



# Safety-efficiency trade-offs in the cotton xylem: acclimatization to different soil textures

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**Abstract:** The acclimatization of plant xylem to altered environmental conditions has attracted considerable attention from researchers over several decades. Plants growing in natural environments must seek a balance between water uptake and the water loss of leaves from evaporation. Thus, the adaptation of xylem to different soil textures is important in maintaining plant water balance. In this study, we investigated the xylem changes of cotton (*Gossypium herbaceum* L.) xylem in sandy, clay and mixed soils. Results showed that soil texture had a significant effect on xylem vessel diameter and length of stems and roots. Compared with *G. herbaceum* growing in the clay soil, those plants growing in the sandy soil developed narrower and shorter xylem vessels in their roots, and had a higher percentage of narrow vessels in their stems. These changes resulted in a safer (i.e. less vulnerable to cavitation), but less-efficient water transport system when soil water availability was low, supporting the hydraulic safety versus efficiency trade-off hypothesis. Furthermore, in sandy and mixed soils, the root: shoot ratio of *G. herbaceum* increased twofold, which ensures the same efficiency of leaves. In summary, our finding indicates that the morphological plasticity of xylem structure in *G. herbaceum* has a major role in the acclimatization of this plant species to different soil textures.

**Keywords:** acclimatization; soil texture; xylem structure; hydraulic acclimation; safety vs. efficiency

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High availability of water in soil resulted in a less-efficient hydraulic structure (i.e. xylem) in plants (Mencuccini, 2003). However, recent research showed that plants growing in porous soils with low water availability also developed a less-efficient hydraulic system (Holste et al., 2006). And another research demonstrated that plants growing under different conditions coordinated their water supply and demand through long-term hydraulic acclimatization and morphological adaptations (e.g. root:leaf ratio), which resulted in the same hydraulic conductance per unit of leaf area (Li et al., 2005). Although the efficiency of hydraulic system under different environmental conditions was studied (Nardini et al., 1998; Ewers et al., 2000; Oliveras et al., 2003; Martínez-Vilalta et al., 2004; Li et al., 2005; Holste et al., 2006; Alameda et al., 2012; Plavcová and Hacke, 2012; Lens et al., 2013; Głab, 2014), a consensus has yet to emerge. Given that the xylem structure directly determines hydraulic efficiency, characterizing the xylem structure in different plant species is needed.

Long-term acclimatization of xylem structures (e.g. vessel diameter, vessel length, end-wall

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resistivity and other properties) to environmental gradients was also studied. Generally, the adaptiveness of xylem structure is thought to be constrained by a trade-off between xylem safety (less vulnerable to cavitation) and conductive efficiency. The xylem comprises a series of vessels of different diameters and lengths, and wider vessels mean a greater hydraulic efficiency (Pittermann and Sperry, 2003; Jansen et al., 2009, 2011). The separate vessels are connected by pit membranes and, in a given length of xylem; longer vessels have a reduced number of pit membranes and, therefore, decreased end-wall resistance (Tyree et al., 1994; Markesteijn et al., 2011). Consequently, plants with long, wide xylem vessels have more-efficient water transport compared with plants with short, narrow xylem vessels; and this has important implications for plant evolution (Markesteijn et al., 2011). However, plants with long, wide xylem vessels are more vulnerable to cavitation compared with plants with short, narrow xylem vessels (Tyree et al., 1994; Markesteijn et al., 2011). Moreover, vulnerability to cavitation is related not only to the size of the pitted area (Sperry et al., 2006) (a larger area implies higher probability of containing large pores), but also to pit characteristics, such as porosity and thickness (Jansen et al., 2009).

It has been shown that the root-specific hydraulic conductance for cotton growing in sandy soil was less than those plants growing in clay soil (Li et al., 2005), although the mechanism behind this phenomenon was unclear. In addition, the xylem structure of woody plants was significantly correlated with soil water availability (Maherali et al., 2004; Christensen-Dalsgaard et al., 2007). The theory of soil-root contact suggests that roots in sandy soil are only partially effective in absorbing water, because the surface area of root that is exposed to large, air-filled soil pores is unable to take up water (Li et al., 2005). Thus, sandy soil has lower water availability compared with clay soil. Therefore, based on the safety versus efficiency trade-off, we hypothesized that plant growing in sandy soil developed short and narrow xylem vessels in order to enhance the xylem safety, compared with plants growing in clay soil.

