Environmental and Experimental Botany 66 (2009) 341–346

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Hydraulic conductance and vulnerability to cavitation in corn (*Zea mays* L.) hybrids of differing drought resistance

Yangyang Li[a,*], John S. Sperry[b], Mingan Shao[a]

[a] *State Key Laboratory of Soil Erosion and Dryland Farming in the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University, Yangling, Shaanxi 712100, China*
[b] *Department of Biology, University of Utah, 257S 1400E, Salt Lake City, UT 84112, USA*

ARTICLE INFO

Article history:
Received 23 September 2008
Received in revised form 13 January 2009
Accepted 1 February 2009

Keywords:
Hydraulic conductivity
Vulnerability
Cavitation
Corn

ABSTRACT

Water transport through the xylem is essential for replacing water loss during transpiration, thus preventing desiccation and permitting photosynthesis. The occurrence of cavitation and embolism due to drought impairs transport to the transpiring leaves. Most research in this discipline has been conducted on woody plants. Less attention has been given to cavitation of crops and its physiological significance for understanding crop water relations. In this paper, hydraulic conductance and vulnerability of xylem to cavitation were studied in corn hybrids with different drought resistances. The results indicated that stems of drought-resistant 'Pioneer 3902' not only had a higher conductivity on both a stem area and leaf area basis but also had a greater resistance to cavitation. The estimated xylem pressure at 63.2% loss of conductivity (Weibull fitting parameter *b*) and at 50% loss of conductivity (P_{50}) in 'Pioneer 3902' were about 0.2 MPa lower than in 'Pride 5'. Higher conductivity in 'Pioneer 3902' was mainly attributed to more vascular bundles per stem area rather than greater vessel diameter. The central bundles and peripheral vascular bundles showed the same degree of cavitation although the vessels of central bundles were generally larger than in peripheral bundles.

1. Introduction

Xylem hydraulic properties are important for the general functioning of plants because they exert a strong influence on carbon uptake (Zimmermann, 1983). When soil moisture decreases, the tension in the water column becomes too great, embolisms form within the xylem vessels, and cavitation occurs, rendering the xylem conduit in which it occurs dysfunctional. The cause of embolism by water stress can be explained by the "air-seeding" mechanism: air is aspirated into a vessel via pit membranes between adjacent vessels, disrupting cohesion of the water column, thereby causing retraction of the water column and leaving behind a vessel filled with water vapor and air (Zimmermann, 1983; Tyree and Sperry, 1989). The vulnerability of woody plants to cavitation has been extensively studied, but little research has been conducted on crops (Sperry et al., 2003). Limited studies on rice (Stiller et al., 2003), soybean (Sperry, 2000), sugarcane (Neufeld et al., 1992), sunflower (Stiller and Sperry, 2002) indicated crops also suffered considerable cavitation within their physiological range of xylem pressure. Thus, it is very necessary to investigate the role of cavitation in crop water relations.

Corn (*Zea mays* L.) is a widely cultivated cereal crop throughout the world. Because of its shallow root system, high soil evaporation and transpiration during the growing stages, it is sensitive to water deficiency. Hence, improving the drought-resistance of corn is important for its survival and yield increase in water-limited areas. Researches on woody plants have indicated that resistance to cavitation may be an advantageous characteristic for drought-resistant varieties (Tyree and Ewers, 1991; Cochard, 1992; Pockman and Sperry, 2000). But it is not clear if this holds true for crops. If cavitation resistance is positively related with drought-resistance in corn, the trait could be useful in the selection and improvement of drought-resistant varieties.

Few studies on cavitation in corn indicate that it is of common occurrence. Tyree et al. (1986) have detected cavitation events in corn stems growing under field conditions using ultrasonic acoustic techniques. Using cryomicroscopy, McCully (1999) and McCully et al. (1998) found that daily embolism and refilling in roots of well-watered field-grown corn plants was a normal occurrence and might be a component of hydraulic signaling. The acoustic method requires verification by other techniques because of limited listening distance and the potential for acoustic emissions to be produced by events other than cavitation in vessels. The cyromicroscopy method is very informative because it directly observes

---

* Corresponding author at: Institute of Soil and Water Conservation, Chinese Academy of Sciences, 26 Xinong Road, Yangling, Shaanxi 712100, China.
Tel.: +86 29 87012884; fax: +86 29 87016082.
E-mail address: yyli@ms.iswc.ac.cn (Y. Li).

0098-8472/$ – see front matter. Crown Copyright © 2009 Published by Elsevier B.V. All rights reserved.
doi:10.1016/j.envexpbot.2009.02.001

the embolism, but Cochard et al. (2000) have reported that large numbers of air-filled vessels seen with the cryo-SEM technique can be artifacts of the freezing procedure. Neither the acoustic nor cryo-methods directly measure the impact of cavitation on water transport capabilities. Cochard (2002b) did this and found the degree of xylem embolism in corn leaves always remained below 10% in situ, this is greatly inconsistent with the above results acquired by other techniques (Tyree et al., 1986; McCully, 1999; McCully et al., 1998). Further research is needed to evaluate the importance of embolism in corn.

