, water storage capacity and NPQ, is necessary for future study.

Additional file

Additional file 1: Table S1. Species measured, growth form, midday leaf water potential (Ψ_{min}), the percentage loss of conductivity (*PLC*), the Ψ at which a 50% loss in conductivity occurs (Ψ_{50}), the method used to determine PLC, the ecosystem where the measurement was conducted, and the reference. (DOCX 38 kb)

Abbreviations
HJ: Huajiang site; K_{init}: initial leaf hydraulic conductance; MAP: mean annual precipitation; PD: Puding site; PLC: percentage loss of conductivity; PSII: photosystem II; $\Psi_{predawn}$: Predawn leaf water potential

Availability of data and materials
All data and materials can be obtained by requesting from the author.

Authors' contributions
DF and SZ contributed equally to this paper. HY, QW and XX carried out the experiment, DF, XW and SZ performed the statistical analyses and drafted the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]College of Forestry, Beijing Forestry University, Beijing 100083, China. [2]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China. [3]Inner Mongolia Forestry Monitoring and Planning Academy, Hohhot 010020, China. [4]China Meteorological Administration, Beijing 100081, China.

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