On the basis of safety versus conducting efficiency trade-off in xylem, conducting efficiency represents the hydraulic conductivity (e.g.  $K_{pl}$ ), rather than the leaf-specific hydraulic conductance (e.g.  $K_{L,pl}$ ) (Mencuccini, 2003). Thus, different soil textures lead to variances in the hydraulic supply of xylem due to long-term acclimatization. However, plants can increase the root to shoot ratio for ensuring a sufficient water supply to the leaves (Li et al., 2005). Research found that decreased  $K_{pl}$  resulted in the xylem network being less efficient and, thus, it will support fewer leaves, decreasing the potential for CO<sub>2</sub> assimilation (Smith and Sperry, 2014; Mencuccini, 2015).

In this study, cotton plants were grown under three soil textures. Plastic adaptation of xylem (i.e. vessel diameter, length, density, etc. in both roots and shoots), hydraulic conductance or resistance (root, shoot and whole plant) and plant morphology (root to shoot weight ratio and root length to leaf area ratio) were examined. We hypothesize that (1) plants growing in sandy soil will develop a less-efficient hydraulic system compared with plants growing in clay soil; and (2) at the whole-organism level, the lower efficiency of hydraulic system will be compensated by the other plasticity of plants (e.g. plant hydraulic conductance per leaf area) that enable the leaves to take up water regardless of soil textures.

## 1 Materials and methods

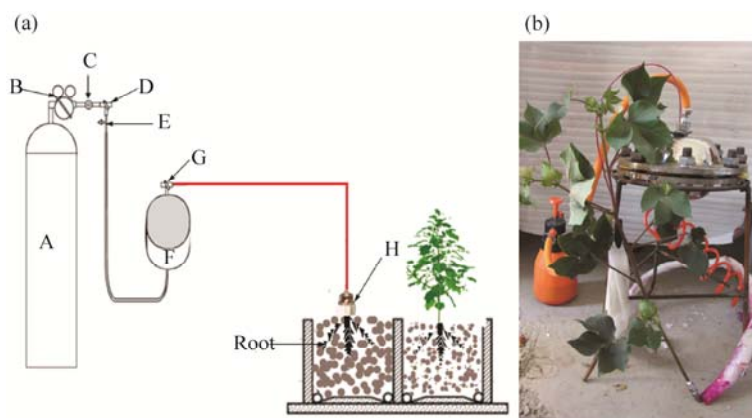
### 1.1 Soil textures

The experiment was carried out at Fukang National Field Scientific Observation and Research Station for Desert Ecosystems (44°17'N, 87°56'E; 475 m asl), Chinese Academy of Sciences in 2011. The station is located in the southern periphery of the Gurbantunggut Desert, in the hinterland of the Eurasian continent. Three kinds of soil texture were taken from local fine-textured soil (hereafter referred to as clay), nearby desert sand (hereafter referred to as sandy) and a mixture of the two types of soil in a ratio 1:1 (hereafter referred to as mixed). The particle size distributions of the sandy soil and clay soil were determined by a laser diffraction system (Sympatec GmbH, System-Partikel-Technik, Clausthal-Zellerfeld, Germany). The particle diameters of the sandy soil were <500 µm and those of the clay soil were <50 µm (Li et al., 2005).

The soil texture gradient results in a partial physical discontinuity at the soil-root interface for the movement of water and nutrients from soil to roots. Therefore, the sandy soil would have lower resource availability than that of clay soil (Xie et al., 2012).