In this paper, the ‘Pioneer 3902’ corn hybrid was compared with ‘Pride 5’ hybrid in terms of their water conducting capacity and vulnerability to cavitation. The ‘Pioneer 3902’ hybrid has the better drought performance by lowering threshold stem water potential related to stomatal closure, maintaining photosynthesis longer and recovering faster after re-watering than ‘Pride 5’ (Nissanka et al., 1997). Otherwise, the two hybrids are morphologically and phenologically similar (Tollenaar, 1991). To measure vulnerability to cavitation we used the new centrifugal method presented by Cochard (2002a) and Cochard et al. (2005). In this technique, the loss of hydraulic conductivity in a stem is measured while the stem is spinning in a centrifuge and the xylem sap is under negative pressure at the stem center. This method is consistent with older techniques (Li et al., 2008), but has the potential to be much faster in assembling the relationship between conductivity loss and xylem pressure (a “vulnerability curve”).

2. Materials and methods

2.1. Materials

Corn varieties ‘Pioneer 3902’ and ‘Pride 5’ were planted in small pots in September 20, 2006. Seedlings were transplanted three times to gradually bigger pots to stimulate the root development. The soil consisted of 22% topsoil, perlite, and wood mulch each, 17% vermiculite, 11% peat mulch and 6% sand. Plants were grown in a greenhouse with day/night temperature 25/15 ± 3 °C, photosynthetic photon flux density 850 μmol m^{-2} s^{-1}, relative humidity 40–60%, and watered frequently to minimize water stress and embolism. When plants were developed to the silking stage, 28-cm long stems adjacent to the first ear were cut underwater for use with leaves and ears removed.

2.2. Vulnerability curve

A vulnerability curve shows the relationship between percentage loss of hydraulic conductivity and xylem pressure. When the centrifugal method is used, the xylem pressure is most negative in the middle of the stem and rises to atmospheric pressure at the either end. Considering the different vascular structure in the node and internode in a corn stem, it was necessary to test whether placing the node or internode at the center makes a difference for the vulnerability curve. For stems with the node in the center, the node was the first one below the node bearing the lowermost ear. For stems with the internode in the center, the internode was the one immediately below the ear. All stems were cut with fresh razors under water to 275 mm, which was the length accommodated by the centrifuge rotor (Li et al., 2008). Since the corn stem has an odd cross-section with a V-shaped wedge, leaks at two ends were prevented by filling the cavity with plumber’s putty and wrapping the parts with Teflon tape. The stems were flushed with 20 mM KCl under 100 kPa pressure for 30 min to remove any native embolism, and then attached to a tubing manifold filled with filtered (0.2 μm) KCl solution to measure the initial conductivity (K_i). The mass flow was gravimetrically induced by 4–6 kPa hydraulic head, and quantified with a balance interfaced with computer. K_i was calculated as the quotient of the mass flow rate of solution through the segment and pressure gradient along the segment (the gravity method, for which a hydraulic head is used to drive water through the segment during the conductivity determination). The stem was then placed in the centrifuge rotor and spun in a centrifuge (Sorvall RC-5C, Thermo Fisher Scientific, Waltham, MA, USA) to generate a xylem pressure (P) of −0.5 MPa at the stem center. The stem was held at that pressure for 3 min before the hydraulic conductivity at −0.5 MPa was measured with the 20 mM KCl solution while the stem was still rotating. The P was then decreased to a more negative value, held for 3 min, and the conductivity was measured as before. The experiment was stopped when about 90% of the conductivity at −0.5 MPa had been lost. All conductivity including K_i was expressed as stem specific conductivity (K_s) based on stem cross-section area and leaf specific conductivity (K_l) based on the leaf area supported by the stem. Leaf area was measured by a LI-3100 area meter (Li-Cor Inc., Lincoln, NE, USA).

A Weibull function was used to describe the relationship of conductivity and xylem pressure: $K = K_{max}\ \exp(-(-x/b)^c)$ as well as the vulnerability curve (PLC vs. xylem pressure, PLC is calculated based on estimated K_{max}): $PLC/100 = 1 - \exp(-(-x/b)^c)$. The K_{max} represents the conductivity in the absence of any embolism, x is xylem pressure, and b and c are curve fitting parameters. Normally, K_i would be used to set K_{max}, but as noted in the Results section, we found that K_i tended to be less than K obtained by centrifugation at the first pressure of −0.5 MPa and sometimes at −0.8 MPa either. This suggests that in the absence of embolism formation, centrifugation may tend to increase conductivity relative to the

Table 1

Weibull function parameters and xylem pressure at 50% loss of hydraulic conductivity (P_{50}) for two hybrids.

Hybrids	Weibull function parameters			P_{50} ± S.E. (MPa)
	K_{max} ± S.E. (mg s^{-1} kPa^{-1} mm^{-1})	b ± S.E. (MPa)	c ± S.E.	
K_s curves				
Pioneer 3902	0.44 ± 0.03*	2.01 ± 0.06*	3.13 ± 0.29	−1.77 ± 0.07*
Pride 5	0.31 ± 0.03	1.77 ± 0.08	2.68 ± 0.24	−1.54 ± 0.09
K_l curves				
Pioneer 3902	(3.72 ± 0.26) × 10^{-4} *	2.02 ± 0.06*	3.19 ± 0.28	−1.79 ± 0.07*
Pride 5	(2.88 ± 0.26) × 10^{-4}	1.79 ± 0.08	2.72 ± 0.22	−1.56 ± 0.08
PLC curves				
Pioneer 3902	–	2.01 ± 0.06*	3.18 ± 0.28	−1.78 ± 0.07*
Pride 5	–	1.79 ± 0.08	2.70 ± 0.22	−1.56 ± 0.08

Parameters shown for the stem area-specific conductivity (K_s), leaf area-specific conductivity (K_l) and percentage loss of conductivity (PLC) vulnerability curves. The Weibull “b” parameter is the absolute value of the xylem pressure at 63.2% loss of conductivity; “c” relates to the steepness of the curve (high “c” = steep curve); K_{max} is the estimated maximum conductivity in the absence of any embolism. Mean ± S.E. for n = 10–12 stems per hybrid.

* Significant difference between hybrids at the 0.05 level based on independent-samples t-test.

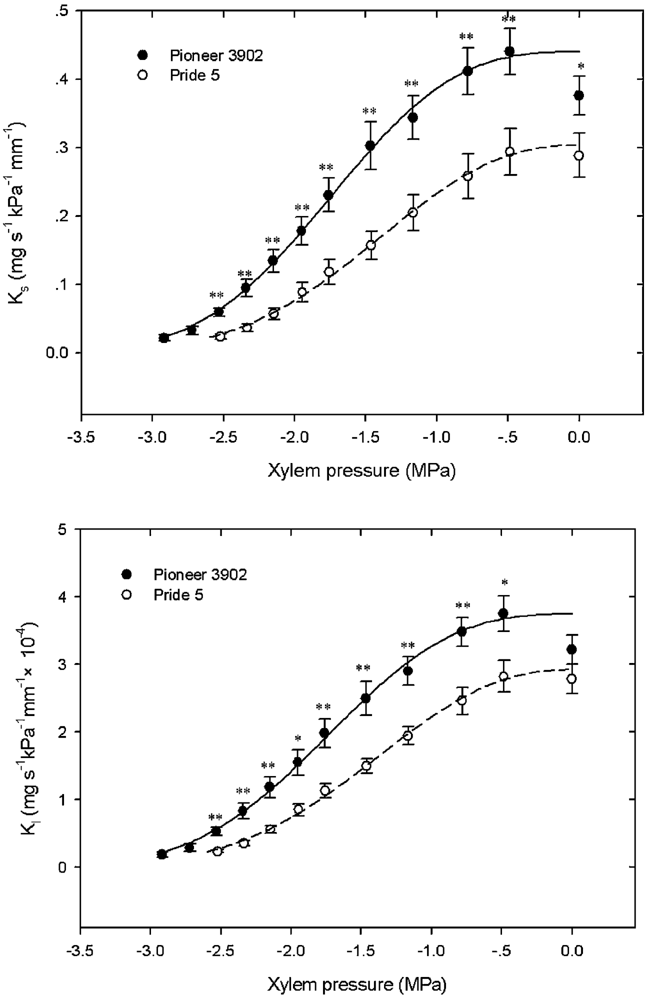

Fig. 1. The decline of conductivity per stem area (K_s, above) and of conductivity per leaf area supplied (below, K_l) with negative xylem pressure in the two corn hybrids. The asterisks near 'Pioneer 3902' indicated significant difference at 0.05 level (*) or 0.01 level (**) between two hybrids by independent-samples *t*-test. The lines are Weibull function curve fits. The K_s or K_l at 0 MPa was measured by a hydraulic head. Mean ± S.E. for the same set of n = 10–12 stems for each hybrid.

gravity method in corn. Because of this ambiguity, we treated K_{max} as a curve fitting parameter. The parameter b is the absolute value of the xylem pressure where K_{max} is reduced by 63.2%, and c represents the steepness for the curve slope at b with higher values representing steeper slopes. Thus a small b means that the xylem is more vulnerable to cavitation, and a large c means the cavitation occurs over small range of pressure. Vulnerability between hybrids were compared by the mean conductivities at each xylem pressure (Fig. 1), the Weibull b, c, and K_{max} parameters and xylem pressure at 50% loss of conductivity (P_{50}) based on the Weibull fit (Table 1).