## 1.2 Plant materials

A total of 75 pots (1 m×1 m×1 m) were filled with either sandy, clay or mixed soils (25 pots per soil texture). Cotton (*Gossypium herbaceum* L.) seeds were sown on 15 May 2010, and only one plant was left to grow in each pot after emergence. All pots for each soil texture were placed in an open field. Prior to sowing and after filling the pots with soil, we watered and drained all the pots continuously for 10 d in order to wash out salt or nutrients. All the potted plants were kept well-watered and treated with pesticide to avoid physiological stress during the growing period. Soils in arid regions are generally nutrient-poor. For avoiding nutrient deficiency during plant growth, we irrigated with a modified Hoagland nutrient solution (0.4 mmol/L  $\text{NH}_4\text{H}_2\text{PO}_4$ , 2.4 mmol/L  $\text{KNO}_3$ , 1.6 mmol/L  $\text{Ca}(\text{NO}_3)_2$ , 0.8 mmol/L  $\text{MgSO}_4$ , 0.1 mmol/L Fe-EDTA, 0.023 mmol/L  $\text{B}(\text{OH})_3$ , 0.0045 mmol/L  $\text{MnCl}_2$ , 0.0003 mmol/L  $\text{CuCl}_2$ , 0.0015 mmol/L  $\text{ZnCl}_2$ , 0.0001 mmol/L  $\text{MoO}_3$ ) (Xie et al., 2012). Water filled the experiment devices once a week for all three soil textures, and water amount was measured by a water meter (Fig. 1). Pots were watered and drained continuously for 5 h in order to wash out fertilizer residue prior to fertilization (see details in Fig. 2).



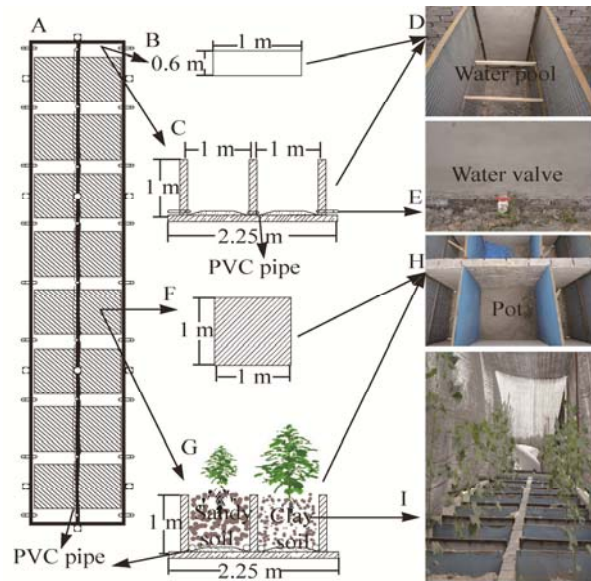
**Fig. 1** Schematic diagram (a) and photo (b) of the apparatus used to inject a standard paint suspension into roots or stems. A, air tank; B, pressure regulator; C, needle valve; D, three-way ball valve; E, pressure release valve; F, captive air tank, a rubber diaphragm that separates the air from water in the tank; G, water valve; H, high-pressure watertight connectors to the root system or stem segments.

## 1.3 Measurement of hydraulic conductance in roots and shoots

Measurements of hydraulic conductance were carried out 50 d after seed emergence (i.e. before the plants reached the reproductive stage). Basal stem diameter (D) and height (H) were measured for 15 plants from each soil treatment. Shoot conductance was measured using a high-pressure flow meter (HPFM; Dynamax Company, USA) connected to the shoot base (Tyree et al., 1998; Choat et al., 2008). Stem conductance was measured by one transient mode of the HPFM (Tyree et al., 1995; Tsuda and Tyree, 1997). Conductance measurements were also performed on the root system using a similar protocol.