2.3. Xylem anatomical characteristics

The initial conductivity, K_i, was measured by the gravity method on different sets of six stems as above. Six transverse sections (one per stem for a total of six) were taken at mid-segment from six stems for each hybrid. The number of bundles, and average vessel lumen diameter were measured by image analysis software (ImagePro, Media Cybernetics, Carlsbad, CA) on digital images of freehand sections. Vessel diameters (D) were calculated as that of a circle with the same area (S) as the vessel lumen: $D = 2(S/\pi)^{0.5}$. A preliminary dye experiment with phloxine B showed that almost all vessels were functional after flushing. Transverse sections were divided into four 90° sectors, and all bundles were counted under 4× magnification under the microscope. Diameters of all vessels in at least one sector were measured under 40× magnification, and their hydraulic conductivity calculated according to the Hagen–Poiseuille equation: $K_{hp} = (\pi/128\eta)\sum_{i=1}^{n} D_i{}^4$, in which η is the viscosity of water (MPa s^{-1}), n is the number of vessels. This Hagen–Poiseuille conductivity was expressed per stem cross-sectional area for comparison with measured conductivity of the same stems.

2.4. Spatial pattern of xylem embolism

The water-conducting system of the corn stem is composed of scattered vascular bundles, and vessels in the central vascular bundles were larger than in the peripheral bundles. An experiment was conducted to test the relative vulnerability of central vascular bundles and peripheral bundles. Two similar stems of each hybrid, both 275 mm long, were flushed, one stem was used as a control (CK), and the other was spun on the centrifuge to induce 50% loss of conductivity based on vulnerability curve. A solution of 0.1% safranin was siphoned through the two stems under a 75 cm hydraulic head for 1.5 h, water was then siphoned through the stems for 0.5 h to chase dye from the conducting vessels to minimize dye spread, and then sections were made at *ca.* 180 mm from the dye injection end. The dyed bundles were counted under 4× microscope, and the ratio of functional bundles was acquired (R). Percentage loss of functional bundles (PLFB) was calculated as follows:

$$\text{PLFB\%} = \frac{R_{CK} - R_{50\%}}{R_{CK}} \times 100$$

The percentage loss of central functional bundles and peripheral functional bundles was calculated in the same manner. Four stem pairs per hybrid were compared.

2.5. Statistics

The SPSS 11.0 statistical package (SPSS Inc., Chicago, IL, USA) was used for all statistics. A two-way ANOVA was applied first to each pair of vulnerability curves to test the effect of stem position and differences between hybrids. Results indicated no difference of stem position for both hybrids, so all vulnerability curve parameters (K_s, K_l, PLC, P_{50}, and Weibull curve parameters) were pooled. An independent-samples *t*-test was used to compare these parameters between hybrids. The independent-samples *t*-test was also used to compare anatomical structure and the percentage loss of functional bundles between hybrids and between central vs. peripheral bundles within the same hybrid. A paired-samples *t*-test was used to compare the difference between measured K_i vs. estimated K_{max}, K_i vs. conductivity at −0.5 MPa ($K_{0.5}$) and K_i vs. conductivity at −0.8 MPa ($K_{0.8}$) for the same hybrid.

3. Results

3.1. Water transport capability and vulnerability to cavitation

Fig. 1 shows the decrease of K_s and K_l of the two hybrids as a function of the xylem pressure in the centrifuge. The initial conductivity measured after flushing but before centrifugation (K_i, plotted on the zero pressure axis in Fig. 1) was somewhat less than the K measured during centrifugation at −0.5 MPa and −0.8 MPa for 'Pioneer 3902' (paired-samples *t*-test, $P < 0.01$). This tendency was also noted for some other woody species previously (Li et al., 2008). Because of this potential confounding factor, we did not use K_i to set K_{max} in the Weibull function, but solved for K_{max} in the curve fitting process.

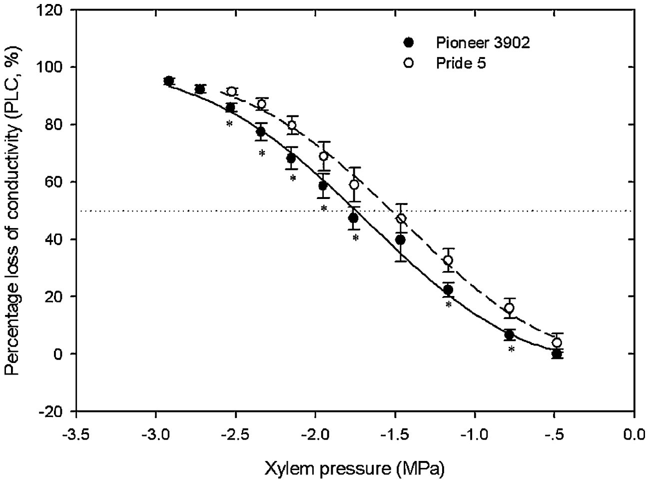

Fig. 2. Xylem vulnerability curves of the stems of two corn hybrids. Percentage loss of conductivity (PLC) is calculated based on individual estimated K_{max} by Weibull function. The reference line corresponds to 50% PLC. Significant symbols, lines, and error bars are same as in Fig. 1.

No difference was found in Weibull curve parameters whether stems were centered on their nodes or internodes in the centrifuge rotor, nor was effect of stem position significant in the ANOVA. However, the ANOVA between hybrids was significant, with independent-samples *t*-tests indicating greater conductivities at all compared pressures in the better drought performer, 'Pioneer 3902,' than in 'Pride 5'. This was true whether conductivity was expressed per stem cross-sectional area or per leaf area supplied (Fig. 1). The Weibull K_{max} estimate was greater in 'Pioneer 3902' (Table 1), and this was consistent with its greater measured K_i (Fig. 1, symbols on zero pressure axis). 'Pioneer 3902' not only maintained greater conductivity across compared xylem pressure range but also showed less relative loss of conductivity with pressure (Fig. 2 and Table 1). PLC for 'Pioneer 3902' was significantly lower than 'Pride 5' at seven of nine tested xylem pressures (Fig. 2). The Weibull "*b*" value, which indicates the absolute value of the pressure at 63.2% loss of conductivity from K_{max}, was significantly higher in 'Pioneer 3902' (2.01, 2.02 and 2.01 for the K_s, K_l and PLC curves respectively) than 'Pride 5' (1.77, 1.79 and 1.79 for K_s, K_l and PLC curves respectively). No difference of Weibull "*c*" value representing the steepness for the curve at *b* was detected between hybrids. Pressures at 50% loss of conductivity calculated from the curves (P_{50}) also indicated greater resistance to cavitation in 'Pioneer 3902' (−1.77 MPa, −1.79 MPa and −1.78 MPa for K_s, K_l and PLC curves respectively) than in 'Pride 5' (−1.54 MPa for K_s curve, −1.56 MPa for both K_l and PLC curves) (Table 1). These results suggest that both water transport capability and resistance to cavitation were associated with the better performance of 'Pioneer 3902' during drought.

Greater conducting capacity in 'Pioneer 3902' was also indicated by a greater Hagen–Poiseuille conductivity per stem area than in 'Pride 5'; the difference being significant at the $P = 0.082$ level (Table 2). The estimated K_{max} was 17.0% lower than the Hagen–Poiseuille value in 'Pioneer 3902' and 24.4% lower in 'Pride 5', a significant difference at $P = 0.066$ level (Table 2). These percentages corresponded to percentage of xylem resistance contributed by deviations in vessel structure from ideal capillaries. They indicated greater hydraulic resistance that was presumably contributed by inter-conduit pitting in 'Pride 5' than in 'Pioneer 3902'.

The greater conducting capacity of 'Pioneer 3902' was associated with more vascular bundles per stem area than 'Pride 5' and a greater cross-sectional area of xylem vessels per stem area. There was no significant difference between vessel diameters of both hybrids, whether comparing central or peripheral vessels (Table 2).

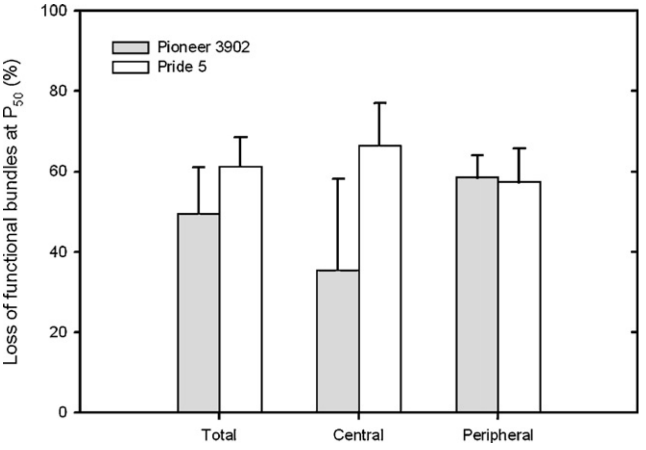

Fig. 3. The percentage loss of conducting bundles corresponding to approximately 50% loss of conductivity. Percentages are shown for the total stem, central, and peripheral sections. Mean ± S.E. for $n = 4$ stems per hybrid.

3.2. Spatial pattern of xylem embolism

When stems were stressed to approximately 50% loss of conductivity, dye perfusions indicated that 'Pioneer 3902' lost 49.54 ± 11.47% functional bundles, while 'Pride 5' lost 61.28 ± 7.37% (Fig. 3), a non-significant difference. Central bundles and peripheral regions lost a similar proportion of conducting bundles in both hybrids. This suggested that the smaller diameter of vessels in the peripheral bundles did not necessarily confer a greater resistance to cavitation.