## 1.4 Measurement of plant morphological traits

Leaves and roots (intact cotton root systems were excavated to determine their length) were scanned, and leaf area (including green petioles) and root length were computed by CI-400 CIAS (Computer Imaging Analysis Software; CID Co., Logan, UT, USA). Then the plants were divided into roots, stems (including non-green petioles) and leaves (including green petioles),



**Fig. 2** Schematic diagram of the experiment. A, plan of the experimental apparatus; B, plan of the water pool; C, cross section of the water pool; D, water pool; E, water valve; F, pots; G, cross section of the pots; H, photograph of the pots; and I, experimental plants. The experimental containers (A) were constructed using cement. Each container was divided into  $2 \times 8$  cells. Each cell contained a pot and a water pool. Each pot ( $1 \text{ m} \times 1 \text{ m} \times 1 \text{ m}$ ) was located between two water pools ( $0.6 \text{ m} \times 1 \text{ m} \times 1 \text{ m}$ ). A steel mesh (covered with nylon) was used to separate the pot from the water pools, and all water pools in the device were connected by PVC pipes (the length of PVC was 1.2 m; the left hand pools were also connected to the right hand pools by PVC pipes (C). Thus the water could flow through the whole device. The left pot was filled with sandy soil and the right pot with clay soil (G, I).

which were dried to a constant weight, and root mass (MR), stem mass (MS) and leaf mass (ML) were measured. The ratios of root, stem and leaf mass to total mass, leaf area (leaf area per mass) and specific root length (root length:root mass) were also calculated.

### 1.5 Distribution of vessel length

For determining the proportion of open vessels at different lengths in the stem and main root segments, we estimated vessel length distribution in similar-sized stems and root segments ( $n=5$  for stems and  $n=3$  for roots in each soil texture). For filling the opened conduits, we injected a pigment red suspension (1:100 pigment-to-water) into the stems and main root according to previous methods (Zimmermann and Jeje, 1981; Ewers and Fisher, 1989; Sperry et al., 2005). The stems or main roots were then cut to expose the injected surface, and the painted vessels per xylem area were counted (Sperry et al., 2005). The numbers were converted to the vessel length distributions according to the method described by the Sperry lab, available at [http://biologylabs.utah.edu/sperry/methods.html#vessel\\_lengths](http://biologylabs.utah.edu/sperry/methods.html#vessel_lengths).

Injection into the stems and main root (10-cm long) was operated using a custom-built pressure chamber, keeping the injecting pressure stable for 24 h (root injection details are shown in Fig. 1). A cross-section of each stem was photographed with a camera attached to a fluorescence microscope, and the image was analyzed using Image-Pro Plus software (Media Cybernetics, Silver Spring, MD, USA).

### 1.6 Measurements of vessel diameter

Vessel diameter was measured using the cross-section of each stem and root. Basal stem and root (root diameter=0.5 mm) cross-sections ( $20\text{-}\mu\text{m}$  in thickness) were prepared using a sliding microtome and stained with toluidine blue. The cross-section was photographed with an Olympus BX51 microscope and the captured images were analyzed by Image Pro plus (Media

Cybernetics, Silver Spring, MD, USA). The total vessel area:section area, diameter of vessel and vessel density were measured for each cross-section.

### 1.7 Statistical analysis

All statistical analyses were performed using MATLAB software (MATLAB, R2012a, The MathWorks, Inc, USA). One-way analysis of variance (ANOVA) was performed to compare difference between treatments.

## 2 Results

### 2.1 Plant morphology

The soil textures resulted in significant variations in morphology of cotton plants (Table 1). The plants growing in the clay soil had the greatest basal stem diameter, height, leaf area and root length, followed by those plants growing in the mixed soil, and then those growing in the sandy soil. In addition, the plants growing in the sandy soil had the greatest root length:leaf area and root:shoot mass ratio, and these were lowest in the plants growing in the clay soil.

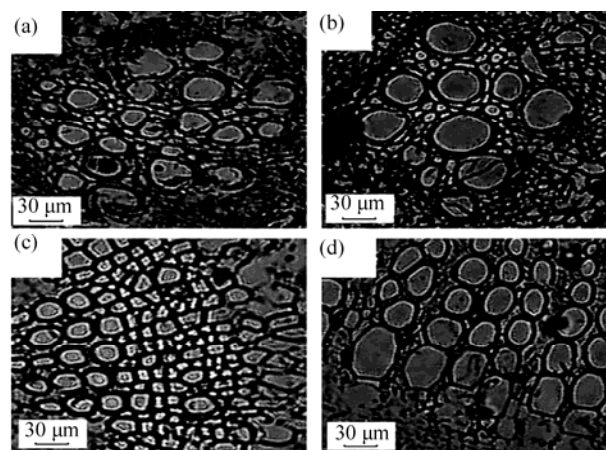
**Table 1** Effects of different soil textures on morphological characteristics of cotton plants

Item	Sandy soil	Mixed soil	Clay soil
Stem basal diameter (mm)	3.1±0.45 <sup>a</sup>	3.6±0.88 <sup>a</sup>	5.8±0.88 <sup>b</sup>
Height of plant (cm)	14.9±1.78 <sup>a</sup>	20.5±5.05 <sup>b</sup>	33.2±6.57 <sup>c</sup>
Leaf area (cm <sup>2</sup> )	83.5±14.69 <sup>a</sup>	211.5±15.18 <sup>b</sup>	323.4±3.73 <sup>c</sup>
Length of root (m)	35.0±3.36 <sup>a</sup>	33.2±3.12 <sup>b</sup>	46.4±4.71 <sup>b</sup>
Root length/leaf area (cm/cm <sup>2</sup> )	42.4±4.60 <sup>a</sup>	16.2±3.50 <sup>b</sup>	7.2±2.10 <sup>c</sup>
Root mass/shoot mass (g/g)	0.74±0.07 <sup>a</sup>	0.47±0.09 <sup>b</sup>	0.34±0.06 <sup>c</sup>

Note: Each value represents mean±SE (*n*=15). Different letters indicate a significant difference among different soil textures at *P*<0.05 level.

### 2.2 Xylem structure in roots and stems

The soil textures had a dramatic effect on the structure of root xylem. Root xylem vessel diameter (Fig. 3), the total root xylem vessel area:section area ratio, the number of vessel in the signal root (Table 2) and root xylem vessel length (Fig. 4) were all significantly lower for plants growing in the sandy soil compared with those plants growing in the other soils.

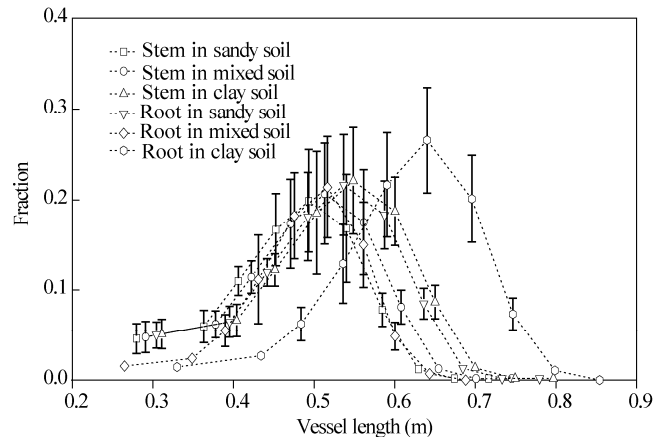


**Fig. 3** Photographs of transverse sections of root and stem xylem in cotton plants. Root xylem (root diameter=0.5 mm) from cotton growing in the sandy soil (a) and clay soil (b), and stem xylem (stem basal) of cotton growing in the sandy soil (c) and clay soil (d) at 100×(Olympus BX51 microscope).