4. Discussion

In this research, a new variant of the centrifugation method in which xylem conductivity is measured while the stem is spinning has been used to construct the vulnerability curves of corn stems. Our previous work on woody plants with diverse xylem anatomy has shown that this "spinning" method generally consistent with

Table 2
Comparison of xylem structure in two corn hybrids.

	Pioneer 3902	Pride 5
Vascular bundles per stem area (mm^{-2})	4.39 ± 0.14[*]	3.85 ± 0.28
Vessel diameter (μm)		
Central metaxylem	54.02 ± 3.35	52.78 ± 4.01
Peripheral metaxylem	43.46 ± 1.70	41.20 ± 2.35
Central protoxylem	30.10 ± 1.38	28.46 ± 2.23
Peripheral protoxylem	23.38 ± 1.29	22.07 ± 0.93
Vascular bundle area per stem area (%)	1.93 ± 0.25[*]	1.41 ± 0.16
HP conductivity, K_{hp} (mg mm^{-1} kPa^{-1} s^{-1})	0.53 ± 0.12	0.41 ± 0.10
Measured conductivity, K_i (mg mm^{-1} kPa^{-1} s^{-1})	0.33 ± 0.03[*]	0.26 ± 0.03
Modelled conductivity, K_{max}	0.44 ± 0.04[*]	0.31 ± 0.04
$(1 - K_{max}/K_{hp}) \times 100$ (%)	16.88 ± 1.05	24.56 ± 2.25

"HP" conductivity (K_{hp}) refers to the Hagen–Poiseuille value for ideal capillaries of the same cross-sectional area as the stem vessels. The K_i is the measured initial conductivity per stem area after stems were flushed to remove embolism. K_{max} is the estimated maximum conductivity in the absence of any embolism on different set of stems (Fig. 1). The bottom row gives the percentage that the K_{max} are below the K_{hp}. This presumably represents the percent of the total xylem resistance that results from water flow through vessel end-walls and other obstructions. Mean ± S.E. for $n = 6$ stems for both hybrids.

[*] Significant difference between two hybrids according to independent-samples *t*-test ($P < 0.05$).

the traditional centrifugal method where xylem conductivity is measured using a small hydraulic head between periods of centrifugation (the "gravity method"; Li et al., 2008). As in our previous study, we observed a slight increase of conductivity at the start of the vulnerability curve in some, but not all materials. The measured conductivity at −0.5 MPa and −0.8 MPa during spinning was higher than the initial K_i gravity measurement for 'Pioneer 3902', though not significantly so for 'Pride 5'. It seems the degree of the conductivity increase is highly variable and species- or variety-dependent. The increase of conductivity may result from distortion of the pit membrane by either the direct action of centrifugation or by greater drag forces caused by the generally greater pressure gradients in spinning stems. Slight stretching of the membrane may increase its porosity, and enhance water conduction. A transient increase in conductivity has been observed with increased pressure gradients in some species and attributed to the same cause (Sperry and Tyree, 1990). Further research is necessary to explain the phenomenon and why it differs between species.

A key issue about the spinning technique is its applicability to species with a significant number of long vessels that extend from the cut ends to the middle of the segment and beyond. Cochard et al. (2005) have shown that the centrifuge technique is reliable for species having relatively short xylem conduits. The longest corn vessels are up to 10–15 cm long with a median length of about 2 cm (Zimmermann and Jeje, 1981). Thus, even the longest vessel length is only about half of the stem segment length in our centrifugal method (275 mm), reducing the chance of any artifact associated with long vessels. Furthermore, we found no difference between stems centered on their nodes or internodes, despite the likelihood that these configurations would differ in the number of vessels running from the ends to beyond the middle of the segment. Moreover, our previous work could discover no obvious evidence of a vessel length artifact, because we obtained the same vulnerability curves in ring-porous *Fraxinus pensylvanica* and *Quercus gambelii* stems with relatively long vessels whether we used Cochard's spinning method, the old gravity method, the air-injection method, or the native PLC method (Li et al., 2008). Recent work by Taneda and Sperry (2008) further supports the validity of vulnerability curves from ring-porous species *Q. gambelii*. These observations give confidence in the reliability of the spinning method for comparing the vulnerability of the two corn cultivars.

Although corn water relations have been extensively studied, the implication of hydraulic traits for drought resistance is not well demonstrated. Our present research showed that cavitation resistance in stems of two hybrids corresponded to their relative drought-resistance, the same as in many woody plants (Tyree and Ewers, 1991; Cochard, 1992; Pockman and Sperry, 2000). Based on the average vulnerability curves (Fig. 2), 'Pioneer 3902' would lose 1.43%, 13.97% and 42.16% of its maximum conductivity at −0.5 MPa, −1.0 MPa and −1.6 MPa, corresponding to mid-day stem water potentials for well-watered and droughted corn plants (Nissanka et al., 1997) and a typical leaf water potential at stomatal closure for corn (Cochard, 2002b). Correspondingly, 'Pride 5' would lose 6.07%, 23.02% and 53.97% of its conducting capacity at these stress levels. Neufeld et al. (1992) also reported that drought-tolerant sugarcane cultivars maintained higher conductivity at low leaf water potentials than the drought-susceptible cultivars. Differences between the corn hybrids would be accentuated during periods of relatively intense moisture stress when stem water potential was lower than −1.0 MPa. The threshold stem water potential corresponding to stomatal closure was found to be lower for 'Pioneer 3902' than for 'Pride 5' (Nissanka et al., 1997). Greater cavitation avoidance would further amplify the conductivity advantage of 'Pioneer 3902' relative to 'Pride 5'. The better water conducting ability of 'Pioneer 3902' is consistent with visual observations of less wilting of top leaves and stem shrinkage than 'Pride 5'. Hence, partly due to higher stem conductance and higher cavitation resistance, 'Pioneer 3902' may be able to maintain relatively higher stomatal conductance than 'Pride 5' over a broad range of water potentials.

The degree of embolism predicted by our vulnerability curves was consistent with what Tyree et al. (1986) found in unirrigated corn plants with the acoustic technique, generally as many as 50% of the stem vessels embolized when xylem water potential fell below −1.5 MPa to −1.8 MPa. In contrast, Cochard (2002b) found the degree of xylem embolism in corn leaves always remained below 10% in situ, and leaf cavitation resistance was not related to grain yield under drought conditions for four corn hybrids. We do not know whether this results from stem xylem being generally more vulnerable than leaf xylem in corn, or whether our cultivars were more vulnerable than the four genotypes studied by Cochard.

'Pioneer 3902' is a more recent "stay-green" hybrid that maintains its green leaf area for photosynthate production and soil nitrogen uptake during grain filling (Ma and Dwyer, 1998). 'Pride 5' is an older hybrid with earlier leaf senescence. In sorghum, stay-green lines also had a higher yield of grain and biomass under terminal drought (Borrell et al., 2000). The stay-green trait of maize and sorghum has been used to improve yield of these two crops under water-scarce environments (Tollenaar and Wu, 1999; Bruce et al., 2002). It is possible that the higher hydraulic conductivities we observed in 'pioneer 3902' help to promote its stay-green abilities.

In woody species, larger vessels tend to be more vulnerable to cavitation than smaller ones (Hacke et al., 2006). Corn stems are composed of two different sizes of scattered vascular bundles. The peripheral bundles are generally crowded, have narrower vessels, and are provided with heavy sclerotic sheaths, whereas the central bundles are widely-spaced, have wider vessels, and lack massive sheaths. In our experiments, cavitation occurred in both central and peripheral bundles to a similar extent. In general, the two metaxylem vessels of a bundle and persisting protoxylem conduits cavitated together, suggesting that vessels within one bundle embolized as a unit. But is still not clear where and how cavitation occurred within the bundles and its relation to pit membrane structure.

There is evidence for a tradeoff between water transport efficiency and safety in woody plants (Tyree et al., 1994; Hacke et al., 2006). In corn, we did not see this tradeoff. 'Pioneer 3902' had greater water transport capability and also was more resistant to cavitation. Hypothetically, it is the total area of pits in a vessel that largely influences the vessel's cavitation resistance, while conductivity is influenced by the length and width of the conduit lumen and the number of vessels per stem area. Hence, it is possible to have high hydraulic conductance and be resistant to cavitation by limiting the amount of pitting or by packing more vessels per unit area (Hacke et al., 2006). 'Pioneer 3902' achieved its greater hydraulic conductivity by having more vascular bundles per stem area rather than having bigger vessels, thus possibly minimizing any safety vs. efficiency tradeoff at the vessel level.

Acknowledgements

We would like to thank Prof. Mattijs Tollenaar in University of Guelph, Canada who provided all corn seeds, and three anonymous reviewers whose suggestions greatly improved the manuscript. This project was funded by the State Key Fundamental Research Planning of China (2007CB106803) to M.A. Shao and NSF IBN-0416297 to J.S. Sperry and a research grant from State Key Laboratory of Soil Erosion and Dryland Farming to Y.Y. Li (10501-189).

References

Borrell, A.K., Hammer, G.L., Henzell, R.G., 2000. Does maintaining green leaf area in sorghum improve yield under drought. II. Dry matter production and yield. Crop Sci. 40, 1037–1048.

Bruce, W.B., Edmeades, G.O., Barker, T.C., 2002. Molecular and physiological approaches to maize improvement for drought tolerance. J. Exp. Bot. 53, 13–25.