**Table 2** Effects of different soil textures on the xylem structures of cotton roots

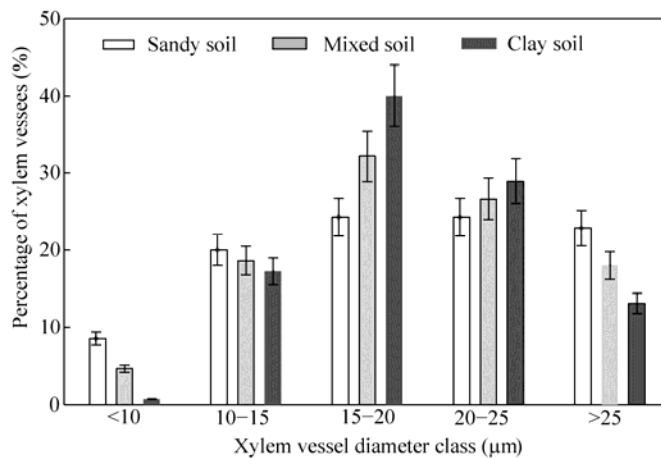
Item	Sandy soil	Mixed soil	Clay soil
Vessel diameter of root xylem ( $\mu\text{m}$ )	19.30 $\pm$ 4.60 <sup>a</sup>	22.14 $\pm$ 5.21 <sup>a</sup>	26.84 $\pm$ 5.31 <sup>b</sup>
Total vessel area/section area ( $\text{cm}^2/\text{cm}^2$ )	4.8 $\pm$ 0.84 <sup>a</sup>	5.0 $\pm$ 0.72 <sup>a</sup>	5.4 $\pm$ 0.60 <sup>b</sup>
Number of vessels in signal root	20 $\pm$ 5 <sup>a</sup>	16 $\pm$ 3 <sup>a</sup>	11 $\pm$ 2 <sup>b</sup>
Vessel length (cm)	1.36 $\pm$ 0.58 <sup>a</sup>	1.78 $\pm$ 0.56 <sup>b</sup>	2.39 $\pm$ 0.67 <sup>b</sup>

Note: Each value represents mean $\pm$ SE ( $n=3$ ). The average vessel length was determined by the vessel length distributions shown in Fig. 2. Different letters indicate significant difference among different soil textures at  $P<0.05$  level.



**Fig. 4** Vessel length distribution of stems ( $n=5$ ) and roots ( $n=3$ ) for the cotton plants growing in different soils. Vertical bars indicate standard errors.

For basal stem xylem, the vessel diameter, total vessel area:section area ratio and stem xylem vessel length were not significantly different among the three soil textures (Figs. 3 and 4; Table 3). However, there was an effect of soil texture on the distribution of vessel diameter in stem xylem (Fig. 5). There were a higher percentage of large vessels in plants growing in the clay soil than plants growing in the sandy soil, whereas the plants growing in mixed soil did not differ significantly from either of the other two.



**Fig. 5** Percentage of xylem vessel in different diameter classes (diameter ranged from  $<10$  to  $>25$   $\mu\text{m}$ ) for cotton growing in different soils. All the vessels from five basal stems were measured in each treatment, with 160–450 vessels per stem. Vertical bars indicate standard errors.

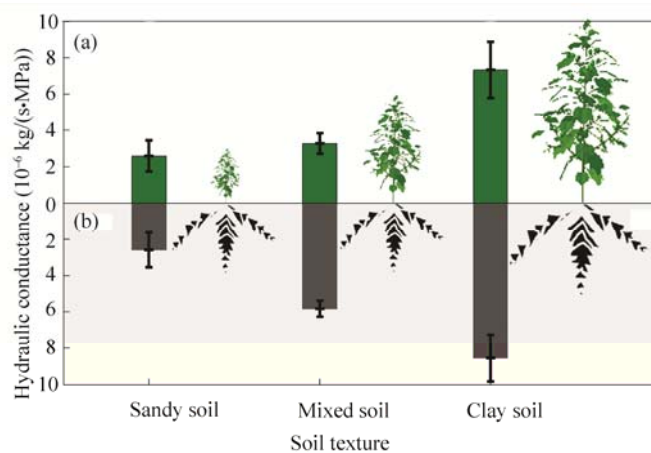
**Table 3** Effects of different soil textures on characteristics of basal stem xylem in cotton