Cochard, H., 1992. Vulnerability of several conifers to air embolism. Tree Physiol. 11, 73–83.

Cochard, H., 2002a. A technique for measuring xylem hydraulic conductance under high negative pressures. Plant Cell Environ. 25, 815–819.

Cochard, H., 2002b. Xylem embolism and drought-induced stomatal closure in maize. Planta 215, 466–471.

Cochard, H., Bodet, C., Ameglio, T., Cruiziat, P., 2000. Cryo-scanning electron microscopy observations of vessel content during transpiration in walnut petioles. Facts or artifacts? Plant Physiol. 124, 1191–1202.

Cochard, H., Damour, G., Bodet, C., Tharwat, I., Poirier, M., Améglio, T., 2005. Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. Physiol. Plantarum 124, 410–418.

Hacke, U.G., Sperry, J.S., Wheeler, J.K., Castro, L., 2006. Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiol. 26, 689–701.

Li, Y., Sperry, J.S., Taneda, H., Bush, S., Hacke, U.G., 2008. Evaluation of centrifugal methods for measuring xylem cavitation in conifers, diffuse- and ring-porous angiosperms. New Phytol. 177, 558–568.

Ma, B.L., Dwyer, L.M., 1998. Nitrogen uptake and use of two contrasting maize hybrids differing in leaf senescence. Plant Soil 199, 283–291.

McCully, M.E., 1999. Root xylem embolisms and refilling. Relation to water potentials of soil, roots, and leaves, and osmotic potentials of root xylem sap. Plant Physiol. 119, 1001–1008.

McCully, M.E., Huang, C.X., Ling, L.E.C., 1998. Daily embolism and refilling of xylem vessels in the roots of field-grown maize. New Phytol. 138, 327–342.

Neufeld, H.S., Grantz, D.A., Meinzer, F.C., Goldstein, G., Crisosto, G.M., Crisosto, C., 1992. Genotypic variability in vulnerability of leaf xylem to cavitation in water-stressed and well-irrigated sugarcane. Plant Physiol. 100, 1020–1028.

Nissanka, S.P., Dixon, A., Tollenaar, M., 1997. Canopy gas exchange response to moisture stress in old and new maize hybrid. Crop Sci. 37 (1), 172–181.

Pockman, W.T., Sperry, J.S., 2000. Vulnerability to stem cavitation and the distribution of sonoran desert vegetation. Am. J. Bot. 87, 1287–1299.

Sperry, J.S., 2000. Hydraulic constraints on plant gas exchange. Agric. Forest Meteorol. 104, 13–23.

Sperry, J.S., Stiller, V., Hacke, U.W., 2003. Xylem hydraulics and the soil-plant-atmosphere continuum: opportunities and unsolved issues. Agron. J. 95, 1362–1370.

Sperry, J.S., Tyree, M.T., 1990. Water-stress-induced xylem embolism in three species of conifers. Plant Cell Environ. 13, 427–436.

Stiller, V., Lafitte, H.R., Sperry, J.S., 2003. Hydraulic properties of rice and the response of gas exchange to water stress. Plant Physiol. 132, 1698–1706.

Stiller, V., Sperry, J.S., 2002. Cavitation fatigue and its reversal in intact sunflower plants. J. Exp. Bot. 53, 1155–1161.

Taneda, H., Sperry, J.S., 2008. A case study of water transport in co-occurring ring- vs. diffuse-porous trees: contrasts in water status, conducting capacity, cavitation, and vessel refilling. Tree Physiol. 28, 1641–1651.

Tollenaar, M., 1991. Physiological basis of genetic improvement of maize hybrids in Ontario from 1959 to 1988. Crop Sci. 31, 119–124.

Tollenaar, M., Wu, J., 1999. Yield improvement in temperate maize is attributable to greater stress tolerance. Crop Sci. 39, 1597–1604.

Tyree, M.T., Davis, S.D., Cochard, H., 1994. Biophysical perspective of xylem evolution: is there a trade off of hydraulic efficiency for vulnerability to dysfunction? IAWA J. 15, 335–360.

Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants. New Phytol. 119, 345–360.

Tyree, M.T., Fiscus, E.L., Wullschleger, S.D., Dixon, M.A., 1986. Detection of xylem cavitation in corn (*Zea mays*) under field conditions. Plant Physiol. 82, 597–599.

Tyree, M.T., Sperry, J.S., 1989. Vulnerability of xylem to cavitation and embolism. Annu. Rev. Plant Physol. Plant Mol. Biol. 40, 19–38.

Zimmermann, M.H., 1983. Xylem Structure and the Ascent of Sap. Springer-Verlag, Berlin.

Zimmermann, M.H., Jeje, A.A., 1981. Vessel-length distribution in stems of some Amercian woody plants. Can. J. Bot. 59, 1882–1892.