Item	Sandy soil	Mixed soil	Clay soil
Vessel diameter of stem basal xylem ( $\mu\text{m}$ )	20.22 $\pm$ 7.63 <sup>a</sup>	19.14 $\pm$ 6.21 <sup>a</sup>	20.20 $\pm$ 7.19 <sup>a</sup>
Total vessel area/section area ( $\text{cm}^2/\text{cm}^2$ )	2.80 $\pm$ 0.92 <sup>a</sup>	3.75 $\pm$ 1.12 <sup>b</sup>	4.10 $\pm$ 1.10 <sup>b</sup>
Density of vessels (vessels/ $\text{mm}^2$ )	122 $\pm$ 11 <sup>a</sup>	119 $\pm$ 14 <sup>a</sup>	114 $\pm$ 12 <sup>a</sup>
Average vessel length (cm)	1.25 $\pm$ 0.42 <sup>a</sup>	1.30 $\pm$ 0.34 <sup>a</sup>	1.39 $\pm$ 0.37 <sup>a</sup>

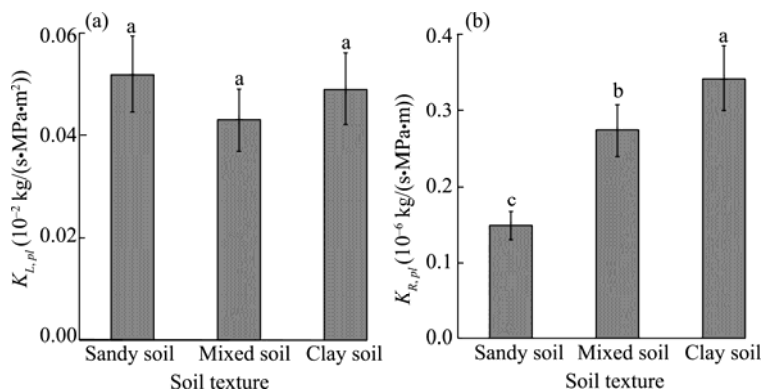
Note: Each value represents mean $\pm$ SE ( $n=5$ ). Different letters indicate significant difference among different soil textures at  $P<0.05$  level.

### 2.3 Hydraulic conductance

Soil textures resulted in significant variations in water-flow characteristics (Fig. 6). The plants growing in the clay soil had the greatest shoot, root and whole-plant hydraulic conductance, followed by those growing in the mixed soil, with the lowest in plants growing in the sandy soil. The  $K_{R,pl}$  value of plants growing in the sandy soil was 31% of that of plants growing in the clay soil, which was probably due to the smaller percentage of larger vessels in the former. However, because of its reduced leaf area, the plants growing in the sandy soil had similar leaf-specific hydraulic conductance compared with those plants growing in the clay soil (Fig. 7).



**Fig. 6** Shoot (a) and root (b), hydraulic conductance and morphologies for the cotton plants growing in different soil textures. Vertical bars indicate standard errors ( $n=15$ ).



**Fig. 7** Leaf-specific conductance ( $K_{L,pl}$ ; a) and root-specific conductance ( $K_{R,pl}$ ; b) for cotton growing in different soil textures. Vertical bars indicate standard errors ( $n=15$ ). Columns with different letter are significantly different among different soil textures at  $P<0.05$  level.

### 3 Discussion

#### 3.1 Safety versus efficiency trade-off

The results of our study showed that cotton plants growing in different-textured soils can result in significant variations in xylem vessel diameter, length and other characteristics. Compared with plants growing in the clay soil (Fig. 5), the plants growing in the sandy soil developed narrower and shorter root vessels (Fig. 3; Table 2), and had a higher percentage of narrow stem vessels. The changes of morphology resulted in a safer, but less-efficient (i.e. absolute value of hydraulic supply, rather than the leaf-specific hydraulic efficiency of the vascular system; Fig. 6) water transport system when soil water availability was low. Narrow vessels of plants growing in the sandy soils have the potential to reduce hydraulic conductance substantially as a result of Hagen-Poiseuille's law (Tyree et al., 1994; Mencuccini, 2003). However, vessels that are narrower and shorter could potentially enhance water transport safety in plants (Tyree et al., 1994; Hacke et al., 2006; Jansen et al., 2009). Our results revealed the trade-off of vessels in terms of water conducting efficiency and cavitation safety. We did not measure vulnerability to cavitation in this study. However, vulnerability to cavitation is related to inter-vessel pit area (Oliveras et al., 2003; Hacke et al., 2006; Zhu and Cao, 2009), and relies on pit characteristics such as porosity and thickness (Jansen et al., 2009). A larger pit area implies a higher probability of cavitation vulnerable pores. Thus, long and wide vessels (Figs. 3 and 4) are more efficient for transporting water compared with narrow and short vessels (Figs. 3 and 4; Tables 2 and 3), but would be more vulnerable to cavitation. These findings support our first hypothesis that plants growing in sandy soil will develop a less-efficient hydraulic system compared with plants growing in clay soil.

At a cellular scale, there has been progress in identifying the anatomical features that underlie cavitation resistance and xylem hydraulic conductivity. The structure of pits between xylem conduits is crucial because it determines the cavitation resistance of a species and its xylem conductivity. The area of photo-assimilating leaves is constrained by the capacity of xylem conduction (Plavcová and Hacke, 2012). The anatomical features of conduit pitting and wall structures that confer greater protection from cavitation also tend to reduce the conductivity of the xylem per unit area, establishing a safety versus efficiency trade-off (Hacke et al., 2004; Sperry and Hacke, 2004). Species with traits that optimize this trade-off (i.e. increasing the conductivity for a given safety trade-off) should be more competitive compared with species without such traits. For example, conifers have advantages over angiosperms that compensate for their lack of multi-cellular vessels: the torus-margo-type of pit membrane in conifers has greater conductivity for a given air-seeding resistance than that of the homogenous type of pit membrane found in angiosperms (Hacke et al., 2004; Pittermann et al., 2005). The simpler tracheid-based xylem of conifers achieves a given cavitation resistance at a considerably lower wood density than that seen in angiosperms, resulting in conifers being more efficient under stress. At the species level, more work is needed to determine whether finer-scale variations in pit and conduit structure can explain the relative success of individual conifer and angiosperm species in arid regions.

#### 3.2 Morphological adjustment

In this study, the increase in root:shoot ratios in plants growing in mixed versus sandy soils (twofold variation; Fig. 6 and Table 1), which partly compensated for the reduced  $K_{L,pl}$  values, enabled the leaves to grow identically in different soils (Fig. 7a). These findings support our second hypothesis. Recent studies have also highlighted that the area of assimilating leaves or morphological adjustment is constrained by the xylem conductance capacity (Plavcová and Hacke, 2012; Smith and Sperry, 2014; Mencuccini, 2015). By contrast, a study by Holste et al. (2006) showed that plants have lower leaf-specific hydraulic conductance under reduced resource availability. Moreover, Mencuccini (2003) suggested that increasing resource availability was prone to the induction of less-efficient hydraulic systems. We did not measure wood density and xylem reinforcement parameters in this study. However, recent study had also confirmed that wood density and xylem reinforcement affected both mechanical stability and cavitation resistance (Holste et al., 2006).



The effects of soil texture on the structural properties of xylem showed some similar patterns. Compared with the control, *Phaseolus vulgaris* growing in porous soil was inclined to develop a higher percentage of small vessel and a lower percentage of large vessels, which resulted in a decrease of  $K_{R,pl}$  (Holste et al., 2006). Our study also revealed the similar trend in cotton under lower water availability.

## 4 Conclusions

The purpose of this paper was to examine how cotton xylem structures acclimatize to different soil textures. In a control experiment, we examined the acclimatization of the xylem, hydraulic conductance or resistance and plant morphology of cotton plants to different soil textures. We found that: (1) plants growing in the sandy soil developed a less-efficient hydraulic system compared with plants growing in the clay soil; and (2) at the whole-organism level, the lower efficiency of the hydraulic system was compensated by the higher plasticity or flexibility of other phenotypic characteristics (e.g. plant hydraulic conductance per leaf area) that enabled the leaves to take up enough water regardless of the soil texture. In summary, the current study has shown that the acclimatization of structural characteristics of xylem and the plasticity of the whole-plant morphology has major role in determining plant water economy.

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